Climatically driven changes in primary production propagate through trophic levels

Running head: Consumer abundance tracks primary productivity.

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ABSTRACT

Climate and land-use change are the major drivers of global biodiversity loss. Their effects are particularly acute for wide-ranging consumers, but little is known about how these factors interact to affect the abundance of large carnivores and their herbivore prey. We analyzed population densities of a primary and secondary consumer (mule deer, *Odocoileus hemionus*, and mountain lion, *Puma concolor*) across a climatic gradient in western North America by combining satellite-based maps of plant productivity with estimates of animal abundance and foraging area derived from Global Positioning Systems telemetry data (GPS). Mule deer density exhibited a positive, linear relationship with plant productivity ($r^2 = 0.58$), varying by a factor of 18 across the climate-vegetation gradient (38-697 individuals / 100 km²). Mountain lion home range size decreased in response to increasing primary productivity and consequent changes in the abundance of their herbivore prey (range: 20-450 km²). This pattern resulted in a strong, positive association between plant productivity and mountain lion density ($r^2 = 0.67$). Despite varying densities, the ratio of prey to predator remained constant across the climatic gradient (mean ± SE = 363 ± 29 mule deer / mountain lion), suggesting that the determinacy of the effect of primary productivity on consumer density was conserved across trophic levels. As droughts and longer-term climate changes reduce the suitability of marginal habitats, consumer home ranges will expand in order for individuals to meet basic nutritional requirements. These changes portend decreases in the abundance of large-bodied, wide-ranging wildlife through climatically-driven reductions in carrying capacity, as well as increased human-wildlife interactions stemming from anthropogenic land use and habitat fragmentation.
Climate and land-use change are altering the global distribution of ecosystem productivity and biodiversity (Pimm et al., 2014; Haddad et al., 2015). As expansion and intensification of human land use fragments natural habitats (Theobold et al., 2013, Haddad et al. 2015), coupled climate-vegetation models predict lower and more variable productivity in arid and semi-arid regions worldwide (Seager et al., 2012; Garfin et al., 2013). Although confidence is high that climate change will threaten rare species with narrow habitat requirements or small geographic ranges (e.g. Laidre, et al., 2015; Stewart et al., 2015; White et al., 2018), comparatively little is known about how these changes will affect the abundance of widely distributed species with broad environmental tolerances, or how these effects will transfer through food chains.

The effect of primary productivity on consumer abundance is among the most fundamental relationships in ecology (Lindeman 1942; Albrecht 1957; Huston & Wolverton 2011). Only a small fraction of matter from each trophic level is consumed and assimilated at successively higher levels, leading to exponential declines in biomass and energy through food chains (Lindeman 1942; Hatton et al., 2015). The productivity-abundance relationship is dictated by the energetics of foraging: in landscapes where food is concentrated, consumers can meet their caloric requirements within small home ranges; but when food resources are scarce or diffuse, consumers must expand their foraging radii to integrate productivity over larger areas (Duncan et al., 2015).

These relationships are well understood in small, experimental systems (e.g. Moe et al., 2005), however, the transmission of climatic effects from plants to herbivores and carnivores has not
been evaluated over scales relevant to the conservation of large, wide-ranging, or migratory species. For populations occupying marginal or fragmented habitats, climatic changes will increase vulnerability to extirpation (Blois et al., 2013) and/or compromise the ability of individuals to track forage resources seasonally (Haddad et al., 2015; McGuire, 2016). As such, these deficiencies warrant greater attention, as many ecologically and economically important consumers (e.g., big game, agricultural pests, human commensals, and livestock) are abundant and widely distributed habitat generalists.

The physiological constraints imposed by high energetic demands and low production efficiencies mean that carnivores are generally limited by prey density (Carbone et al., 2011), and as such, the distribution and abundance of predator and prey are correlated. To evaluate this general hypothesis, we analyzed population densities of a large herbivore (mule deer, Odocoileus hemionus) and its principal predator (mountain lion, Puma concolor) against a satellite index of plant productivity (Normalized Difference Vegetation Index, or NDVI; Rouse et al., 1973, Turner 2014) across a climate and productivity gradient in western North America. Drawing upon ecological energetic theory (Lindeman 1942; Huston & Wolverton 2011), we predicted that herbivore abundance would track spatial gradients in primary productivity. In response, carnivore home range should decrease - and population density increase - with positive changes in primary productivity. To illustrate these relationships we mapped predicted population densities of both species with respect to primary production across a climate-vegetation gradient. Finally, we predicted that the effects of changes in plant productivity would attenuate through the food chain, diminishing in strength or determinacy from primary to secondary consumers of plant biomass.
Study region. Analyses focused on three major arid ecoregions in western North America: the Great Basin, Colorado Plateau, and Mojave Desert (Fig. 1). Collectively, the region is forecasted to undergo warming and drying in the coming century (Seager et al., 2012; Garfin et al., 2013), which will further exacerbate already steep gradients in primary productivity. Anthropogenic water demand is also projected to escalate in response to continued human population growth and land-use change (MacDonald 2010; Theobold et al., 2013). The focal region spans 9° of latitude and encompasses > 3,300 m in elevational relief (757 m in the Grand Canyon to > 4,100 m in the Uinta Mountains), with commensurate variability in climate. Mean monthly temperatures range from -12 to 9° C in winter, and from 5 to 41° C in summer. Precipitation ranges from 179 to 732 mm/yr, with approximately 42% (range = 30-55%) falling as winter snow. A summer peak in rainfall associated with the North American Monsoon accounts for 28% of the annual total (range = 18-46%), the effect of which is most pronounced in the southern and eastern portions of the study region (Forzieri et al. 2014).

