Predicting diet quality and genetic diversity of a desert-adapted ungulate with NDVI

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ABSTRACT

Diet quality influences ungulate population dynamics but is difficult to measure at fine temporal or spatial resolution using field-intensive methods such as fecal nitrogen (FN). Increasingly, the remotely sensed vegetation index NDVI is used to represent potential ungulate diet quality, but NDVI's relationship with diet quality has yet to be examined for herbivores in desert environments. We evaluated how strongly NDVI was associated with diet quality of desert bighorn sheep (*Ovis canadensis nelsoni*) in the Mojave Desert using FN data from multiple years and populations. We considered effects of temporal resolution, geographic variability, and NDVI spatial summary statistic on the NDVI-diet quality relationship. NDVI was more reliably associated with diet quality over the entire growing season than with instantaneous diet quality for a population. NDVI was also positively associated with population genetic diversity, a proxy for long-term, population-level effects of diet quality. We conclude that NDVI is a useful diet quality indicator for Mojave Desert bighorn sheep and potentially other desert ungulates. However, it may not reliably track diet quality if NDVI data are too spatially coarse to detect microhabitats providing high-quality forage, or if diet is strongly influenced by forage items that are weakly correlated with landscape greenness.

1. Introduction

Diet quality has an important influence on the population dynamics of ungulates. Many studies have demonstrated the link between diet quality and individual body mass or body condition, which in turn affect survival and reproduction rates (Parker et al., 2009). The nutritional quality of ungulate diets depends on the nutrient content of available forage species, which frequently varies spatially and temporally (Albon and Langvatn, 1992; Festa-Bianchet, 1988; McNaughton, 1990). This variation largely reflects changes in plant phenology and is particularly evident in arid environments where precipitation is scant and geographically variable with a strong stochastic element (Bender, 1982; Noy-Meir, 1973), leading to pulses in forage growth and diet quality that can vary greatly in space and time. Accurately characterizing diet quality of ungulate populations in such environments may require sampling over broad areas at relatively fine spatial resolution (e.g., tens to hundreds of meters) and temporal resolution (e.g., days to weeks) to account for this heterogeneity; infrequent sampling may fail to capture pulses in diet quality that drive ungulate population dynamics, and geographically sparse sampling may fail to include localized hotspots of high forage quality.

Traditional methods of measuring diet quality limit researchers' ability to simultaneously maximize temporal and spatial resolution of diet quality sampling. Methods that assess diet quality by analyzing diet composition and nutrient content of forage plants can be too data-intensive to allow the development of data sets large enough to investigate temporal and spatial variation. Fecal indices of diet quality (most commonly fecal nitrogen, FN) have gained widespread acceptance as measures of ungulate diet quality (Leslie et al., 2008) and provide an indirect measure of diet quality at a much lower cost and time investment. Wehausen (1995) elucidated a causal mechanism that linked percent FN and apparent digestibility in a curvilinear relationship that was corroborated by data from domestic sheep and cattle, making FN a potentially meaningful index of diet quality for some ungulates. Yet,

fecal indices still require extensive field sampling that limits the spatial and temporal extent and resolution for most studies.

The relationship between plant phenology and nutrient quality of herbivore diets has led to the use of remotely sensed vegetation indices such as the Normalized Difference Vegetation Index (NDVI) as alternative measures that may track ungulate diet quality. NDVI is a measure of vegetation greenness, based on reflectance in the red (RED) and near-infrared (NIR) regions of the electromagnetic spectrum, and is correlated with several variables that appear to be relevant to ungulate diet quantity and quality, including net primary productivity, plant biomass, and leaf area index (Pettorelli et al., 2011). It offers several advantages over other diet quality methods, including fine spatial and temporal resolution, global coverage, data available as far back as 1981 from the Landsat program, typically low (or no) data acquisition cost, and perhaps most significantly, no field sampling or laboratory analysis once validated. These characteristics make NDVI a potentially powerful tool for examining diet quality at higher resolution and over longer time periods and larger spatial extents than would be possible with traditional field-based methods, thereby offering excellent opportunities for long-term monitoring. NDVI is not without limitations, however: it does not directly quantify any biological variable, and factors such as the scale of imagery (Teillet et al., 1997), atmospheric conditions (Kaufman and Tanre, 1992), and differences in soil type (Huete and Tucker, 1991) can affect its relationship to biological variables.

NDVI is increasingly used as a proxy for diet quality in studies of ungulate populations, and has been related to individual- and population-level characteristics such as body condition (Ryan et al., 2012), body mass (Herfindal et al., 2006; Mysterud et al., 2008), conception rate (Rasmussen et al., 2006; Trimble et al., 2009), and breeding phenology (Wittemyer et al., 2007). However, the relationship between NDVI and diet quality may differ among species and environments, so it is critical to verify and elucidate the details of this relationship before applying NDVI as a diet quality indicator in new situations. Only a few studies have related NDVI to empirical measures of ungulate diet quality such as FN: Hamel et al. (2009) found that NDVI predicted yearly variation in the timing of peak fecal crude protein for mountain goats (*Oreamnos americanus*) and Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in a Canadian alpine ecosystem; Ryan et al. (2012) found NDVI to be a positive predictor of FN for African buffalo (*Syncerus caffer*) in a South African savanna ecosystem; and Lendrum et al. (2014) observed corresponding increases in NDVI and FN for mule deer (*Odocoileus hemionus*) during spring migration in northwestern Colorado, USA.

Here, we use a long-term FN dataset to evaluate the association between NDVI and diet quality for an ungulate adapted to arid environments, the desert bighorn sheep (*O. canadensis nelsoni*), in the Mojave Desert, USA. FN has served well as an indicator of bighorn sheep diet quality in previous studies (Blanchard et al., 2003; Irwin et al., 1993; Rubin et al., 2002; Wehausen, 1992, 2005), but NDVI could greatly expand research opportunities if found to be a suitable proxy for diet quality. The Mojave Desert is characterized by relatively widespread winter precipitation and spatially heterogeneous summer monsoon thunderstorms (Bender, 1982). Temperature patterns create a temporally predictable winter—spring growing season, but inter-annual and geographic variation in the timing and amount of precipitation results in large variation in forage growth and nutrient availability within the growing season (Wehausen, 2005). Bighorn sheep populations inhabit discrete and often isolated mountain ranges separated by broad valleys that are less hospitable (Bleich et al., 1990; Schwartz et al., 1986), limiting their opportunity to shift to areas supporting higher diet quality when there is intermountain variation in

nutrient availability. Previous research in this system has shown that diet quality is strongly associated with reproductive success, as measured by lamb:ewe ratios (Wehausen, 2005). Additionally, populations inhabiting mountain ranges with lower maximum elevation and precipitation (where diet is presumably poorer) have higher extinction probability (Epps et al., 2004) and lower genetic diversity (Epps et al., 2006) than those in mountain ranges with higher maximum elevation and precipitation. These findings, along with forecasted increases in temperature and aridity for the region (Bernstein et al., 2008; Seager et al., 2007), suggest that more widespread data on diet quality in the region could aid in both retrospective and prospective analyses of bighorn sheep population dynamics.

