1   **Climatically driven changes in primary production propagate through trophic levels**

2   Running head: Consumer abundance tracks primary productivity.

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38   **ABSTRACT**

39

40   Climate and land-use change are the major drivers of global biodiversity loss. Their effects are

41   particularly acute for wide-ranging consumers, but little is known about how these factors

42   interact to affect the abundance of large carnivores and their herbivore prey. We analyzed

43   population densities of a primary and secondary consumer (mule deer, *Odocoileus hemionus*, and

44   mountain lion, *Puma concolor*) across a climatic gradient in western North America by

45   combining satellite-based maps of plant productivity with estimates of animal abundance and

46   foraging area derived from Global Positioning Systems telemetry data (GPS). Mule deer density

47   exhibited a positive, linear relationship with plant productivity ($r^2 = 0.58$), varying by a factor of

48   18 across the climate-vegetation gradient (38-697 individuals / 100 km^2). Mountain lion home

49   range size decreased in response to increasing primary productivity and consequent changes in

50   the abundance of their herbivore prey (range: 20-450 km^2). This pattern resulted in a strong,

51   positive association between plant productivity and mountain lion density ($r^2 = 0.67$). Despite

52   varying densities, the ratio of prey to predator remained constant across the climatic gradient

53   (mean $\pm$ SE = 363 $\pm$ 29 mule deer / mountain lion), suggesting that the determinacy of the effect

54   of primary productivity on consumer density was conserved across trophic levels. As droughts

55   and longer-term climate changes reduce the suitability of marginal habitats, consumer home

56   ranges will expand in order for individuals to meet basic nutritional requirements. These changes

57   portend decreases in the abundance of large-bodied, wide-ranging wildlife through climatically-

58   driven reductions in carrying capacity, as well as increased human-wildlife interactions

59   stemming from anthropogenic land use and habitat fragmentation.

60

INTRODUCTION

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

85   been evaluated over scales relevant to the conservation of large, wide-ranging, or migratory

86   species. For populations occupying marginal or fragmented habitats, climatic changes will

87   increase vulnerability to extirpation (Blois *et al*., 2013) and/or compromise the ability of

88   individuals to track forage resources seasonally (Haddad *et al*., 2015; McGuire, 2016). AS such,

89   these deficiencies warrant greater attention, as many ecologically and economically important

90   consumers (e.g., big game, agricultural pests, human commensals, and livestock) are abundant

91   and widely distributed habitat generalists.

92

93   The physiological constraints imposed by high energetic demands and low production

94   efficiencies mean that carnivores are generally limited by prey density (Carbone *et al*., 2011),

95   and as such, the distribution and abundance of predator and prey are correlated. To evaluate this

96   general hypothesis, we analyzed population densities of a large herbivore (mule deer, *Odocoileus*

97   *hemionus*) and its principal predator (mountain lion, *Puma concolor*) against a satellite index of

98   plant productivity (Normalized Difference Vegetation Index, or NDVI; Rouse *et al*., 1973,

99   Turner 2014) across a climate and productivity gradient in western North America. Drawing

100   upon ecological energetic theory (Lindeman 1942; Huston & Wolverton 2011), we predicted that

101   herbivore abundance would track spatial gradients in primary productivity. In response,

102   carnivore home range should decrease - and population density increase - with positive changes

103   in primary productivity. To illustrate these relationships we mapped predicted population

104   densities of both species with respect to primary production across a climate-vegetation gradient.

105   Finally, we predicted that the effects of changes in plant productivity would attenuate through

106   the food chain, diminishing in strength or determinacy from primary to secondary consumers of

107   plant biomass.

108 **MATERIALS AND METHODS**

109

110 *Study region.* Analyses focused on three major arid ecoregions in western North America: the

111 Great Basin, Colorado Plateau, and Mojave Desert (Fig. 1). Collectively, the region is forecasted

112 to undergo warming and drying in the coming century (Seager *et al*., 2012; Garfin *et al*., 2013),

113 which will further exacerbate already steep gradients in primary productivity. Anthropogenic

114 water demand is also projected to escalate in response to continued human population growth

115 and land-use change (MacDonald 2010; Theobold *et al*., 2013). The focal region spans 9° of

116 latitude and encompasses > 3,300 m in elevational relief (757 m in the Grand Canyon to > 4,100

117 m in the Uinta Mountains), with commensurate variability in climate. Mean monthly

118 temperatures range from -12 to 9° C in winter, and from 5 to 41° C in summer. Precipitation

119 ranges from 179 to 732 mm/yr, with approximately 42% (range = 30-55%) falling as winter

120 snow. A summer peak in rainfall associated with the North American Monsoon accounts for

121 28% of the annual total (range = 18-46%), the effect of which is most pronounced in the southern

122 and eastern portions of the study region (Forzieri et al. 2014).

123

124 Common plant communities include succulents and evergreen shrubs in the lowest and driest

125 areas (< 1,540 m; *Yucca sp.*, *Larrea tridentata*, *Coleognye ramosissima*, *Artemisia tridentata,*).

126 At middle elevations (1,540-2,460 m) these shrublands grade into piñon-juniper woodlands

127 (*Pinus sp.*, *Juniperus sp.*). Above 2,150 m, increased moisture and shorter growing seasons

128 support montane and subalpine communities dominated by aspen and mixed conifer forests

129 (*Populus tremuloides, Pinus ponderosa, Pseudotsuga menziesii, Picea engelmannii, Abies*

130 *lasiocarpa*). Alpine conditions generally prevail above ~ 3,300 m.