Common plant communities include succulents and evergreen shrubs in the lowest and driest areas (< 1,540 m; Yucca sp., Larrea tridentata, Coleogyne ramosissima, Artemisia tridentata). At middle elevations (1,540-2,460 m) these shrublands grade into piñon-juniper woodlands (Pinus sp., Juniperus sp.). Above 2,150 m, increased moisture and shorter growing seasons support montane and subalpine communities dominated by aspen and mixed conifer forests (Populus tremuloides, Pinus ponderosa, Pseudotsuga menziesii, Picea engelmannii, Abies lasiocarpa). Alpine conditions generally prevail above ~ 3,300 m.
Vegetation data

Primary production. We used NDVI to quantify primary productivity and plant phenology (Rouse et al., 1973). This remotely sensed index is sensitive to variation in leaf tissue and chlorophyll, and has been used to model consumer-habitat relationships in tropical, temperate, and arctic systems (Pettorelli et al., 2011, and references therein). Daily, 500-m resolution estimates of red and near-infrared surface reflectance spanning the study region compiled from 15 March, 2000 to 31 December, 2012 were drawn from the MOderate-resolution Imaging Spectroradiometer (MODIS) sensors aboard the Aqua and Terra satellites (https://ladsweb.modaps.eosdis.nasa.gov/api/v1/productPage/product=MOD09GA). Image data were masked for snow, cloud, and high aerosols and then corrected for Bidirectional Reflectance Distribution Function (BRDF) effects using the Ross-Li-Magnan model (Vermote et al., 2009). BRDF parameters were estimated from a master dataset (2000-2012) using a monthly moving window. Data gaps smaller than 16 days were filled using locally weighted scatterplot smoothing (LOWESS) to produce a BRDF-corrected, daily, 500-m resolution series of red and near-infrared reflectance estimates for each pixel. NDVI values were rescaled from 0-1.

Plant phenology. The “stack” of daily NDVI layers constituted the master dataset from which phenological variables were derived. We estimated three metrics of relevance to primary consumers: the start (SOS), peak (POS), and end of the growing season (EOS). For large herbivores, these seasonal events can be used to predict birth timing (Stoner et al., 2016), autumn migration (Monteith et al., 2011), and overwinter survival (Hurley et al., 2014). Here, we defined POS as the mean date across years on which the highest NDVI value was recorded for a

1 Accessed July 2013.
given pixel. SOS and EOS were defined as the inflection points on the ascending and descending arms of the phenological growth curve, respectively. These points equate to the date of the maximum rate of change in NDVI over time, and were measured as the date at which the first derivative approximated zero. Dates of inflection points occurred between the first snow-free day and POS (for SOS), and between POS and the lowest NDVI value in autumn (for EOS). Because of the coarse spatial resolution, we did not use NDVI as an evaluation of specific forage plants, but as an index of total ecosystem productivity (Pettorelli et al., 2011).

Animal data

Primary and secondary consumers. Intraspecific variation in the demography of primary (herbivores) and secondary (large-bodied carnivores) consumers is most readily evaluated using common, widely distributed species with generalized habitat requirements. Assessments are further strengthened when each focal species unambiguously falls within a single trophic level (i.e. obligate herbivore or carnivore), both are of a similar body mass, overlap in distribution, and exhibit direct behavioral interactions such as a predator-prey relationship. The mule deer is a common herbivore whose populations are closely monitored because of its economic value as a game species and an agricultural pest. The mountain lion is a large felid and the principal predator of mule deer in our study region. These species are sympatric from central Mexico to the Yukon Territory in Canada, and occupy the range of biomes found between the tropics and the boreal zone. Locally, both species may co-occur in agricultural and near-urban environments. Among females, mule deer tend to be heavier than mountain lions (51 ± 6 kg vs. 36 ± 8 kg; Mackie et al., 2003; Pierce & Bleich, 2003). Nevertheless, mule deer are the most commonly reported prey item in North American mountain lion diets and the strongest predictor of their
distribution, abundance, and population trends (Pierce & Bleich, 2003; Laundré et al., 2007; Pierce et al., 2012). Moreover, *Odocoileus* (including *O. virginianus*) and *Puma* are the most widely distributed ungulate and terrestrial carnivore genera in the western hemisphere. The tight coupling of their ecological relationship is evidenced by the concurrent expansion of their respective northern ranges (Pierce & Bleich, 2003) and their parallel patterns of body size in relation to latitude (Huston & Wolverton, 2011).