The ability to assess the relationship between NDVI and population dynamics is hampered by a lack of demographic data such as population size estimates or recruitment rates for most Mojave Desert bighorn sheep populations. However, genetic diversity has been characterized for most populations in the region and may serve as a proxy for long-term population dynamics. Genetic diversity measures the extent of heritable variation in a population or species, and differences in neutral (i.e., non-expressed) genetic diversity among populations are a function of both gene flow (the amount of dispersal and subsequent reproduction between populations, influenced by population connectivity) and genetic drift (the random loss of alleles that occurs faster in smaller populations). After accounting for differences in connectivity, the remaining variation in genetic diversity among populations should primarily reflect population demographic history: populations that remain consistently large through time will have higher genetic diversity than smaller and less stable populations. This is a fundamental prediction of population genetic theory and is supported by a large body of empirical research (Crow and Kimura, 1970; Frankham, 1996; Soulé, 1976). The effect of population size and stability on genetic diversity should be especially acute in metapopulations, where periodic extinctions and recolonizations by a small number of individuals can dramatically reduce genetic diversity via inbreeding, random genetic drift, and founder effects (Frankham et al., 2002; Pannell and Charlesworth, 2000).

We use fecal nitrogen data from five populations and genetic data from 22 bighorn sheep populations in the Mojave Desert to test four hypotheses about the relationships between NDVI, diet quality, and genetic diversity of Mojave Desert bighorn sheep that may also be relevant to many other ungulate species and regions: *(1) The relationship between NDVI and diet quality differs for populations occupying different habitat patches.* Previous research suggests that populations of a species in different locations may exhibit different relationships between NDVI and diet quality (Martinez-Jauregui et al., 2009). For instance, two habitat patches could have similar NDVI values but contain different forage plant species and consequently support different levels of ungulate diet quality. *(2) NDVI is a better predictor of diet quality at the temporal resolution of the entire growing season than at the resolution of individual samples representing instantaneous diet quality on a given day.* The location of bighorn sheep within a patch may vary between areas of higher and lower forage quality on a daily basis, such that a patch-level summary statistic of NDVI on any particular day may not accurately represent the actual diet quality experienced by bighorn sheep. NDVI summarized at an intermediate temporal resolution, such as a growing season, could better reflect diet quality by integrating daily fluctuations over a longer, critical time period. *(3) At a given point in time, diet quality is more highly correlated with the highest NDVI within a habitat patch than with average NDVI within the patch.* Patch-level summaries of NDVI values should reflect the degree to which animals find and utilize areas with the best forage, so measures of average NDVI within an area may poorly represent

diet quality if NDVI is spatially heterogeneous and animals preferentially feed in locations with the highest NDVI values. *(4) Long-term NDVI conditions in a habitat patch are positively associated with genetic diversity of the population occupying that patch.* If NDVI is strongly associated with diet quality at the growing-season level, it may be possible to use NDVI to evaluate the long-term impact of habitat patches' forage quality on bighorn sheep populations, with genetic diversity serving as a proxy for demographic data.

2. Methods and materials

2.1. Study area

Our study area encompassed 23 currently occupied habitat patches in the Mojave Desert of southern California and Nevada (Fig. 1) for which bighorn sheep genetic data (Epps et al., 2006, 2005) and/or FN data were available. The study area includes transitional environments that represent varying mixtures of Mojave Desert characteristics and Great Basin Desert (to the north) or Sonoran Desert (to the south and southeast) characteristics.
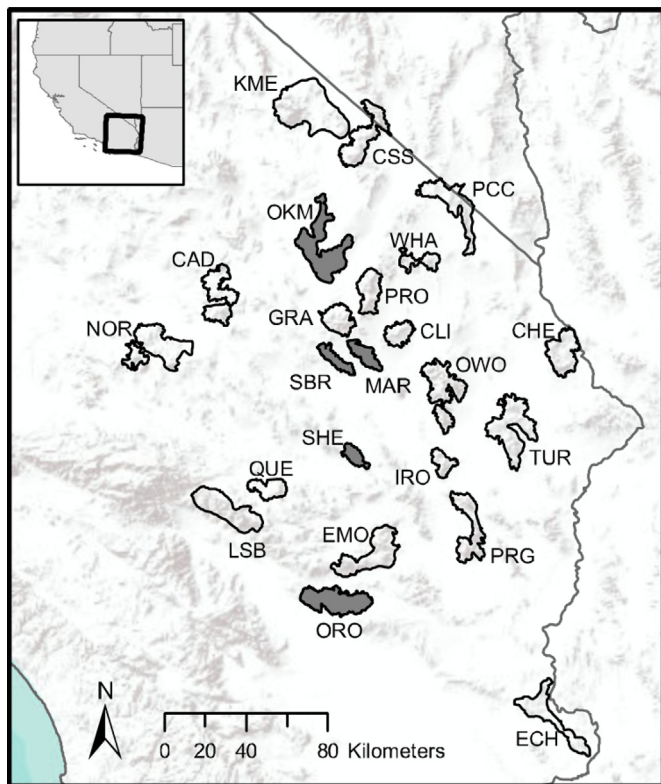
Fig. 1. Bighorn sheep populations and their associated habitat patches considered in this study. Filled dark gray polygons represent populations in which fecal nitrogen (FN) data were collected and used to analyze the relationship between diet quality and Normalized Difference Vegetation Index (NDVI). Unfilled polygons represent populations in which genetic data (but not FN data) were collected and used to analyze the relationship between genetic diversity and NDVI. Genetic data were also collected in all FN-sampled populations except the Sheephole Mountains. Patch abbreviations: CAD — Cady Mountains, CHE — Chemehuevi Mountains, CLI — Clipper Mountains, CSS — Clark Mountains/South Spring Range, ECH — East Chocolate Mountains, EMO — Eagle Mountains, GRA — Granite Mountains, IRO — Iron Mountains, KME — Kingston Mountains/Mesquite Range, LSB — Little San Bernardino Mountains, MAR — Marble Mountains, NOR — Newberry Mountains/Ord Mountains, OKM — Old Dad Peak/Kelso Mountains/Marl Mountains/Club Peak/Indian Spring, ORO — Orocopia Mountains, OWO — Old Woman Mountains, PCC — Piute Range/Castle Peaks/Castle Mountains, PRG — Palen Mountains/Riverside Granite Mountains, PRO — Providence Mountains, QUE — Queen Mountain, SBR — South Bristol Mountains, SHE — Sheephole Mountains, TUR — Turtle Mountains, WHA — Woods Mountains/Hackberry Mountains.