131

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[1]). 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

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[1] Accessed July 2013.

153   given pixel. SOS and EOS were defined as the inflection points on the ascending and descending

154   arms of the phenological growth curve, respectively. These points equate to the date of the

155   maximum rate of change in NDVI over time, and were measured as the date at which the first

156   derivative approximated zero. Dates of inflection points occurred between the first snow-free day

157   and POS (for SOS), and between POS and the lowest NDVI value in autumn (for EOS). Because

158   of the coarse spatial resolution, we did not use NDVI as an evaluation of specific forage plants,

159   but as an index of total ecosystem productivity (Pettorelli *et al*., 2011).

160

161   **Animal data**

162   *Primary and secondary consumers*. Intraspecific variation in the demography of primary

163   (herbivores) and secondary (large-bodied carnivores) consumers is most readily evaluated using

164   common, widely distributed species with generalized habitat requirements. Assessments are

165   further strengthened when each focal species unambiguously falls within a single trophic level

166   (i.e. obligate herbivore or carnivore), both are of a similar body mass, overlap in distribution, and

167   exhibit direct behavioral interactions such as a predator-prey relationship. The mule deer is a

168   common herbivore whose populations are closely monitored because of its economic value as a

169   game species and an agricultural pest. The mountain lion is a large felid and the principal

170   predator of mule deer in our study region. These species are sympatric from central Mexico to

171   the Yukon Territory in Canada, and occupy the range of biomes found between the tropics and

172   the boreal zone. Locally, both species may co-occur in agricultural and near-urban environments.

173   Among females, mule deer tend to be heavier than mountain lions (51 ± 6 kg vs. 36 ± 8 kg;

174   Mackie *et al*., 2003; Pierce & Bleich, 2003). Nevertheless, mule deer are the most commonly

175   reported prey item in North American mountain lion diets and the strongest predictor of their

176   distribution, abundance, and population trends (Pierce & Bleich, 2003; Laundré *et al*., 2007;

177   Pierce *et al*., 2012). Moreover, *Odocoileus* (including *O. virginianus*) and *Puma* are the most

178   widely distributed ungulate and terrestrial carnivore genera in the western hemisphere. The tight

179   coupling of their ecological relationship is evidenced by the concurrent expansion of their

180   respective northern ranges (Pierce & Bleich, 2003) and their parallel patterns of body size in

181   relation to latitude (Huston & Wolverton, 2011).

182

183   *Herbivore density*. Mule deer habitat, jurisdiction, and demographic, data were obtained from the

184   Utah Division of Wildlife Resources (UDWR) and the Western States and Provinces Mule Deer

185   Mapping Project (WAFWA 2004). Methods detailing extrapolations of state-based population

186   estimates to the study region are detailed in Appendix S1. We calculated habitat area using the

187   intersection of a species-distribution model (WAFWA 2004) with the state-based wildlife

188   monitoring unit polygons (Fig. 1; Table 1). Resulting polygons represented total mule deer

189   habitat within a WMU and its associated estimate of density. We used these polygons to sample

190   POS NDVI, which provided an index of primary productivity for each density estimate.

191   Measures of NDVI were averaged spatially within a sampling polygon and through time (2000-

192   2012; Appendix S2). Five units were dropped from the sampling frame due to lack of data or

193   because they fell outside the range of NDVI common to both focal species.

194

195   *Carnivore capture and marking*. From 2002-2012 we outfitted 73 female mountain lions with

196   GPS collars. These animals spanned 10 study sites in three ecoregions: the Great Basin (n = 4),

197   Colorado Plateau (n = 5), and the Mojave Desert (n = 1). Two of the 10 study sites were

198   represented by a small number of marked animals (Shoshone Peak, n = 1; Capitol Reef, n = 2),

199   but were sufficiently similar climatically and botanically to pool individuals with neighboring

200   study sites (Shoshone Peak with the Sheep Range, and Capitol Reef with Zion). Individual study

201   sites are illustrated in Fig. 1 and described in Table 2. GPS sampling schedules recorded 4-8

202   fixes / day. Capture and marking techniques are detailed in Stoner *et al*. (2006) and Mattson *et*

203   *al*. (2011). All captures were conducted using animal handling guidelines endorsed by the

204   American Society of Mammalogists (Sikes and Gannon 2011) with approval from various

205   institutional IACUCs (Utah State University 937-R, Northern Arizona University 02-082-R4,

206   and University of Nevada, R0610-257).

207

208   *Carnivore home range size and density*. We used Local Convex Hulls (LoCoH) to estimate 95%

209   isopleth home ranges (Getz *et al*., 2007) of all resident adult female mountain lions with location

210   data spanning at least one continuous growing season (n = 48). This procedure uses the

211   parameter *k*, which defines the number of nearest neighbors around a root point from which to

212   calculate convex hulls. Getz *et al*. (2007) suggested that the square root of *n* (number of GPS

213   locations) be used as the value for *k* when home ranges contain areas of non-use or hard

214   boundaries. Several home ranges in our dataset contained large unused areas (an open pit mine),

215   or discrete edges (perimeter of the Grand Canyon), which made LoCoH the preferred alternative

216   for home range estimation.