Herbivore density. Mule deer habitat, jurisdiction, and demographic data were obtained from the Utah Division of Wildlife Resources (UDWR) and the Western States and Provinces Mule Deer Mapping Project (WAFWA 2004). Methods detailing extrapolations of state-based population estimates to the study region are detailed in Appendix S1. We calculated habitat area using the intersection of a species-distribution model (WAFWA 2004) with the state-based wildlife monitoring unit polygons (Fig. 1; Table 1). Resulting polygons represented total mule deer habitat within a WMU and its associated estimate of density. We used these polygons to sample POS NDVI, which provided an index of primary productivity for each density estimate. Measures of NDVI were averaged spatially within a sampling polygon and through time (2000-2012; Appendix S2). Five units were dropped from the sampling frame due to lack of data or because they fell outside the range of NDVI common to both focal species.

Carnivore capture and marking. From 2002-2012 we outfitted 73 female mountain lions with GPS collars. These animals spanned 10 study sites in three ecoregions: the Great Basin (n = 4), Colorado Plateau (n = 5), and the Mojave Desert (n = 1). Two of the 10 study sites were represented by a small number of marked animals (Shoshone Peak, n = 1; Capitol Reef, n = 2), but were sufficiently similar climatically and botanically to pool individuals with neighboring
study sites (Shoshone Peak with the Sheep Range, and Capitol Reef with Zion). Individual study sites are illustrated in Fig. 1 and described in Table 2. GPS sampling schedules recorded 4-8 fixes/day. Capture and marking techniques are detailed in Stoner et al. (2006) and Mattson et al. (2011). All captures were conducted using animal handling guidelines endorsed by the American Society of Mammalogists (Sikes and Gannon 2011) with approval from various institutional IACUCs (Utah State University 937-R, Northern Arizona University 02-082-R4, and University of Nevada, R0610-257).

Carnivore home range size and density. We used Local Convex Hulls (LoCoH) to estimate 95% isopleth home ranges (Getz et al., 2007) of all resident adult female mountain lions with location data spanning at least one continuous growing season (n = 48). This procedure uses the parameter $k$, which defines the number of nearest neighbors around a root point from which to calculate convex hulls. Getz et al. (2007) suggested that the square root of $n$ (number of GPS locations) be used as the value for $k$ when home ranges contain areas of non-use or hard boundaries. Several home ranges in our dataset contained large unused areas (an open pit mine), or discrete edges (perimeter of the Grand Canyon), which made LoCoH the preferred alternative for home range estimation.

Juvenile ungulates comprise a critical prey item for female mountain lions in summer and fall (Pierce et al., 2000; Knopff et al., 2010). To capture the distribution of this food resource, we calculated home range as the area used by an individual over the growing season, defined here as the interval between SOS and EOS. We then calculated the mean home range size by study site, and sampled POS NDVI from a polygon representing the union of all individual home ranges for each site (Table 2; Appendix S3).
Home range is relatively simple to measure, and because of this, it has frequently been used to index density (Gros et al., 1996). Home range size and population density are demographic expressions of available energy and are algebraic inverses of one another. Density is defined as the number of individuals / area, and home-range is its reciprocal, i.e., area / individual (Blackburn & Gaston, 2001; Šálek et al., 2015). We used this relationship to model mountain lion density, with two caveats. First, the relation assumes mutually exclusive home ranges between animals (i.e. strict territoriality). If home ranges overlap, then actual density will be underestimated. Second, if home ranges are influenced by external factors that can disrupt social relations, such as hunting, then this index might overestimate actual densities. Mountain lions are subject to both of these potential biases; female home ranges overlap, and the species is managed as a game animal over much of its range. To account for lack of territoriality, we calculated home ranges during the local growing season, which not only captures important food resources, but is smaller than the annual range. This minimizes the inflation of density estimates stemming from the use of overlapping annual home ranges. With respect to social turnover, Maletzke et al. (2014) home range size with respect to residence time, and noted that female home ranges were insensitive to social perturbations produced by hunting.