Variation in precipitation and temperature regimes, and resulting vegetation communities, is largely driven by elevation, which ranges from approximately sea level to 2500 m. Mean annual precipitation is 13.6 cm, but increases with elevation and varies across other geographic gradients. While most precipitation is derived from soaking winter rain storms, summer storms account for at least a third of the annual precipitation (Bender, 1982). Mean annual temperature is 19.9 °C and declines with elevation. Daily temperature range can be as much as 25 °C (Bender, 1982). Vegetation includes shrubs, trees, succulents, and perennial and annual herbs, but is generally sparse; Wallace and Thomas (2008) estimated that the majority of the Mojave Desert has less than 20 percent cover. Shrubs are the dominant plant form and important shrub species include creosote bush (*Larrea tridentata*), catclaw acacia (*Acacia greggii*), burrobush (*Ambrosia dumosa*), and brittlebush (*Encelia farinosa*) at lower elevations, and Mormon tea (*Ephedra* spp.), blackbrush (*Coleogyne ramosissima*), and sagebrush (*Artemisia* spp.) at higher elevations. Perennial grasses are largely absent at lower elevations and increase in cover with elevation; important species are big galleta grass (*Hilaria rigida*), desert needle grass (*Stipa speciosa*), and Indian ricegrass (*Achnatherum hymenoides*). Tree species include Joshua tree (*Yucca brevifolia*), juniper (*Juniperus californica*), and pinyon pine (*Pinus* spp.). Annuals include both winter and summer annual forb and grass species that grow and flower in response to seasonal rainfall (Bender, 1982).

Bighorn sheep habitat in the study area is defined by surface water availability and by the presence of steep, rocky slopes (escape terrain), which occurs mostly in small and discrete mountain ranges within the region; accordingly, patch boundaries were delineated along the margins of mountain ranges where steep slopes transition to flat valleys, using 10% slope as a cutoff as in Epps et al. (2007). Habitat patches ranged in size from 79 to 637 square kilometers (Table A.1). Because movement between habitat patches is infrequent, each population of Mojave Desert bighorn sheep corresponds to a single habitat patch, and we use the terms "patch" and "population" interchangeably.

2.2. NDVI data

We used 8-day composite, 250-m resolution NDVI data from the Moderate Resolution Imaging Spectroradiometer (MODIS). Pre-processed data for the years 2000 through 2011 (MOD09Q1, Level 3, Collection 5, tile h08v05) were obtained from MODIS for the North American Carbon Program (MODIS-for-NACP, http://accweb.nascom.nasa.gov; Gao et al., 2008). Other satellite data offer finer spatial resolution, most notably Landsat Thematic Mapper with 30-m pixels, but we chose MODIS data for several reasons. First, the finer temporal resolution of MODIS data is an important advantage in our study system, where large changes in forage phenology can occur over short time periods. MODIS collects an image of a location every 1–2 days, and the composite dataset we used included the best-quality pixel from every 8-day period. In contrast, Landsat collects an image of a location only once every 16 days, and if conditions are poor at the time of image acquisition (e.g., clouds present), then the time between useable images could be more than a month. Second, Sesnie et al. (2011) found MODIS-derived NDVI to be less sensitive to sun angle and terrain effects when estimating forage phenology in desert bighorn sheep habitat, although a terrain illumination correction for Landsat is now available (Tan et al., 2013) and may negate this advantage of MODIS. Lastly, the pre-processing and accessibility of the MODIS-for-NACP data make them more user-friendly for biologists with limited experience working with remotely sensed data.

We used ArcGIS 10.0 (ESRI, 2010) to calculate three summary statistics from the NDVI values of all pixels with center points

within the boundary of each patch for each 8-day composite image: 1) median NDVI, a hypothesized measure of the average forage quality within the patch; 2) maximum NDVI, which may better reflect diet quality if bighorn sheep tend to seek out the highest-quality forage within the patch; and 3) the 90th percentile of NDVI, which could represent weaker selection of highest-quality forage than maximum NDVI, and is more resistant than maximum NDVI to spuriously high values caused by measurement error.

2.3. Fecal nitrogen data

We used FN measurements for 275 samples collected from 5 populations (Marble Mountains, Old Dad Peak, Orocopia Mountains, South Bristol Mountains, and Sheephole Mountains) from 2000 through 2011, with varying sampling intensity among populations (Fig. A.1). Two populations, Marble Mountains and Old Dad Peak, were sampled at approximately monthly intervals during 2000−2011; samples from other populations were collected less frequently or during fewer years. Each sample was a composite of multiple subsamples (range = 1−14, mean = 5.9; Fig. A.2) from different fecal piles collected over <7 days. Samples consisted of freshly deposited pellets, except for a small proportion (~5%) that were recent pellets (i.e., <7 days old) that were back-dated to the estimated date of deposition on the basis of the condition of pellets and tracks. Equal amounts of fecal material from each subsample were combined to form the composite sample (Jenks et al., 1989). Sampling was focused in areas where most ewes in the population were located at that time of year in an attempt to best represent the ewe population, and sampling locations were mostly consistent from year to year. We could not verify that each subsample was from a different individual; however, individuals move over large areas each day during feeding and thereby individually integrate much of the variation in nutrient availability across the landscape.

Nitrogen content of composite samples was analyzed by the Wildlife Habitat and Nutrition Laboratory at Washington State University with the Kjeldahl method (Horwitz, 1965) for samples from 2000 to 2004, and with the Dumas method of combustion (Helrich, 1990) using a TruSpec C/N Analyzer (LECO Corp., St. Joseph, MI) for samples from 2005 to 2011. FN was measured on an ash-free basis to correct for variation in the amount of inorganic material within pellets, including dirt, which does not contribute to diet quality (Wehausen, 1995). Ash-free FN values were log-transformed to make their relationship with digestibility linear (Wehausen, 1995) and thus more biologically interpretable. Hereafter, we refer to log-transformed, ash-free fecal nitrogen simply as fecal nitrogen or FN.

2.4. Relationship between NDVI and fecal nitrogen

We examined the relationship between FN and NDVI at two temporal resolutions: the sample (essentially a snapshot in time) and the winter−spring primary growing season. We defined the growing season for each year as the period from October 1 of the previous year through June 30 of the stated year, during which the majority of precipitation in the Mojave Desert occurs and potentially initiates sustained plant growth (Beatley, 1974), and when the greatest pulse in diet quality occurs for bighorn sheep in this region (Wehausen, 2005).

2.4.1. Sample level

For each FN sample (n = 275) from each population (n = 5), we identified the NDVI image closest to the FN sample date (calculated as the mean of estimated subsample deposition dates), and used the median, maximum, and 90th percentile NDVI within with the

appropriate habitat patch in those images as potential predictors of FN. Preliminary examination of the data revealed that linearity of the relationships between FN and each of the three NDVI summary statistics was improved by log-transforming values of all summary statistics (Figs. A.3 and A.4). We also improved linearity by back-transforming FN to its original scale via exponentiation for the sample-level analysis; however, we also present results in terms of log-transformed FN because of its direct biological relationship to diet quality.

We calculated the Pearson correlation coefficient between FN and each NDVI summary statistic for each population to determine which correlated best with bighorn sheep diet quality. We conducted all further analyses with the summary statistic most highly correlated with FN for the majority of populations. Because FN data exhibited a clear pattern of serial autocorrelation within populations (Fig. 2), we fit linear models of the FN-NDVI relationship using generalized least squares with a Gaussian correlation structure to account for autocorrelation of residuals. Models were fit in R (R Development Core Team, 2014) using the *nlme* package (Pinheiro et al., 2011). We constructed three linear models of the FN-NDVI relationship: a model including NDVI, population, and their interaction as covariates, which allowed the FN-NDVI relationship to have different slopes and different intercepts among populations (*separate lines*); a model including NDVI and population, but no interaction, as covariates, which allowed only intercepts to differ among populations (*parallel lines*); and a model including only NDVI as a covariate, such that a single regression line was fit to all populations (*equal lines*). We used likelihood ratio tests to select the best-fitting model.