217   Juvenile ungulates comprise a critical prey item for female mountain lions in summer and fall

218   (Pierce *et al*., 2000; Knopff *et al*., 2010). To capture the distribution of this food resource, we

219   calculated home range as the area used by an individual over the growing season, defined here as

220   the interval between SOS and EOS. We then calculated the mean home range size by study site,

221   and sampled POS NDVI from a polygon representing the union of all individual home ranges for

222   each site (Table 2; Appendix S3).

223   Home range is relatively simple to measure, and because of this, it has frequently been used to

224   index density (Gros *et al*., 1996). Home range size and population density are demographic

225   expressions of available energy and are algebraic inverses of one another. Density is defined as

226   the number of individuals / area, and home-range is its reciprocal, i.e., area / individual

227   (Blackburn & Gaston, 2001; Šálek *et al*., 2015). We used this relationship to model mountain

228   lion density, with two caveats. First, the relation assumes mutually exclusive home ranges

229   between animals (i.e. strict territoriality). If home ranges overlap, then actual density will be

230   underestimated. Second, if home ranges are influenced by external factors that can disrupt social

231   relations, such as hunting, then this index might overestimate actual densities. Mountain lions are

232   subject to both of these potential biases; female home ranges overlap, and the species is managed

233   as a game animal over much of its range. To account for lack of territoriality, we calculated

234   home ranges during the local growing season, which not only captures important food resources,

235   but is smaller than the annual range. This minimizes the inflation of density estimates stemming

236   from the use of overlapping annual home ranges. With respect to social turnover, Maletzke *et al*.

237   (2014) home range size with respect to residence time, and noted that female home ranges were

238   insensitive to social perturbations produced by hunting.

239   *Analyses.* We used regression approaches to analyze consumer density and home range as

240   functions of POS NDVI. NDVI measured at the peak-of-season served as the common index of

241   primary productivity for both response variables. We limited our analyses to the range of POS

242   NDVI values shared by each species in our dataset (~ 0.25-0.65), which included observations

243   from 25 mule deer and 8 mountain lion populations.

244   A generalized linear mixed model (R package lme4; Bates *et al*., 2015) was used to evaluate the

245   relationship between POS NDVI and mountain lion home range size. POS NDVI was considered

246   a fixed effect, with study site treated as a random effect, and individual animals serving as

247   within-site replicates. We compared random intercept to random intercept-random slope models,

248   using AIC as the basis for final model selection, as we were more interested in prediction than

249   variable determination of competing models. Prediction intervals were estimated using the R

250   package merTools (Knowles & Frederick, 2016). Given the nested nature of the underlying

251   design, focus of the prediction intervals was on the factor 'site.'

252   We used analysis of covariance (ANCOVA) to test for interactions between the mule deer and

253   mountain lion density models. Because our focal species represented different trophic levels,

254   densities varied by more than two orders of magnitude. To accommodate this difference and

255   illustrate relationships on a common scale, we conducted ANCOVA analyses on $\log_{10}$

256   transformed data. Predictions of population density (no. / 100 km^2) were derived from

257   regressions on untransformed data.

258   We first tested for an interaction effect using 'species' as factor levels; presence of an interaction

259   would indicate that the slopes of the regression lines differed, and lead to the conclusion that the

260   factor 'species' varied with POS NDVI. Lack of interaction would indicate species density

261   changed at a constant rate, i.e., had similar slopes, with respect to POS NDVI. For each

262   regression we tested model assumptions formally using the Shapiro-Wilk test and visually by

263   inspecting model residuals and qqnorm plots.

264   We used the root-mean-square-error (RMSE) to quantify model uncertainty. This metric is

265   equivalent to the standard deviation of a linear model. All statistical analyses were conducted

266   using R base packages unless otherwise noted (R Development Core Team 2013). Spatial models

267   were created in ArcGIS (v. 10.3), using the Albers Equal Area Conic and the North American

268   Datum of 1983.

269   **RESULTS**

270   *Regional variability in primary productivity*. Growing season length, as calculated from the

271   NDVI stacks, reflected the range of climatic conditions within the study region, averaging $175 \pm$

272   34 days ($\pm$ SD). The standard deviation in POS NDVI reflects interannual variation. Higher

273   mean annual POS NDVI was positively correlated with high interannual variability ($r_{Spearman} =$

274   0.57), reflecting the prevalence of deciduous vegetation in more productive systems. However,

275   the coefficient of variation (CV) was negatively correlated with mean POS NDVI, indicating that

276   xeric systems dominated by evergreen shrub cover or annual grasses displayed the highest

277   relative interannual variation ($r_{Spearman} = $ -0.32; see Fig. 1 for spatial distribution of POS NDVI).

278

279   *Effects of primary production on herbivore population density*. As predicted, mule deer density

280   increased linearly with primary production (Fig. 2). Primary productivity at the peak-of-season

281   explained 58% of the variation in mule deer abundance ($df = 1, 23$; $F = 31.3$; $P < 0.001$).

282   Predicted densities ranged from 38 / 100 km^2 at POS NDVI $= 0.25$ (95% CI $= 0$-178 / 100 km^2)

283   to 697 / 100 km^2 at POS NDVI $= 0.65$ (95% CI $= 554$-840 / 100 km^2). Densities were lowest in

284   water-limited systems such as deserts and alpine areas, but up to 18 times greater in mesic,

285   montane systems (Fig. 3a). This effect was surprisingly strong given the wide variation in plant

286   community composition, forage palatability, and canopy height across the region.