Analyses. We used regression approaches to analyze consumer density and home range as functions of POS NDVI. NDVI measured at the peak-of-season served as the common index of primary productivity for both response variables. We limited our analyses to the range of POS NDVI values shared by each species in our dataset (~ 0.25-0.65), which included observations from 25 mule deer and 8 mountain lion populations.
A generalized linear mixed model (R package lme4; Bates et al., 2015) was used to evaluate the relationship between POS NDVI and mountain lion home range size. POS NDVI was considered a fixed effect, with study site treated as a random effect, and individual animals serving as within-site replicates. We compared random intercept to random intercept-random slope models, using AIC as the basis for final model selection, as we were more interested in prediction than variable determination of competing models. Prediction intervals were estimated using the R package merTools (Knowles & Frederick, 2016). Given the nested nature of the underlying design, focus of the prediction intervals was on the factor ‘site.’

We used analysis of covariance (ANCOVA) to test for interactions between the mule deer and mountain lion density models. Because our focal species represented different trophic levels, densities varied by more than two orders of magnitude. To accommodate this difference and illustrate relationships on a common scale, we conducted ANCOVA analyses on log10 transformed data. Predictions of population density (no. / 100 km²) were derived from regressions on untransformed data.

We first tested for an interaction effect using ‘species’ as factor levels; presence of an interaction would indicate that the slopes of the regression lines differed, and lead to the conclusion that the factor ‘species’ varied with POS NDVI. Lack of interaction would indicate species density changed at a constant rate, i.e., had similar slopes, with respect to POS NDVI. For each regression we tested model assumptions formally using the Shapiro-Wilk test and visually by inspecting model residuals and qqnorm plots.
We used the root-mean-square-error (RMSE) to quantify model uncertainty. This metric is equivalent to the standard deviation of a linear model. All statistical analyses were conducted using R base packages unless otherwise noted (R Development Core Team 2013). Spatial models were created in ArcGIS (v. 10.3), using the Albers Equal Area Conic and the North American Datum of 1983.

RESULTS

Regional variability in primary productivity. Growing season length, as calculated from the NDVI stacks, reflected the range of climatic conditions within the study region, averaging 175 ± 34 days (± SD). The standard deviation in POS NDVI reflects interannual variation. Higher mean annual POS NDVI was positively correlated with high interannual variability ($r_{\text{Spearman}} = 0.57$), reflecting the prevalence of deciduous vegetation in more productive systems. However, the coefficient of variation (CV) was negatively correlated with mean POS NDVI, indicating that xeric systems dominated by evergreen shrub cover or annual grasses displayed the highest relative interannual variation ($r_{\text{Spearman}} = -0.32$; see Fig. 1 for spatial distribution of POS NDVI).

Effects of primary production on herbivore population density. As predicted, mule deer density increased linearly with primary production (Fig. 2). Primary productivity at the peak-of-season explained 58% of the variation in mule deer abundance ($df = 1, 23; F = 31.3; P < 0.001$). Predicted densities ranged from 38 / 100 km$^2$ at POS NDVI = 0.25 (95% CI = 0-178 / 100 km$^2$) to 697 / 100 km$^2$ at POS NDVI = 0.65 (95% CI = 554-840 / 100 km$^2$). Densities were lowest in water-limited systems such as deserts and alpine areas, but up to 18 times greater in mesic, montane systems (Fig. 3a). This effect was surprisingly strong given the wide variation in plant community composition, forage palatability, and canopy height across the region.
Effects of primary production on carnivore home range area and population density. Following expectations, mountain lion home range size decreased with increasing plant productivity (Fig. 4). Growing season home range size for individual adult females varied from 20 to 450 km², a > 20-fold difference in intraspecific spatial requirements. Comparison of the random intercepts versus the random intercepts – random slopes models indicated the random intercepts model better fit the data ($P = 0.03$). The random intercepts model indicated a significant negative relationship of female mountain lion home range size with POS NDVI (estimate = -257.7, $F = 7.8$, $P < 0.01$). As with mule deer, the effect of POS NDVI was notable in light of the wide variation in terrain, land use, plant and animal community composition, and other environmental factors.