2.4.2. Season level

We used areas-under-the-curve to compare FN and NDVI over the yearly growing season (Oct. 1 − June 30, 273 days). FN was sampled for all or most of the months during the growing season from 2001 through 2011 for only two populations, Marble Mountains and Old Dad Peak (Fig. A.1), so this analysis was limited to 22 season-level FN observations (11 per population). We constructed growing-season FN curves for Marble Mountains and Old Dad Peak by fitting a piecewise polynomial spline (essentially a smooth curve connecting consecutive data points) to the series of monthly FN measurements for each population with the *splines* package in R (R Development Core Team, 2014); in cases where FN samples were not available for every month of the growing season (Fig. A.1), we interpolated between the previous and subsequent monthly values when constructing curves. Similarly, we constructed growing-season NDVI curves by fitting splines through NDVI values (again, using the summary statistic most highly correlated with FN values from the sample-level analysis) from 8-day composite images within the growing season. We explored the FN-NDVI relationship at the season level by calculating the area under the growing-season FN curve (integrated FN, or IFN) and the area under the growing-season NDVI curve (integrated NDVI, or INDVI), excluding the portion of the year outside of the growing season. We log-transformed INDVI to make its relationship with IFN more linear. As in the sample-level analysis, we then fit three linear regression models that allowed the relationship between IFN and INDVI to differ between the two populations to varying degrees (i.e., separate, parallel, or equal lines). Because we observed no pattern of serial autocorrelation at the season level, we used ordinary least squares to fit linear regression models and extra-sum-of-squares F-tests to select the best-fitting model.

2.5. Characteristics of FN and NDVI curves

We calculated several statistics to measure how closely seasonal
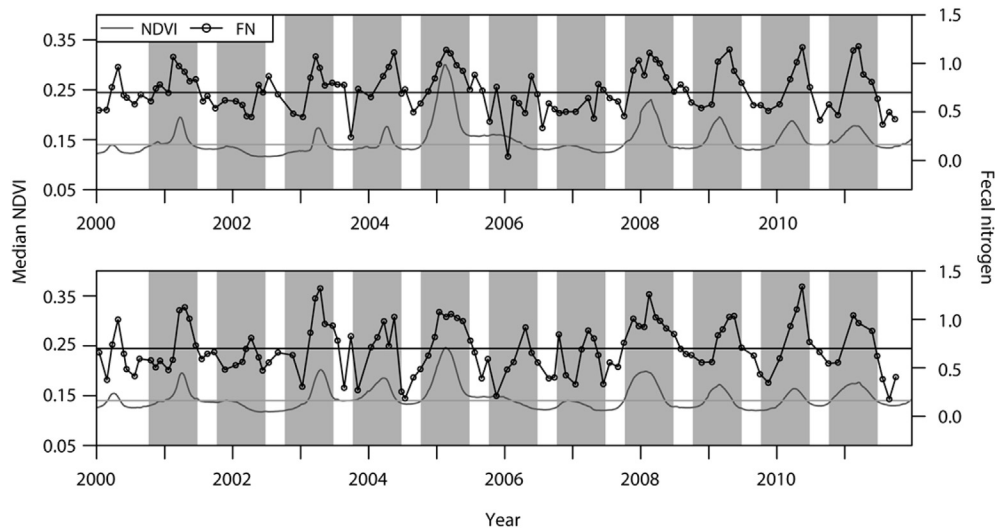
Fig. 2. Median Normalized Difference Vegetation Index (NDVI) and fecal nitrogen (FN) for the Marble Mountains (top) and Old Dad Peak (bottom) populations. Tick marks on x-axis are placed at Jan. 1 of each year. Gray vertical bands show Oct. 1 − June 30 growing seasons. Horizontal black and gray lines show baseline levels of FN and NDVI, respectively, used to determine width of growing season peaks.

changes in NDVI tracked changes in FN in the Marble Mountains and Old Dad Peak patches. First, we calculated the difference in the date of peak NDVI and peak FN for each growing season. Second, we examined the percentage of IFN and INDVI associated with each month of the growing season by integrating FN and NDVI splines for each month individually, using the minimum FN or NDVI value observed during 2001−2011 growing seasons in each patch as a baseline level for integrations to maximize the signal:noise ratio. We calculated the mean monthly percentages and 95% confidence intervals for each month to describe how FN and NDVI were temporally distributed within the growing season and the degree of consistency between the FN and NDVI distributions.

Lastly, we examined the degree to which IFN and INDVI were influenced by two characteristics of the FN and NDVI curves: the maximum value reached during the growing season (i.e., peak height) and the duration above summer baseline level (i.e., peak width). We estimated baseline values of FN = 0.7 and median NDVI = 0.14 from the curves in Fig. 2, then calculated peak width for each growing season as the number of days between the closest points on either side of the peak date at which the spline dropped below the threshold value. We regressed IFN and INDVI against their respective peak heights and peak widths, and calculated the change in R^2 associated with removing each of these explanatory variables from the regression model as an indicator of the relative influence of peak height and width on total area under the curve.

2.6. Relationship between NDVI and genetic diversity

We used existing genetic data (Epps et al., 2005) from 22 populations in the Mojave Desert (Fig. 1) to determine whether long-term NDVI of habitat patches was correlated with genetic diversity. Our genetic dataset included genotypes of 399 individuals at 14 microsatellite loci, representing 4 to 37 individuals per population. Details of genotyping procedures can be found in Epps et al. (2005). We used the program FSTAT (Goudet, 2001) to calculate two common genetic diversity metrics for each population, expected heterozygosity (H_e) and allelic richness (A_r); we used rarefaction to correct A_r for variation in sample size among populations.

To characterize long-term diet quality for these populations, we calculated INDVI of each patch for each growing season from 2001 through 2011 using the same method described for the season-level analysis in Section 2.4.2. We then calculated the median of yearly INDVI values for each patch during these 11 years. We used linear regression to estimate the association between NDVI and genetic diversity, with H_e or A_r as the response variable and median INDVI as the predictor variable. Because relationships between genetic indices and median INDVI were nonlinear and could not be made linear by logarithmic transformation, we fit quadratic linear regression models by adding a squared term for median INDVI.

We also included population connectivity as a predictor variable because genetic diversity can be strongly influenced by the gene flow; populations that are more connected to neighboring populations receive more new alleles via immigration, which counteracts the loss of genetic diversity that occurs through genetic drift. Previous research on the Mojave bighorn sheep metapopulation has demonstrated that genetic diversity is higher in populations that are separated from their neighbors by shorter distances (Epps et al., 2006) and that gene flow between populations decreases with distance and the presence of dispersal barriers such as interstate highways (Epps et al., 2005). We considered four network-based connectivity metrics from Creech et al. (2014) that describe connectivity of Mojave bighorn sheep populations at local or regional scales (Appendix A); however, we used only the connectivity metric with the highest correlation with A_r or H_e (Table A.2) in regression models because all connectivity metrics were highly correlated ($r \geq 0.75$).