287

288 *Effects of primary production on carnivore home range area and population density*. Following

289 expectations, mountain lion home range size decreased with increasing plant productivity (Fig.

290 4). Growing season home range size for individual adult females varied from 20 to 450 km^2, a >

291 20-fold difference in intraspecific spatial requirements. Comparison of the random intercepts

292 versus the random intercepts – random slopes models indicated the random intercepts model

293 better fit the data ($P = 0.03$). The random intercepts model indicated a significant negative

294 relationship of female mountain lion home range size with POS NDVI (estimate = -257.7, $F =$

295 7.8, $P < 0.01$). As with mule deer, the effect of POS NDVI was notable in light of the wide

296 variation in terrain, land use, plant and animal community composition, and other environmental

297 factors.

298

299 Mountain lion population density increased with primary productivity ($df = 1, 6$; $F = 6.3$; $P =$

300 0.04; Fig. 2), ranging from 0.0 / 100 km^2 at POS NDVI = 0.25 (95% CI = 0.0-1.4 / 100 km^2) to

301 2.3 / 100 km^2 where POS NDVI = 0.65 (95% CI = 1.2-3.5 / 100 km^2). The reciprocal of

302 growing-season home range was a good index of density, as these values captured the range of

303 estimates derived using intensive mark-recapture techniques in this and other North American

304 ecosystems (0.3-3.2 / 100 km^2; Logan & Sweanor 2001; Stoner *et al.*, 2006). At the low end of

305 this range, we documented mountain lion presence and reproduction in Mojave Desert

306 ecosystems with mean POS NDVI as low as 0.28, but below this value, the model showed

307 substantial uncertainty (Fig. 3b). Low productivity and high inter-annual variability were

308 generally associated with large, variable home ranges and low population densities. Thus, sites

309   with mean POS NDVI = 0.28 (± 0.02) might be near the lower limits of primary productivity

310   capable of supporting an adequate prey base for an obligate carnivore of this body mass.

311

312   *Propagation of primary productivity across trophic levels.*

313   We anticipated that the productivity constraint would weaken from mule deer to mountain lions

314   due indirect coupling of carnivores to plant productivity. To evaluate this hypothesis formally,

315   we compared regression coefficients between the mule deer and mountain lion models. There

316   was no evidence of an interaction between POS NDVI and the factor 'species,' indicating that

317   both species' slopes were positive over the measured range of POS NDVI ($F = 0.48$, $P = 0.49$;

318   Fig. 2). Statistically, despite the large difference in y-intercepts (mule deer = 1.08; mountain lion

319   = -1.12), regression slopes were approximately parallel within the scale of x-values common to

320   both species.

321

322   Regardless of the wide range of edaphic and botanical conditions among sites, determination of

323   the thermodynamic constraint was conserved through the trophic system over the measured

324   range of primary productivity. Quantifying the strength of the producer-consumer relationship,

325   similar coefficients of determination (mule deer: $r^2 = 0.58$; mountain lion: $r^2 = 0.67$) and variation

326   (RMSE: mule deer 0.24, mountain lion = 0.15) suggest a consistent degree of constraint

327   spanning trophic levels. Although densities varied with POS NDVI, the ratio of prey to predator

328   remained constant (mean ± SE = 363 ± 29 mule deer / mountain lion). This broadly confirms the

329   theoretical expectation of energy and biomass loss through food chains (Lindeman 1942; Huston

330   & Wolverton 2011).

331

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

355   mechanism driving this relationship. The effect of prey density on carnivore home range size and

356   abundance is well supported empirically in both temperate and tropical systems (Herfindal *et al.*,

357   2005; Jędrzejewski *et al.*, 2007; Duncan *et al.*, 2015; Šálek *et al.*, 2015), with or without

358   migratory prey (Karanth *et al.*, 2004; Loveridge *et al.*, 2009; Simcharoen *et al.*, 2014). Our

359   results confirm this general observation, but also account for the differences in primary

360   productivity underlying these patterns.

361

362   Other investigators have hypothesized that consumers at the highest trophic levels may be

363   particularly vulnerable to climate change (Blois *et al.*, 2013). Much of the evidence for this

364   argument comes from species with highly specialized, temperature-sensitive habitat

365   requirements, such as polar bears and sea ice (*Ursus maritimus*; Laidre *et al.*, 2015). Our results

366   lend support to this premise, and suggest that the pattern may be more general. The focal

367   consumers studied here exhibit wide thermal tolerances, and represent one of the most broadly

368   distributed predator-prey relationships in the western hemisphere. When considering the

369   principle of energy loss across trophic levels, rather than being buffered by trophic distance,

370   changes in primary productivity may be conserved from primary to secondary consumers. Given

371   that large carnivores are thermodynamically constrained to live at exceptionally low densities,

372   relatively small declines in primary production may result in disproportionately large reductions

373   in herbivore prey. This is most likely to manifest as increased home range size, reduced fertility,

374   and ultimately, lower population density.