Mountain lion population density increased with primary productivity ($df = 1, 6; F = 6.3; P = 0.04$; Fig. 2), ranging from 0.0 / 100 km² at POS NDVI = 0.25 (95% CI = 0.0-1.4 / 100 km²) to 2.3 / 100 km² where POS NDVI = 0.65 (95% CI = 1.2-3.5 / 100 km²). The reciprocal of growing-season home range was a good index of density, as these values captured the range of estimates derived using intensive mark-recapture techniques in this and other North American ecosystems (0.3-3.2 / 100 km²; Logan & Sweanor 2001; Stoner et al., 2006). At the low end of this range, we documented mountain lion presence and reproduction in Mojave Desert ecosystems with mean POS NDVI as low as 0.28, but below this value, the model showed substantial uncertainty (Fig. 3b). Low productivity and high inter-annual variability were generally associated with large, variable home ranges and low population densities. Thus, sites
with mean POS NDVI = 0.28 (± 0.02) might be near the lower limits of primary productivity capable of supporting an adequate prey base for an obligate carnivore of this body mass.

Propagation of primary productivity across trophic levels.

We anticipated that the productivity constraint would weaken from mule deer to mountain lions due indirect coupling of carnivores to plant productivity. To evaluate this hypothesis formally, we compared regression coefficients between the mule deer and mountain lion models. There was no evidence of an interaction between POS NDVI and the factor ‘species,’ indicating that both species’ slopes were positive over the measured range of POS NDVI ($F = 0.48, P = 0.49$; Fig. 2). Statistically, despite the large difference in y-intercepts (mule deer = 1.08; mountain lion = -1.12), regression slopes were approximately parallel within the scale of x-values common to both species.

Regardless of the wide range of edaphic and botanical conditions among sites, determination of the thermodynamic constraint was conserved through the trophic system over the measured range of primary productivity. Quantifying the strength of the producer-consumer relationship, similar coefficients of determination (mule deer: $r^2 = 0.58$; mountain lion: $r^2 = 0.67$) and variation (RMSE: mule deer 0.24, mountain lion = 0.15) suggest a consistent degree of constraint spanning trophic levels. Although densities varied with POS NDVI, the ratio of prey to predator remained constant (mean ± SE = 363 ± 29 mule deer / mountain lion). This broadly confirms the theoretical expectation of energy and biomass loss through food chains (Lindeman 1942; Huston & Wolverton 2011).
DISCUSSION

Trophic propagation

Water balance limits vegetation productivity, composition, and phenology in arid and semi-arid ecosystems (Albrecht, 1957; Sexton et al., 2006; Huston, 2012) and these effects propagate through food chains from herbivores to large carnivores. Spatial variation in mule deer abundance was largely explained by a simple, remotely-sensed index of primary productivity, which ultimately affected the home range size and population density of its principal predator.

Herbivores depend directly on vegetation for food, and as such, we anticipated a strong relationship between NDVI and mule deer abundance. However, we predicted that the NDVI-consumer relationship would weaken at higher trophic levels as carnivore relations with vegetation were mediated through their herbivore prey. We found little evidence that the constraints imposed by primary production attenuate with trophic level. Indeed, despite indirect coupling to vegetation, and in contrast to our hypothesis, POS NDVI proved a similarly strong predictor of density for both species. Although the herbivore and carnivore regression slopes were separated by 2.5 orders of magnitude, the determinacy of the model relationships were similar, and the ratio of predator to prey did not change over the range of productivity.

The effects on carnivores were not due to vegetation directly, but were transferred across trophic levels through changes in the density of prey biomass. Juvenile ungulates are sensitive to stochastic (Duncan et al., 2012) and deterministic (Stoner et al., 2016) fluctuations in primary productivity. Given the importance of mule deer fawns to mountain lion recruitment (Laundré et al. 2007; Pierce et al., 2012) the relative abundance of this food resource was the likely
mechanism driving this relationship. The effect of prey density on carnivore home range size and abundance is well supported empirically in both temperate and tropical systems (Herfindal et al., 2005; Jędrzejewski et al., 2007; Duncan et al., 2015; Šálek et al., 2015), with or without migratory prey (Karanth et al., 2004; Loveridge et al., 2009; Simcharoen et al., 2014). Our results confirm this general observation, but also account for the differences in primary productivity underlying these patterns.

Other investigators have hypothesized that consumers at the highest trophic levels may be particularly vulnerable to climate change (Blois et al., 2013). Much of the evidence for this argument comes from species with highly specialized, temperature-sensitive habitat requirements, such as polar bears and sea ice (Ursus maritimus; Laidre et al., 2015). Our results lend support to this premise, and suggest that the pattern may be more general. The focal consumers studied here exhibit wide thermal tolerances, and represent one of the most broadly distributed predator-prey relationships in the western hemisphere. When considering the principle of energy loss across trophic levels, rather than being buffered by trophic distance, changes in primary productivity may be conserved from primary to secondary consumers. Given that large carnivores are thermodynamically constrained to live at exceptionally low densities, relatively small declines in primary production may result in disproportionately large reductions in herbivore prey. This is most likely to manifest as increased home range size, reduced fertility, and ultimately, lower population density.