To determine whether NDVI or connectivity had greater influence on genetic diversity, we fit single-predictor models (i.e., only NDVI or only connectivity) in addition to our multiple linear regression model, and compared the explanatory power (R^2) of these single-factor models. We used extra-sum-of-squares F-tests to determine the best-fitting model for each genetic diversity index. Although habitat patch size is an important influence on population size (and potentially on genetic diversity) in many wildlife populations, research on the Mojave Desert bighorn metapopulation has shown no effect of patch size on genetic diversity (Epps et al., 2006, 2005), so we did not include patch size in our analysis. Because results could potentially be influenced by spatial autocorrelation in genetic diversity (i.e., if nearby populations exhibit similar genetic diversity), we repeated the analysis using models that included a Gaussian spatial correlation structure, and compared the results to those from non-spatial models.

3. Results

3.1. Sample-level FN versus NDVI

Median NDVI had a higher correlation coefficient with FN than did maximum NDVI or 90th percentile NDVI for three of five populations, and had a correlation coefficient that was within 2 percent of the most highly correlated summary statistic for the remaining two populations (Table A.3). The similarity between the three summary statistics in terms of their correlation with FN reflected the fact that the summary statistics themselves were highly correlated (Fig. A.5). We used the median as our NDVI summary statistic for the remainder of the analyses, and believe it was an appropriate indicator of average forage conditions because NDVI values within patches appeared approximately normally distributed (Fig. A.6).

We found a positive relationship ($p < 0.001$) between FN and median NDVI (Fig. 3, Fig. A.7). The best fitting model was the parallel lines model, in which the intercepts of the FN-NDVI relationships differed among populations (likelihood ratio = 42.91, $p < 0.001$) but the slopes did not (likelihood = 4.99, $p = 0.289$). However, it was clear that the equal lines model would be most appropriate if only considering the two long-term data sets (Marble Mountains and Old Dad Peak), as regression lines were nearly identical for these populations (Fig. 3). Pseudo[2]-R^2 for the best-fitting model was 0.42, suggesting that much of the variation in FN at the sample level remained unexplained.
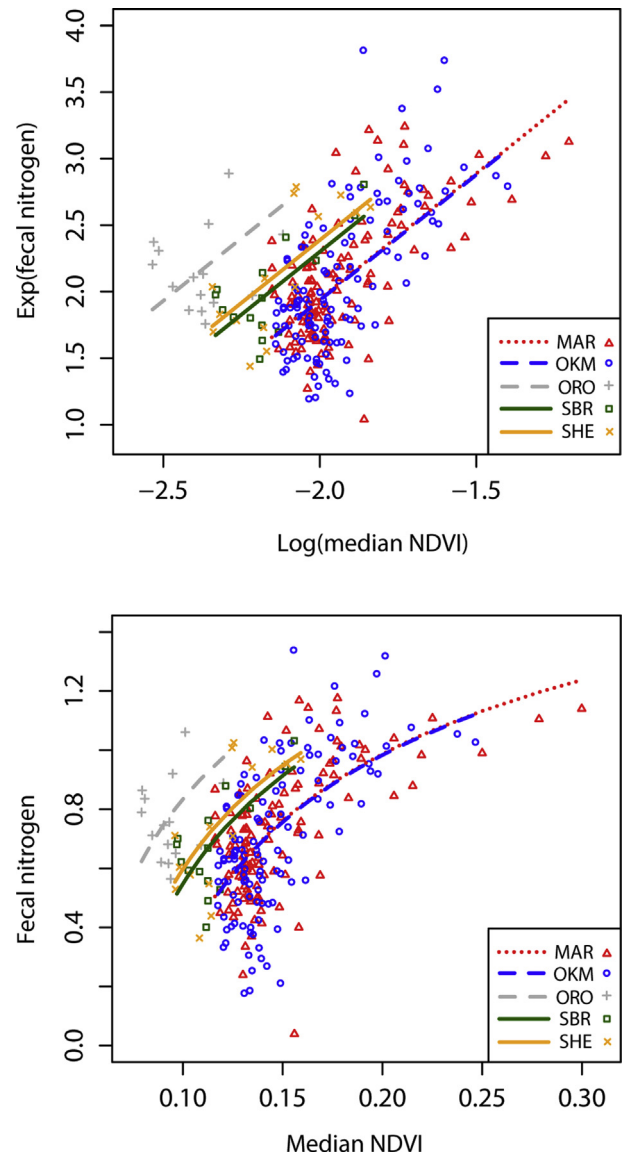
3.2. Season-level FN versus NDVI

We found a highly significant ($p < 0.001$), positive relationship between IFN and INDVI over the full growing season for the Marble Mountains and Old Dad Peak populations (Fig. 4). There was no evidence that the parallel lines model ($F_{1,19} = 0.139$, $p = 0.713$) or separate lines model ($F_{2,18} = 0.396$, $p = 0.679$) fit the data better than the simpler equal lines model, in which the relationship between FN and NDVI was the same for the two populations. R^2 for this best-fitting equal lines model was 0.64, indicating that NDVI explained the majority of season-level variation in FN; thus, NDVI was a better predictor of diet quality at the season level than at the sample level.

3.3. Characteristics of FN and NDVI curves

The peak magnitude and seasonal pattern of NDVI varied among years from 2000 through 2011, but the timing and relative magnitude of peaks in NDVI was similar among patches within the region (Fig. A.8). In the Marble Mountains and Old Dad Peak patches, peak FN typically occurred after peak NDVI (Fig. 2): peak NDVI preceded peak FN in 9 of 11 years in Marble Mountains and 8 of 11 years in Old Dad Peak, with mean lag times of 60 and 48 days, respectively. Mean monthly IFN percentages exceeded mean monthly INDVI percentages at the very beginning and during the last 2−3 months of the growing season, but the pattern was reversed during the middle of the growing season (approximately November through March; Fig. 5).

Both peak width and peak height were highly significant ($p \leq 0.002$) predictors of INDVI, but peak height explained a greater amount of variation in INDVI (Fig. A.9, Table 1). In contrast, peak

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[2] Traditional R^2 cannot be calculated for generalized least squares models; pseudo R^2 presented here is the squared correlation between observed and predicted dependent variable values, a measure of in-sample predictive ability that is similar to traditional R^2 but not related to variance decomposition.
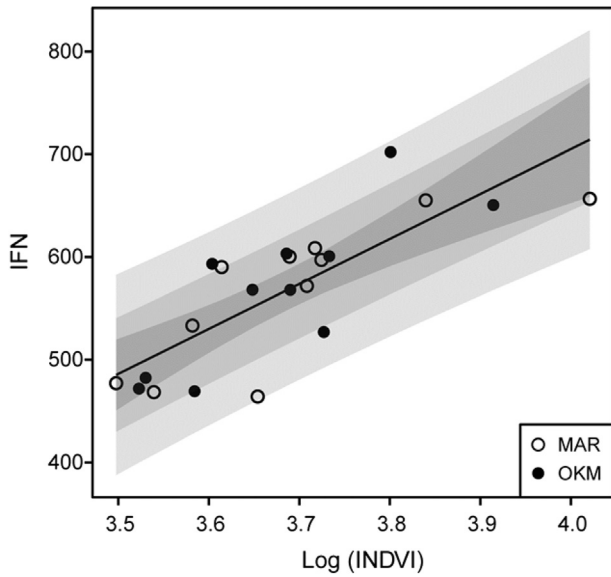