375

376   *Top-down versus bottom-up control*

377 The form of the ecological productivity-density relationship has been debated since the early

378 1970's, and is split between two competing models. The "Ideal Free Distribution" model holds

379 that consumer density should increase linearly with food abundance due to equitable distribution

380 of resources among consumers (Fretwell & Lucas, 1970). Under this scenario, consumer

381 abundance varies, but per-capita resource availability remains relatively constant, regardless of

382 spatial variation in productivity. However, for many carnivore species density appears to saturate

383 in the most productive environments. This alternative model, the "Ideal Despotic Distribution"

384 manifests as a diminishing positive relationship with increasing productivity. This hypothesis has

385 been invoked to explain density-productivity relationships in organisms where social dominance

386 and interference competition play a major role in the appropriation of resources (Beckmann &

387 Berger 2003). The relationship of mountain lion population density to primary productivity

388 observed here is consistent with the Ideal Free Distribution model, in that the relationship

389 between abundance and POS NDVI was linear, with no evidence of a threshold or saturation

390 over the measured range of values. Although density varied with climatically driven changes in

391 POS NDVI, the prey to predator ratio remained constant, further suggesting that food

392 availability, and not social dominance, was the ultimate factor regulating individual spatial

393 requirements and female population density (Pierce *et al*., 2000; Logan & Sweanor 2001).

394 Corroborating other recent efforts (Pettorelli *et al*., 2009; Bårdsen & Tveraa, 2012; Duncan *et*

395 *al*., 2012), our results suggest that although top-down effects remain important at local scales

396 (Tallian *et al*., 2017), demographic processes operate within – or are even governed by - climatic

397 constraints.

398

399 *Implications for ecosystem management*

400   Our results offer a macro-scale view of species abundance patterns in a system that exemplifies

401   the twin stressors of increasing aridity and habitat fragmentation (Seager *et al.*, 2012; Hansen *et*

402   *al*., 2014). As climate change reduces primary productivity, consumer densities are likely to

403   decline through a combination of environmental and anthropogenic forces. Propagations of

404   reductions in primary production will manifest as reduced herbivore population densities. To

405   compensate for decreases in prey abundance, carnivores should expand foraging areas, thereby

406   increasing home range up to some energetically determined asymptote. The consequence of this

407   would be to limit densities at a lower level. Anthropogenic land-use will further modify these

408   patterns in two important ways: increasing the negative effect on populations by increasing the

409   presence of movement barriers, effectively inhibiting dispersal and fragmenting seasonal

410   migration routes (Sawyer *et al*., 2013; Haddad *et al*., 2014), but softening the effect through local

411   increases in primary productivity resulting from irrigation subsidies (Šálek *et al*., 2015). As

412   productivity differences between wild and anthropogenic landscapes increases, both herbivores

413   and carnivores are likely to redistribute to the relatively productive and predictable conditions

414   that characterize agricultural or urban systems (e.g. Beckmann & Berger, 2003; Tuqa *et al*.,

415   2015). Exacerbating lower regional consumer abundance, these interacting forces portend greater

416   human-wildlife conflict as remaining individuals move farther and encounter anthropogenic

417   landscapes with greater frequency (Woodroffe & Ginsburg 1998; Hansen *et al*., 2014).

418

440

441   CONFLICT OF INTEREST

442   The authors declare no conflict of interest.

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612

613　**Table 1**. Environmental and climatic characteristics of 25 wildlife monitoring units in Utah

614　where mule deer abundance was estimated annually from 2007-2012. Monitoring units

615　encompassed habitat conditions found within four major ecoregions in western North America.

no.	Unit name	Ecoregion	Habitat (km^2)	Mean elev (m)	Temperature (°C)		Total ppt (mm)	% ppt winter	% ppt summer
					winter	summer			
1	Beaver	Great Basin	3,228	2,147	0.8	19.1	462	38%	27%
2	Book Cliffs	Colorado Plateau	5,530	2,005	0.3	19.6	377	33%	32%
3	Box Elder	Great Basin	3,086	1,825	-2.3	16.4	359	40%	21%
4	Cache	Great Basin	3,297	2,066	-3.6	19.2	469	40%	21%
5	Central Mtns	Great Basin	7,132	2,254	-4.0	16.9	494	39%	24%
6	Fillmore	Great Basin	3,589	1,902	-0.1	18.2	402	38%	24%
7	Henry Mtns	Colorado Plateau	228	2,605	-3.4	14.6	507	35%	34%
8	Kaiparowitz	Colorado Plateau	2,970	1,872	-6.5	13.3	289	35%	35%
9	Kamas	Great Basin	744	2,535	-3.4	15.4	724	40%	22%
10	La Sal	Colorado Plateau	1,131	2,101	-3.5	14.6	456	36%	33%
11	Monroe Mtn	Great Basin	1,071	2,248	-4.2	13.8	444	36%	31%
12	Morgan-Rich	Great Basin	2,158	2,129	-5.7	14.1	511	37%	23%
13	Mt Dutton	Great Basin	1,499	2,391	-0.4	20.1	490	42%	27%
14	Nine Mile	Colorado Plateau	3,540	2,143	-5.9	12.3	399	33%	30%
15	No. Slope Uintas	So. Rockies	2,698	2,715	-1.5	18.2	610	34%	29%
16	Oquirrh-Stansbury	Great Basin	1,294	1,949	-3.9	15.4	663	42%	18%
17	Panguitch Lake	Colorado Plateau	1,986	2,450	-1.2	18.0	586	45%	25%
18	Paunsaugunt	Colorado Plateau	3,671	1,987	-5.7	13.4	360	43%	29%
19	Pine Valley	Mojave/G. Basin	2,851	1,740	0.2	18.2	444	47%	24%
20	Plateau	Colorado Plateau	4,902	2,525	-1.3	19.1	452	36%	32%
21	San Juan	Colorado Plateau	5,272	1,964	-4.8	14.4	305	37%	35%
22	So. Slope Uintas	So. Rockies	5,704	2,447	-3.8	14.7	506	32%	30%
23	Southwest Desert	Great Basin	4,442	1,926	-3.5	14.1	369	46%	24%
24	West Desert	Great Basin	2,632	1,826	-2.0	17.4	439	39%	21%
25	Zion	Colorado Plateau	3,028	1,937	-1.6	18.3	472	48%	23%

616

617 **Table 2**. Environmental and climatic characteristics of mountain lion study sites in Utah,

618 Arizona, and Nevada. Mountain lion GPS data were collected during 2002-2012 from three

619 major ecoregions in western North America.