Top-down versus bottom-up control
The form of the ecological productivity-density relationship has been debated since the early 1970’s, and is split between two competing models. The “Ideal Free Distribution” model holds that consumer density should increase linearly with food abundance due to equitable distribution of resources among consumers (Fretwell & Lucas, 1970). Under this scenario, consumer abundance varies, but per-capita resource availability remains relatively constant, regardless of spatial variation in productivity. However, for many carnivore species density appears to saturate in the most productive environments. This alternative model, the “Ideal Despotic Distribution” manifests as a diminishing positive relationship with increasing productivity. This hypothesis has been invoked to explain density-productivity relationships in organisms where social dominance and interference competition play a major role in the appropriation of resources (Beckmann & Berger 2003). The relationship of mountain lion population density to primary productivity observed here is consistent with the Ideal Free Distribution model, in that the relationship between abundance and POS NDVI was linear, with no evidence of a threshold or saturation over the measured range of values. Although density varied with climatically driven changes in POS NDVI, the prey to predator ratio remained constant, further suggesting that food availability, and not social dominance, was the ultimate factor regulating individual spatial requirements and female population density (Pierce et al., 2000; Logan & Sweanor 2001).

Corroborating other recent efforts (Pettorelli et al., 2009; Bårdsen & Tveraa, 2012; Duncan et al., 2012), our results suggest that although top-down effects remain important at local scales (Tallian et al., 2017), demographic processes operate within – or are even governed by - climatic constraints.

Implications for ecosystem management
Our results offer a macro-scale view of species abundance patterns in a system that exemplifies the twin stressors of increasing aridity and habitat fragmentation (Seager et al., 2012; Hansen et al., 2014). As climate change reduces primary productivity, consumer densities are likely to decline through a combination of environmental and anthropogenic forces. Propagations of reductions in primary production will manifest as reduced herbivore population densities. To compensate for decreases in prey abundance, carnivores should expand foraging areas, thereby increasing home range up to some energetically determined asymptote. The consequence of this would be to limit densities at a lower level. Anthropogenic land-use will further modify these patterns in two important ways: increasing the negative effect on populations by increasing the presence of movement barriers, effectively inhibiting dispersal and fragmenting seasonal migration routes (Sawyer et al., 2013; Haddad et al., 2014), but softening the effect through local increases in primary productivity resulting from irrigation subsidies (Šálek et al., 2015). As productivity differences between wild and anthropogenic landscapes increases, both herbivores and carnivores are likely to redistribute to the relatively productive and predictable conditions that characterize agricultural or urban systems (e.g. Beckmann & Berger, 2003; Tuqa et al., 2015). Exacerbating lower regional consumer abundance, these interacting forces portend greater human-wildlife conflict as remaining individuals move farther and encounter anthropogenic landscapes with greater frequency (Woodroffe & Ginsburg 1998; Hansen et al., 2014).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Table 1. Environmental and climatic characteristics of 25 wildlife monitoring units in Utah where mule deer abundance was estimated annually from 2007-2012. Monitoring units encompassed habitat conditions found within four major ecoregions in western North America.