Fig. 3. Relationship between fecal nitrogen and Normalized Difference Vegetation Index (NDVI) at the sample level for the Marble Mountains (MAR), Old Dad Peak (OKM), Orocopia Mountains (ORO), South Bristol Mountains (SBR), and Sheephole Mountains (SHE) bighorn sheep populations from 2000 through 2011. Regression lines are from the best-fitting model with equal slopes but different intercepts for the patches. Top panel shows relationship modeled in linear regression analysis: log-transformed NDVI, FN back-transformed to original scale via exponentiation. Bottom panel shows relationship that is most biologically interpretable: NDVI on original scale, FN log-transformed to be linearly related to apparent digestibility. Regression lines for MAR and OKM overlap in figure but are not identical. Individual plots for each population are in Fig. A.7.

width explained considerably more variation in IFN than peak height, which was not a statistically significant ($p > 0.05$) predictor of IFN (Fig. A.9, Table 1). We achieved qualitatively similar results using a range of threshold FN and NDVI values to define peak width, suggesting that the above conclusions were insensitive to the baseline values we selected.

3.4. Genetic diversity versus NDVI

The connectivity metric most strongly correlated with both A_r and H_e, demographic weighted closeness (Table A2), was included as a predictor in regression models and log-transformed to make its

Fig. 4. Relationship between integrated fecal nitrogen (IFN) and log of integrated Normalized Difference Vegetation Index (INDVI) during the Oct.–June growing season for the Marble Mountains (MAR) and Old Dad Peak (OKM) habitat patches between 2001 and 2011. Regression line (solid line) is from the best-fitting model with equal slopes and intercepts for the patches. Dark-shaded region is the 95% pointwise confidence band; medium- and light-shaded regions are 75% and 95% pointwise prediction bands.

relationships with genetic diversity indices linear. A_r and H_e were both positively related to growing-season median INDVI during 2001–2011, after accounting for connectivity (Table 2; Fig. 6), and the relationship was slightly stronger for A_r. For both genetic diversity metrics, the multiple regression model including INDVI and connectivity as predictors was preferred over the INDVI-only model (A_r: $F_{1,18} = 18.344$, $p < 0.001$, H_e: $F_{1,18} = 13.659$, $p = 0.002$) and the connectivity-only model (A_r: $F_{2,18} = 6.980$, $p = 0.006$, H_e: $F_{2,18} = 4.704$, $p = 0.023$). The single-factor model with connectivity as the predictor had higher R^2 than the model with median INDVI as the predictor for both genetic diversity indices (Table 2), suggesting that connectivity had a greater influence on genetic diversity than NDVI. Models accounting for possible spatial autocorrelation provided similar estimates and only marginally higher p-values (Table A.4).

4. Discussion

4.1. Variation among habitat patches

The results of our sample-level analysis supported our hypothesis that FN-NDVI relationships differed among populations (Fig. 3). This result appeared to be mostly driven by the Orocopia Mountains population, which had considerably lower NDVI values than the other four populations considered, but comparable FN values. The Orocopia Mountains are the southernmost population by 60 km and have a climate more characteristic of the Sonoran Desert, where a larger proportion of annual precipitation arrives as summer rains (as opposed to dominant winter precipitation in the Mojave Desert). However, a previous FN analysis for a nearby Sonoran-influenced population (Turtle Mountains; Wehausen, 2005), demonstrated a seasonal nutritional pattern similar to Mojave Desert populations, so major climatic differences probably do not explain the difference in the FN-NDVI relationship among patches. Differences among patches in the forage species consumed by bighorn sheep are a more likely explanation.
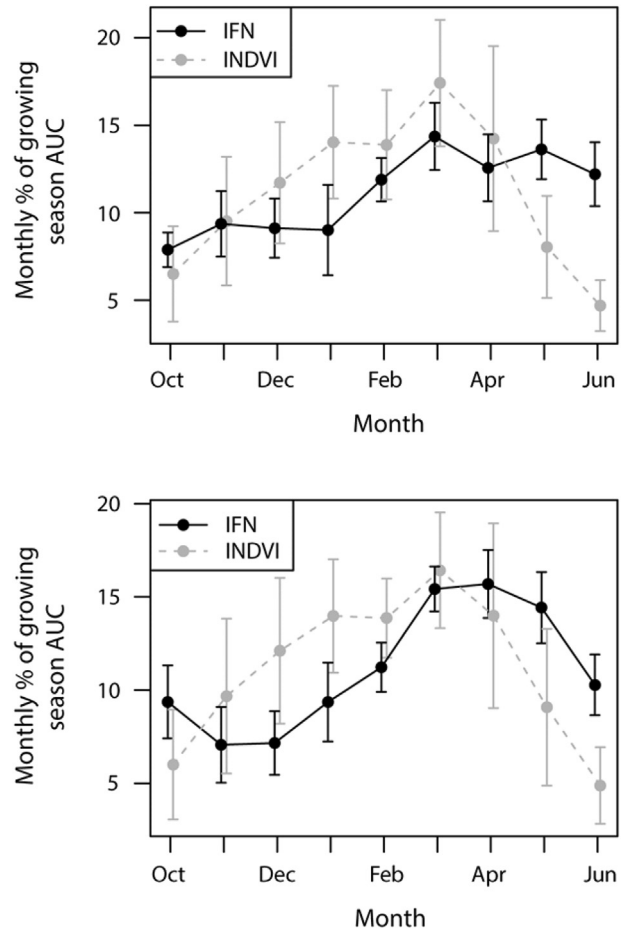
Fig. 5. Mean monthly percentages of total growing season area-under-curve (INDVI or IFN) in the Marble Mountains (top panel) and Old Dad Peak (bottom panel) patches. Points and error bars show means and 95% confidence intervals, respectively, of monthly percentages from 2001 through 2011. N = 11 for each month.

Table 1
Effects of peak height and peak width of FN and NDVI curves on IFN and INDVI, respectively.

Response	Predictor(s)	P[a]	Model R^2	ΔR^{2}[b]
IFN[c]	FN peak height	0.055	0.92	0.02
	FN peak width	<0.001		0.34
INDVI[d]	NDVI peak height	<0.001	0.95	0.28
	NDVI peak width	0.002		0.03

[a] Significance from F-test of $\beta = 0$ for given covariate.
[b] Change in model R^2 when variable is removed from model.
[c] Integrated FN.
[d] Integrated NDVI.