ID	Site	Ecoregion	Habitat (km²)	Mean elev (m)	Mean temp (°C)		Total ppt (mm)	% ppt winter	% ppt summer
					Winter	Summer			
A	Stansbury Mtns (UT)	Great Basin	440	1,723	-2.1	17.3	679	43%	18%
B	Oquirrh Mtns (UT)	Great Basin	658	1,700	-1.7	17.7	721	43%	17%
C	Monroe Mtn (UT)	Great Basin	636	2,366	-4.0	14.0	456	36%	31%
D	Capitol Reef NP (UT)	Colorado Plateau	524	2,389	-4.4	13.6	432	32%	36%
E	Zion NP (UT)	Colorado Plateau	405	2,026	0.3	18.3	473	49%	22%
F	Shoshone Peak (NV)	Great Basin	920	1,362	3.4	21.5	171	51%	23%
G	Sheep Range (NV)	Mojave Desert	1,570	1,743	3.7	21.6	282	56%	18%
H	Kaibab Plateau (AZ)	Colorado Plateau	1,079	2,182	-0.9	16.5	424	44%	31%
I	Grand Cyn NP (AZ)	Colorado Plateau	1,285	1,894	0.8	18.6	333	30%	46%
J	Mogollon Rim (AZ)	Colorado Plateau	2,786	1,960	0.6	17.9	473	42%	38%

620

621 **Figure captions**

622

623 **Fig. 1**. The study region includes portions of the Great Basin, Colorado Plateau, and Mojave

624 Desert ecoregions in western North America. Polygons represent individual study sites for mule

625 deer (black: 2007-2012) and mountain lions (white: 2002-2012). See Tables 1 and 2 for climatic

626 characteristics of each site. Background primary productivity gradient represents NDVI values at

627 the peak of the growing season (POS).

628

629 **Fig. 2.** Peak-of-season NDVI predicts mule deer and mountain lion densities across a climatic

630 gradient spanning three ecoregions in western North America. A $\log_{10}$ transformation was

631 applied to the raw values given the 2.5 orders of magnitude difference in density between mule

632 deer and mountain lions.

633

634 **Fig. 3**. Predicted mule deer (a) and mountain lion (b) densities across a climatic gradient

635 spanning three ecoregions in western North America. Regression models predict species absence

636 from sites with mean Peak-of-Season NDVI ≤ 0.23 (mule deer) and 0.29 (mountain lions). These

637 marginally habitable sites are likely to expand under current climate change projections.

638

639 **Fig. 4**. Mean female mountain lion home range size decreases with increasing primary

640 productivity (bars = 90% CI; gray shading = 90% PI). Data represent the growing season home

641 ranges (~ May-September) of 48 adults, averaged by study site (n = 8). POS NDVI measures

642 denote the highest annual values averaged across years (2000-2012). Data span a climatic

643 gradient representing three ecoregions in western North America.
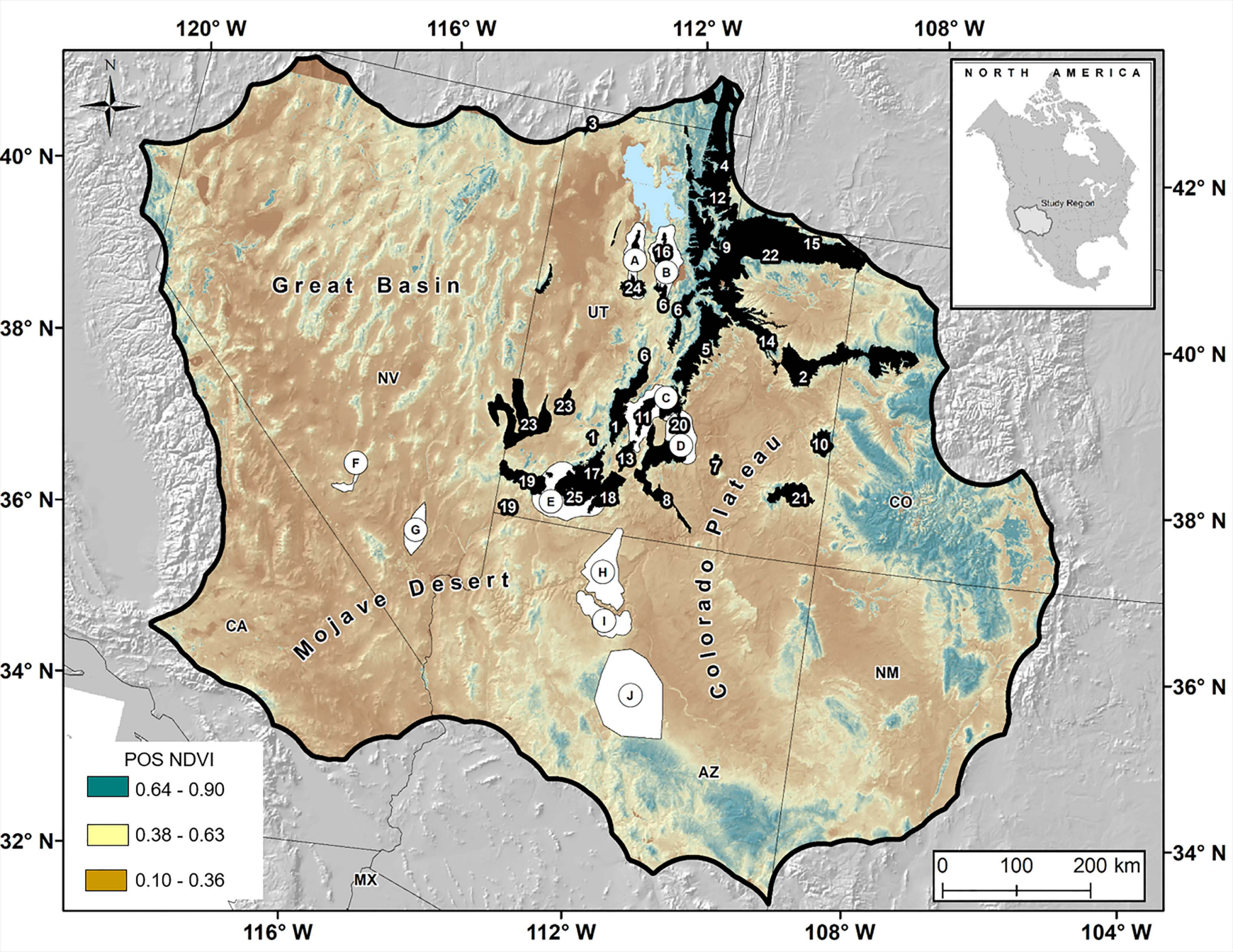
644