<table>
<thead>
<tr>
<th>no.</th>
<th>Unit name</th>
<th>Ecoregion</th>
<th>Habitat (km²)</th>
<th>Mean elev (m)</th>
<th>Temperature (°C)</th>
<th>Total ppt (mm)</th>
<th>% ppt winter</th>
<th>% ppt summer</th>
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<td>494</td>
<td>39%</td>
</tr>
<tr>
<td>6</td>
<td>Fillmore</td>
<td>Great Basin</td>
<td>3,589</td>
<td>1,902</td>
<td>-0.1</td>
<td>18.2</td>
<td>402</td>
<td>38%</td>
</tr>
<tr>
<td>7</td>
<td>Henry Mtns</td>
<td>Colorado Plateau</td>
<td>228</td>
<td>2,605</td>
<td>-3.4</td>
<td>14.6</td>
<td>507</td>
<td>35%</td>
</tr>
<tr>
<td>8</td>
<td>Kaiparowitz</td>
<td>Colorado Plateau</td>
<td>2,970</td>
<td>1,872</td>
<td>-6.5</td>
<td>13.3</td>
<td>289</td>
<td>35%</td>
</tr>
<tr>
<td>9</td>
<td>Kamas</td>
<td>Great Basin</td>
<td>744</td>
<td>2,535</td>
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<td>15.4</td>
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<td>40%</td>
</tr>
<tr>
<td>10</td>
<td>La Sal</td>
<td>Colorado Plateau</td>
<td>1,131</td>
<td>2,101</td>
<td>-3.5</td>
<td>14.6</td>
<td>456</td>
<td>36%</td>
</tr>
<tr>
<td>11</td>
<td>Monroe Mtn</td>
<td>Great Basin</td>
<td>1,071</td>
<td>2,248</td>
<td>-4.2</td>
<td>13.8</td>
<td>444</td>
<td>36%</td>
</tr>
<tr>
<td>12</td>
<td>Morgan-Rich</td>
<td>Great Basin</td>
<td>2,158</td>
<td>2,129</td>
<td>-5.7</td>
<td>14.1</td>
<td>511</td>
<td>37%</td>
</tr>
<tr>
<td>13</td>
<td>Mt Dutton</td>
<td>Great Basin</td>
<td>1,499</td>
<td>2,391</td>
<td>-0.4</td>
<td>20.1</td>
<td>490</td>
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</tr>
<tr>
<td>14</td>
<td>Nine Mile</td>
<td>Colorado Plateau</td>
<td>3,540</td>
<td>2,143</td>
<td>-5.9</td>
<td>12.3</td>
<td>399</td>
<td>33%</td>
</tr>
<tr>
<td>15</td>
<td>No. Slope Uintas</td>
<td>So. Rockies</td>
<td>2,698</td>
<td>2,715</td>
<td>-1.5</td>
<td>18.2</td>
<td>610</td>
<td>34%</td>
</tr>
<tr>
<td>16</td>
<td>Oquirrh-Stansbury</td>
<td>Great Basin</td>
<td>1,294</td>
<td>1,949</td>
<td>-3.9</td>
<td>15.4</td>
<td>663</td>
<td>42%</td>
</tr>
<tr>
<td>17</td>
<td>Panguitch Lake</td>
<td>Colorado Plateau</td>
<td>1,986</td>
<td>2,450</td>
<td>-1.2</td>
<td>18.0</td>
<td>586</td>
<td>45%</td>
</tr>
<tr>
<td>18</td>
<td>Paunsaugunt</td>
<td>Colorado Plateau</td>
<td>3,671</td>
<td>1,987</td>
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<td>13.4</td>
<td>360</td>
<td>43%</td>
</tr>
<tr>
<td>19</td>
<td>Pine Valley</td>
<td>Mojave/G. Basin</td>
<td>2,851</td>
<td>1,740</td>
<td>0.2</td>
<td>18.2</td>
<td>444</td>
<td>47%</td>
</tr>
<tr>
<td>20</td>
<td>Plateau</td>
<td>Colorado Plateau</td>
<td>4,902</td>
<td>2,525</td>
<td>-1.3</td>
<td>19.1</td>
<td>452</td>
<td>36%</td>
</tr>
<tr>
<td>21</td>
<td>San Juan</td>
<td>Colorado Plateau</td>
<td>5,272</td>
<td>1,964</td>
<td>-4.8</td>
<td>14.4</td>
<td>305</td>
<td>37%</td>
</tr>
<tr>
<td>22</td>
<td>So. Slope Uintas</td>
<td>So. Rockies</td>
<td>5,704</td>
<td>2,447</td>
<td>-3.8</td>
<td>14.7</td>
<td>506</td>
<td>32%</td>
</tr>
<tr>
<td>23</td>
<td>Southwest Desert</td>
<td>Great Basin</td>
<td>4,442</td>
<td>1,926</td>
<td>-3.5</td>
<td>14.1</td>
<td>369</td>
<td>46%</td>
</tr>
<tr>
<td>24</td>
<td>West Desert</td>
<td>Great Basin</td>
<td>2,632</td>
<td>1,826</td>
<td>-2.0</td>
<td>17.4</td>
<td>439</td>
<td>39%</td>
</tr>
<tr>
<td>25</td>
<td>Zion</td>
<td>Colorado Plateau</td>
<td>3,028</td>
<td>1,937</td>
<td>-1.6</td>
<td>18.3</td>
<td>472</td>
<td>48%</td>
</tr>
</tbody>
</table>
**Table 2.** Environmental and climatic characteristics of mountain lion study sites in Utah, Arizona, and Nevada. Mountain lion GPS data were collected during 2002-2012 from three major ecoregions in western North America.