We did not observe differences in the FN-NDVI relationship among populations in our season-level analysis, but we compared only two populations that are separated by only 50 km and have similar precipitation patterns and plant communities. Hence, we could not verify whether NDVI would be appropriate for comparing seasonal diet quality between populations that are more geographically distant and thus more likely to exhibit important differences in plant communities and resulting forage quantity, quality, or phenology. On the whole, however, our results suggested that observed relationships between NDVI and diet quality may only apply locally, and spatial extrapolation is risky. It may be necessary to "recalibrate" the relationship between NDVI and diet

Table 2
Models of relationship between genetic diversity and long-term NDVI for 22 bighorn sheep populations in the Mojave Desert.

Response	Predictor(s)	P[a]	Model R^2
A_r	median INDVI[b]	0.007	0.69
	(median INDVI)^2	0.012	
	log(connectivity[c])	<0.001	
A_r	log(connectivity)	<0.001	0.45
A_r	median INDVI	0.153	0.38
	(median INDVI)^2	0.263	
H_e	median INDVI	0.026	0.62
	(median INDVI)^2	0.041	
	log(connectivity)	0.002	
H_e	log(connectivity)	0.001	0.42
H_e	median INDVI	0.243	0.385
	(median INDVI)^2	0.34	

[a] Significance from F-test of $\beta = 0$ for given covariate.
[b] Median of growing-season integrated NDVI values from 2001 through 2011.
[c] Demographic weighted closeness (Appendix A), a network-based measure of population connectivity.
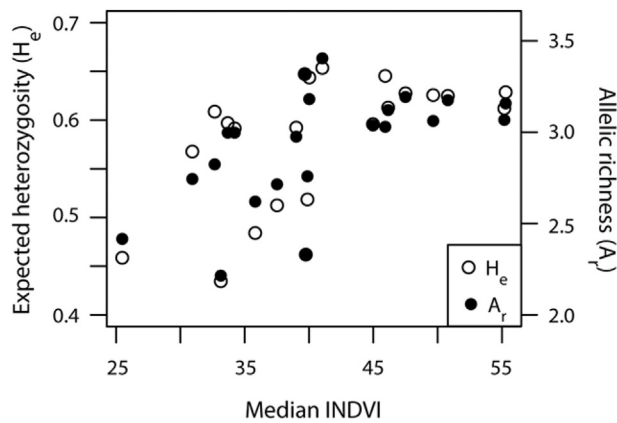
Fig. 6. Relationship between genetic diversity (expected heterozygosity [H_e] and allelic richness [A_r]) and Normalized Difference Vegetation Index (NDVI) for 22 Mojave Desert populations. NDVI is calculated as the median of growing-season integrated NDVI from 2001 through 2011. Partial residual plot (Fig. A.10) suggests a decline in genetic diversity indices at highest INDVI values after accounting for connectivity.

quality by collecting FN samples when applying this method in new areas, which would require a significant initial investment but allow for efficient monitoring of local diet quality over the long term.

4.2. Effects of temporal resolution

We observed weaker relationships between NDVI and FN at the sample level than at the season level. Perhaps the simplest explanation for this finding is that individual FN samples included varying amounts of random error that balanced out when integrated at the season level. However, comparison of FN and NDVI curves suggested that a temporal mismatch in periods of peak NDVI and peak FN played a role in the weaker sample-level relationship. Peak FN typically lagged behind peak NDVI by 1–2 months, and the majority of the area under the curve was in the middle of the growing season for INDVI but shifted toward the end of the growing season for IFN (Fig. 5). The stronger relationship between FN and NDVI when the curves are integrated across the entire growing season suggests that early-season overestimates of diet quality by NDVI somewhat balance later-season diet quality underestimates in years of better plant growth.

4.3. Drivers of NDVI and FN

The difference we observed in the timing of peak FN and peak NDVI most likely reflects a difference in the types of plant growth to which FN and NDVI are most responsive. NDVI peaks in early to mid-spring (Fig. 2), coincident with the period of strongest green-up of annual plants in the Mojave Desert (Beatley, 1974; Wallace and Thomas, 2008). Field notes on forage phenology from the period of fecal sample collection (J. Wehausen, unpublished data) further support this premise: we documented widespread growth of annual plant species in the Marble and Old Dad Peak patches in all eight years in which NDVI exhibited a clear peak and in none of the four years in which NDVI remained near baseline levels throughout the growing season (Fig. 2). In contrast, while FN also responds to the early-season growth of annual and other cold-tolerant species, it appears to respond most strongly to the appearance of highly digestible flowers of perennial species that become available later in the growing season. In the Marble Mountains and Old Dad Peak patches, flowers of the brittlebush shrub are an especially important food source in many years, as are the flowers of various other perennial species such as creosote bush, all of which elevate the nutrient level of bighorn diets during the second half of the growing season (J. Wehausen, personal observation). Thus, NDVI may track diet quality poorly when diets are composed primarily of flowers, perennial plants, or other items whose availability is not synchronized with peak green-up. These differences in nutrient intake tracked by FN and NDVI appear to explain why variation in IFN is mostly driven by the length of the growing season, while variation in INDVI instead reflects variation in peak value during the early green-up period.

We observed several instances in which growing-season pulses in FN were not accompanied by pulses in NDVI. For instance, during the 2002 and 2006 growing seasons in Marble Mountains and Old Dad Peak, there was virtually no increase in NDVI above summer baseline level, but FN still exhibited clear peaks in these growing seasons. This may reflect a reliance on foods not strongly linked with vegetation greenness (e.g., flowers of perennial species), which would have elevated FN in years of poor plant growth. Alternatively, the ability of bighorn sheep to maintain near-normal FN levels in growing seasons with low NDVI may have resulted from selective foraging in microhabitats such as washes where high quality forage was not detectable at the resolution of the NDVI data; this could have elevated FN before NDVI detected a change early in the growing season and at the end of the growing season.

4.4. Summarizing NDVI within a habitat patch

Median NDVI within a habitat patch was more strongly associated with FN than was 90th percentile or maximum NDVI for the majority of patches in our analysis, although correlations with FN for the three summary statistics were very similar in most cases. Given their mobility and nutrient-limited environment, we expected that bighorn sheep would selectively feed in portions of a habitat patch with the highest quality forage (and presumably the highest NDVI) and that this would result in stronger correlation with 90th percentile or maximum NDVI values. There are several plausible explanations for the slightly better performance of median NDVI. First, bighorn sheep may have integrated the fine-scale variation in nutrient availability by moving frequently and sampling multiple microhabitats. Such behavior could have resulted from conflicting habitat needs: dietary requirements are best met in areas of highest-quality forage, but the safest overnight bedding areas (around which bighorn sheep feed in the morning) are in steep terrain, often with poorer forage quality. Second, bighorn sheep could have fed over relatively limited areas of average forage

quality; this explanation is plausible during late spring and summer, when high temperatures can force bighorn sheep to remain close to water sources, but unlikely during other seasons when cooler weather affords greater flexibility in habitat use. Third, the 250-m resolution of our NDVI data may have been too coarse to distinguish microhabitats that provide high-quality forage within pixels of lower average quality. This lack of resolution is consistent with the peaks in FN that we observed during the growing season in years when NDVI remained at low levels throughout the year in the Marble Mountains and Old Dad Peak patches (e.g., 2002, 2006, and 2007 in Fig. 2).