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Supporting Information

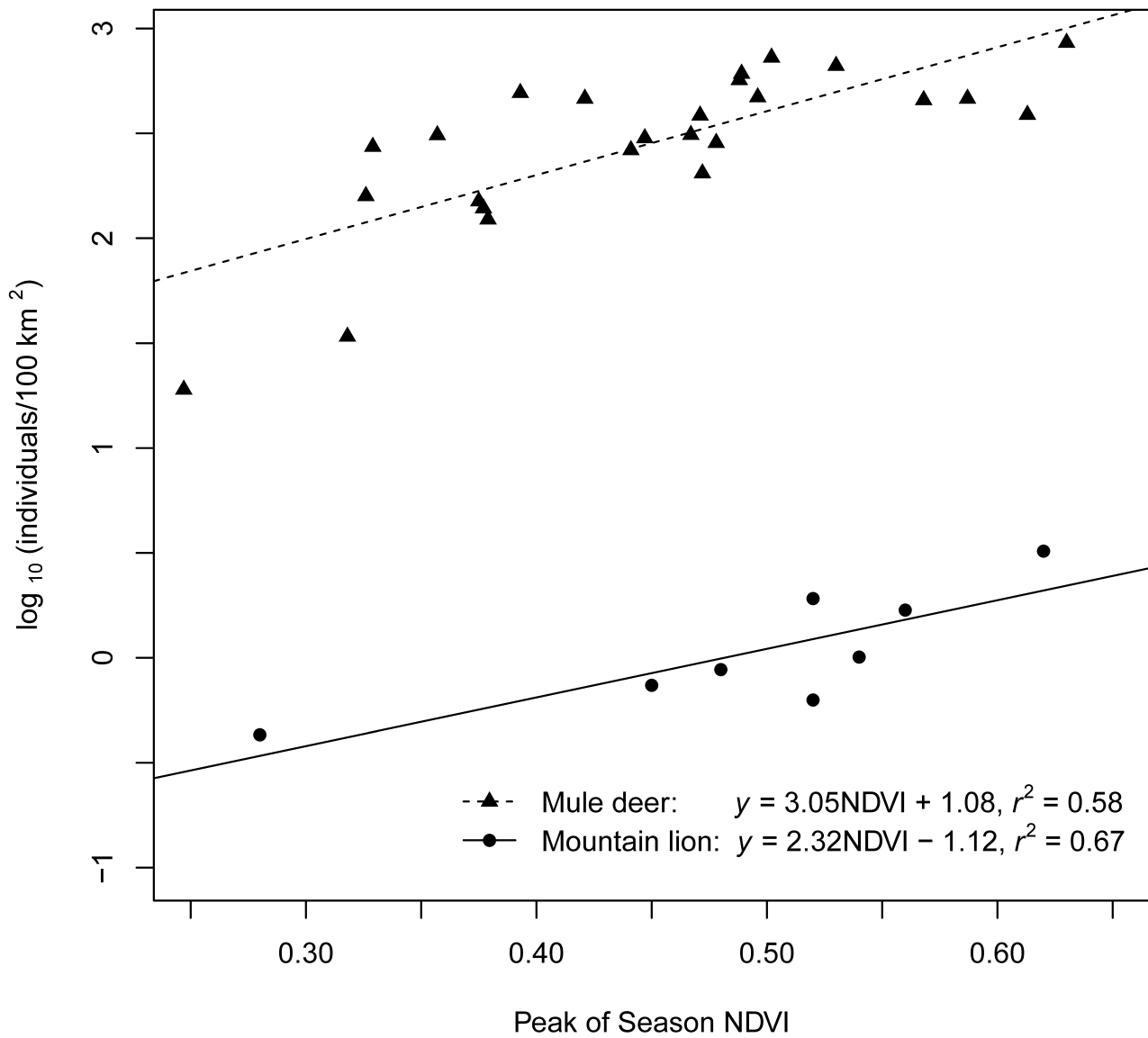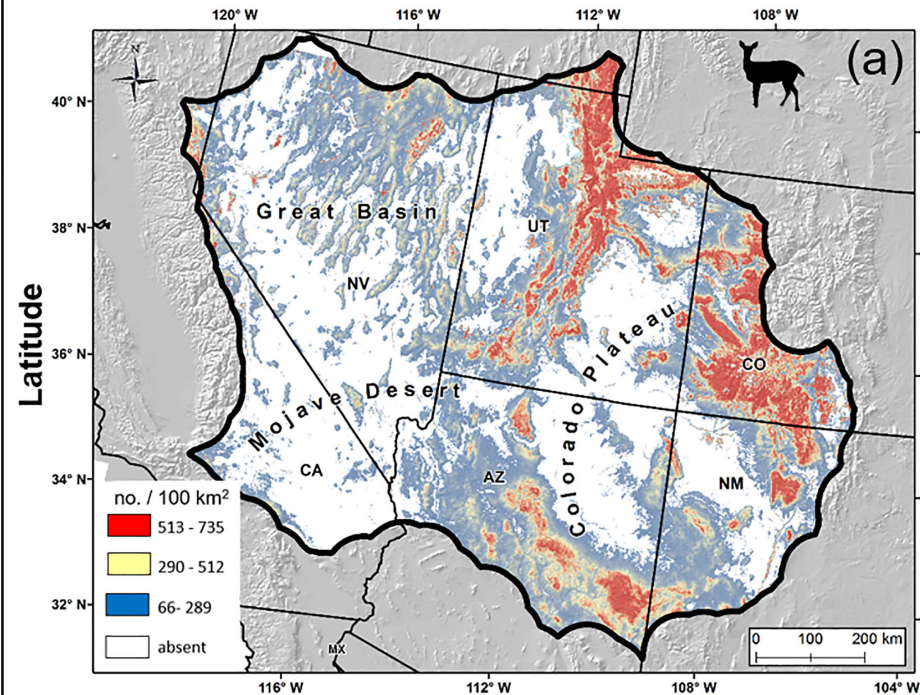*Supporting Information, Appendix S1*. Derivation of Utah mule deer population estimates, 2007-2012.