<table>
<thead>
<tr>
<th>ID</th>
<th>Site</th>
<th>Ecoregion</th>
<th>Habitat (km²)</th>
<th>Mean elev (m)</th>
<th>Mean temp (°C)</th>
<th>Total ppt (mm)</th>
<th>% ppt winter</th>
<th>% ppt summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Stansbury Mtns (UT)</td>
<td>Great Basin</td>
<td>440</td>
<td>1,723</td>
<td>-2.1</td>
<td>17.3</td>
<td>679</td>
<td>43%</td>
</tr>
<tr>
<td>B</td>
<td>Oquirrh Mtns (UT)</td>
<td>Great Basin</td>
<td>658</td>
<td>1,700</td>
<td>-1.7</td>
<td>17.7</td>
<td>721</td>
<td>43%</td>
</tr>
<tr>
<td>C</td>
<td>Monroe Mtn (UT)</td>
<td>Great Basin</td>
<td>636</td>
<td>2,366</td>
<td>-4.0</td>
<td>14.0</td>
<td>456</td>
<td>36%</td>
</tr>
<tr>
<td>D</td>
<td>Capitol Reef NP (UT)</td>
<td>Colorado Plateau</td>
<td>524</td>
<td>2,389</td>
<td>-4.4</td>
<td>13.6</td>
<td>432</td>
<td>32%</td>
</tr>
<tr>
<td>E</td>
<td>Zion NP (UT)</td>
<td>Colorado Plateau</td>
<td>405</td>
<td>2,026</td>
<td>0.3</td>
<td>18.3</td>
<td>473</td>
<td>49%</td>
</tr>
<tr>
<td>F</td>
<td>Shoshone Peak (NV)</td>
<td>Great Basin</td>
<td>920</td>
<td>1,362</td>
<td>3.4</td>
<td>21.5</td>
<td>171</td>
<td>51%</td>
</tr>
<tr>
<td>G</td>
<td>Sheep Range (NV)</td>
<td>Mojave Desert</td>
<td>1,570</td>
<td>1,743</td>
<td>3.7</td>
<td>21.6</td>
<td>282</td>
<td>56%</td>
</tr>
<tr>
<td>H</td>
<td>Kaibab Plateau (AZ)</td>
<td>Colorado Plateau</td>
<td>1,079</td>
<td>2,182</td>
<td>-0.9</td>
<td>16.5</td>
<td>424</td>
<td>44%</td>
</tr>
<tr>
<td>I</td>
<td>Grand Cyn NP (AZ)</td>
<td>Colorado Plateau</td>
<td>1,285</td>
<td>1,894</td>
<td>0.8</td>
<td>18.6</td>
<td>333</td>
<td>30%</td>
</tr>
<tr>
<td>J</td>
<td>Mogollon Rim (AZ)</td>
<td>Colorado Plateau</td>
<td>2,786</td>
<td>1,960</td>
<td>0.6</td>
<td>17.9</td>
<td>473</td>
<td>42%</td>
</tr>
</tbody>
</table>
Figure captions

Fig. 1. The study region includes portions of the Great Basin, Colorado Plateau, and Mojave Desert ecoregions in western North America. Polygons represent individual study sites for mule deer (black: 2007-2012) and mountain lions (white: 2002-2012). See Tables 1 and 2 for climatic characteristics of each site. Background primary productivity gradient represents NDVI values at the peak of the growing season (POS).

Fig. 2. Peak-of-season NDVI predicts mule deer and mountain lion densities across a climatic gradient spanning three ecoregions in western North America. A log10 transformation was applied to the raw values given the 2.5 orders of magnitude difference in density between mule deer and mountain lions.

Fig. 3. Predicted mule deer (a) and mountain lion (b) densities across a climatic gradient spanning three ecoregions in western North America. Regression models predict species absence from sites with mean Peak-of-Season NDVI ≤ 0.23 (mule deer) and 0.29 (mountain lions). These marginally habitable sites are likely to expand under current climate change projections.

Fig. 4. Mean female mountain lion home range size decreases with increasing primary productivity (bars = 90% CI; gray shading = 90% PI). Data represent the growing season home ranges (~ May-September) of 48 adults, averaged by study site (n = 8). POS NDVI measures denote the highest annual values averaged across years (2000-2012). Data span a climatic gradient representing three ecoregions in western North America.
Supporting Information


Supporting Information, Appendix S2. Utah mule deer monitoring units, population estimates, and associated NDVI metrics, 2007-2012.

Supporting Information, Appendix S3. Mountain lion study sites, home range estimates, and associated NDVI metrics, Utah, Nevada, and Arizona, 2002-2012.
\[ \log_{10} \text{(individuals/100 km}^2\text{)} \]

Peak of Season NDVI

- **Mule deer:** \[ y = 3.05 \text{NDVI} + 1.08, \quad r^2 = 0.58 \]
- **Mountain lion:** \[ y = 2.32 \text{NDVI} - 1.12, \quad r^2 = 0.67 \]
Estimate  |  F-value | p-value |
----------|----------|---------|
Intercept | 233.1    | 40.9    | <0.0001 |
NDVI      | -257.7   | 7.8     | 0.0079  |

Growing season home range size (km²)

Peak of season NDVI