4.5. NDVI and genetic diversity

We found evidence for an association between NDVI and genetic diversity of bighorn sheep populations. NDVI was significantly associated with both A_r and H_e of bighorn sheep populations, although to a lesser degree with the latter. Allelic richness tends to respond more quickly to population bottlenecks and other fluctuations than H_e when populations sizes are small (Leberg, 2002), as is the case with desert bighorn sheep (e.g., Epps et al., 2006). Genetic diversity indices had a stronger association with connectivity than with NDVI (Table 2), but this may have been influenced by limitations of our analysis: the duration of our NDVI data may not have been long enough to fully characterize the long-term average and variability of NDVI in habitat patches, and our assumption that recent NDVI was representative of longer-term NDVI may not have been warranted given regional climate change.

4.6. Saturation effect of NDVI

Results from all three temporal scales (sample, growing season, long-term) revealed a pattern of diminishing returns at the upper range of observed NDVI values, whereby further increases in NDVI were associated with negligible increases in diet quality or genetic diversity. We used logarithmic transformations to make these relationships linear for our sample- and season-level analyses, but the saturating pattern implies that bighorn sheep are able to maximize their diet quality even at intermediate levels of NDVI. Differences among populations in our sample-level analysis also support this conclusion; for instance, bighorn sheep in the Orocopia Mountains population had FN levels similar to those in the Marble Mountains and Old Dad Peak populations despite occupying habitat with much lower median NDVI (Fig. 3). However, this pattern could also have arisen if bighorn sheep in the Sonoran-influenced Orocopia Mountains were consuming browse species that were higher in phenolic compounds, which reduce protein digestion and inflate FN (Mould and Robbins, 1981).

The genetic diversity analysis suggested that this saturation effect applies over longer temporal scales. A quadratic relationship fit the data best and implied that both A_r and H_e actually declined slightly with increasing median INDVI for approximately the highest third of the range of median INDVI values observed (Fig. 6, Fig. A.10). However, the small number of data points in this upper range made it difficult to conclude with high confidence that the relationship was quadratic rather than asymptotic. If bighorn sheep are able to maximize diet quality at intermediate NDVI, as suggested by results from all three temporal resolutions examined in this study, this could conceivably lessen the initial negative effects of climate change. Current climate models generally predict increasing temperatures and decreasing precipitation for the southwestern United States (Garfin et al., 2014), but increased aridity may not immediately decrease population persistence in patches that have relatively high NDVI at present, assuming that other climate-influenced factors such as drinking water availability

are not limiting. Conversely, under the less likely scenario that precipitation in some areas increases, persistence probability of bighorn sheep populations may not increase if they have already maximized diet quality at current NDVI levels.

4.7. Limitations

Despite the strongly significant season-level relationship we observed between FN and NDVI, confidence and prediction bands for this relationship (Fig. 4) suggest that care is needed when applying this model in a predictive context. The model appears to adequately distinguish predicted mean FN values (and presumably diet quality) at different NDVI values, as evidenced by the relatively narrow 95 percent confidence band. However, the much wider 95 percent prediction band indicates that it will be difficult to predict FN for any particular growing season and patch with very high confidence using NDVI. Managers will need to balance the ease and availability of NDVI data against its predictive limitations. For instance, knowing with 75 percent confidence that FN is higher in year *x* than year *y* (or in patch *x* than patch *y*) might provide sufficient information to be useful in some applications, and is within the limitations of our model (Fig. 4); in other instances, if greater confidence is needed, MODIS-derived NDVI would not be an appropriate tool. Thus, NDVI is perhaps most appropriate as a coarse-level tool for comparing temporal or geographic variability in bighorn sheep diet quality. At a minimum, however, NDVI can distinguish between growing seasons of very high and very low diet quality (as indicated by FN) with a high level of confidence. Additional years of FN data collection would help to clarify the predictive limits of this relationship.

Several lines of evidence presented above suggest that our ability to predict diet quality was limited by the relatively coarse spatial resolution of the MODIS NDVI data we used. At 250-m resolution, a large fraction of each pixel in our satellite imagery consisted of bare soil or rock rather than vegetation, and we suspect that important microhabitats providing high quality forage were not captured at this resolution. However, the fact that we still observed a strong relationship between FN and NDVI, with seasonal peaks in NDVI corresponding to vegetation green-up, demonstrates that some signal of vegetation was nevertheless present in our NDVI data. This is consistent with many previous studies (e.g., Dall'Olmo and Karnieli, 2002; De La Maza et al., 2009; Santin-Janin et al., 2009; Wallace and Thomas, 2008; Wallace et al., 2008) that have successfully used NDVI data with 250-m or even coarser resolution to study vegetation characteristics in sparsely vegetated areas. Using satellite data of finer spatial resolution (e.g., Landsat TM) would likely improve our ability to accurately characterize diet quality around dates of image acquisition, but the accompanying loss of temporal resolution would compromise the ability to detect rapid shifts in diet quality that occur in the Mojave Desert following precipitation events.

In a recent study of white-tailed deer (*Odocoileus virginianus*), Monteith et al. (2014) found that FN of lactating females was lower than that of non-lactating females and males fed the same diet because lactating females had greater ability to extract nitrogen from forage. The applicability of this finding to other ungulate species has not been tested, but major differences exist between deer and desert bighorn sheep with respect to the structure of the digestive system and the characteristics of forage plants consumed (Krausman et al., 1993). This, plus the fact that virtually all of our FN samples were from ewes and most of these were lactating, leads us to believe that any bias introduced by this issue was minimal. Nonetheless, we recommend that researchers record the sex and lactation status of sampled individuals whenever possible in order to quantify any bias and, if necessary, develop separate models of

the FN-NDVI relationship for individuals of different sex and/or different lactation status.

5. Conclusions

We have demonstrated that NDVI is a useful indicator of seasonal diet quality of desert bighorn sheep in the Mojave Desert, a finding that can help address the logistical challenges of acquiring diet quality data for bighorn populations in this region. Wildlife managers might use such data to identify habitat patches with more favorable forage conditions that should be a higher priority for conservation actions such as reintroductions, addition of artificial water sources, or land use protections; conversely, NDVI could be used to identify patches with poorer forage conditions that do not warrant expending conservation resources. Although we have explored its utility for desert bighorn sheep only, NDVI may also provide a useful diet quality indicator for other desert-adapted ungulates, particularly those that occupy relatively discrete habitat patches or have clearly defined foraging ranges.

Nevertheless, we caution that the convenience of NDVI should not overshadow its apparent limitations. Our analysis suggests that NDVI may fail to reliably track diet quality if: 1) the spatial resolution of NDVI data is too coarse to detect microhabitats providing high quality forage, or 2) diet is strongly influenced by high-quality forage items that are weakly correlated with greenness (e.g., flowers). Thus, a detailed knowledge of dietary habits is critical for assessing the utility of NDVI as a diet quality indicator. Wildlife managers and researchers should understand which forage plants (and plant parts) are utilized at different parts of the year, how they are distributed on the landscape, and how well NDVI reflects the availability and digestibility of these food sources. Finally, we recommend verifying the relationship between NDVI and diet quality with more direct measures such as fecal nitrogen before applying NDVI as a diet quality indicator for a new species or environment.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2015.11.011.

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