Supporting Information, Appendix S2. Utah mule deer monitoring units, population estimates, and associated NDVI metrics, 2007-2012.
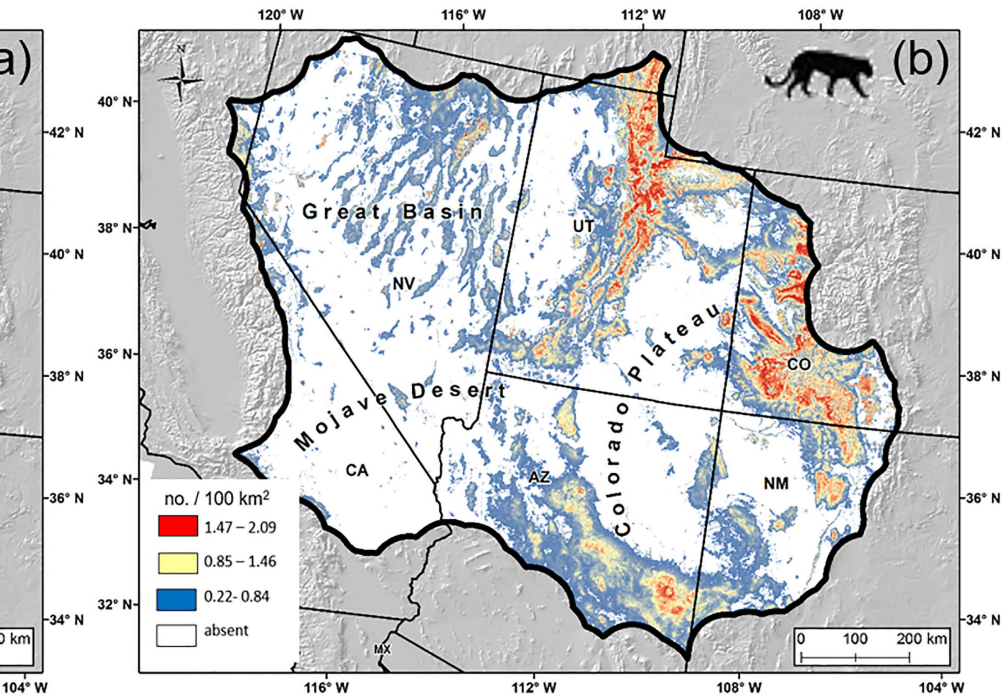
Supporting Information, Appendix S3. Mountain lion study sites, home range estimates, and associated NDVI metrics, Utah, Nevada, and Arizona, 2002-2012.

Mule deer: $y = 3.05\text{NDVI} + 1.08$, $r^2 = 0.58$
Mountain lion: $y = 2.32\text{NDVI} - 1.12$, $r^2 = 0.67$

Mule deer
(*Odocoileus hemionus*)

Mountain lion
(*Puma concolor*)