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Predicted range expansion of Desert Mule Deer under future climate scenarios

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The desert mule deer (*Odocoileus hemionus crooki*) is distributed throughout the southern United States and northern Mexico. As a large herbivore, this subspecies plays a crucial role in maintaining ecological balance. While its distribution is closely linked to water availability and vegetation type, climate change is increasingly altering these factors and shifting potential habitats. This study aimed to model the current potential distribution of *O. h. crooki* and predict distribution changes for the 2021–2040 period in relation to bioclimatic factors. Presence data were compiled from multiple sources, including GBIF, nocturnal sightings, pellet counts, and camera traps. These records were correlated with 19 bioclimatic variables from WorldClim. We utilized 164 presence points, partitioned into 50% (82 points) for model training and 50% for testing. Ecological niche modeling was performed using the kuenm R package, which provides a robust framework for MaxEnt development. Among the selected variables, BIO 9 (mean temperature of the driest quarter) exhibited the highest contribution to the model, given its high permutation value. Under the future climate scenario of extreme warming (BCC-CSM2-MR model, SSP5-8.5 scenario), the potential distribution of the desert mule deer is predicted to increase by 48.51% in the United States and 45.52% in Mexico. However, actual expansion into these newly suitable areas will likely be constrained by human-dimension factors overlooked by macroclimatic models, including transboundary border infrastructure, urban growth, and novel competitive interactions, emphasizing the need to integrate bioclimatic forecasts with regional land-use and adaptation policies.

Keywords: bioclimatic variables, Chihuahuan Desert, ecological niche modeling, MaxEnt

El venado bura del desierto (*Odocoileus hemionus crooki*) se distribuye en el sur de los Estados Unidos y el norte de México. Como gran herbívoro, esta subespecie desempeña un papel crucial en el mantenimiento del equilibrio ecológico. Aunque su distribución está estrechamente vinculada a la disponibilidad de agua y al tipo de vegetación, el cambio climático está alterando cada vez más estos factores y desplazando sus hábitats potenciales. El objetivo de este estudio fue modelar la distribución potencial actual de *O. h. crooki* y predecir los cambios en su distribución para el periodo 2021-2040 en relación con factores bioclimáticos. Los datos de presencia se compilaron de múltiples fuentes, incluyendo GBIF, avistamientos nocturnos, conteo de grupos fecales y fototrampeo. Estos registros se correlacionaron con 19 variables bioclimáticas de WorldClim. Se utilizaron 164 puntos de presencia, divididos en 50% (82 puntos) para el entrenamiento del modelo y 50% para su validación. La modelación del nicho ecológico se realizó utilizando el paquete kuenm de R, que proporciona un marco robusto para el desarrollo de MaxEnt. Entre las variables seleccionadas, la BIO 9 (temperatura media del trimestre más seco) mostró la mayor contribución al modelo, dado su alto valor de permutación. Bajo el escenario climático futuro de calentamiento extremo (modelo BCC-CSM2-MR, escenario SSP5-8.5), se predice que la distribución potencial del venado bura del desierto aumentará un 48.51% en los Estados Unidos y un 45.52% en México. Sin embargo, esta expansión probablemente se verá limitada por factores de índole humana que los modelos macroclimáticos pasan por alto —tales como la infraestructura transfronteriza, el crecimiento urbano y nuevas interacciones competitivas—, subrayando la necesidad de integrar las proyecciones bioclimáticas con las políticas regionales de uso del suelo y de adaptación.

Palabras clave: Desierto Chihuahuense, MaxEnt, modelación de nicho ecológico, variables bioclimáticas.

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Mule deer, one of the biggest ungulates in North America, ranges from Alaska and western Canada through the Rocky Mountains and the Western Plains states of the United States of America and in Mexico occurs in the plateau, the Sonora and Chihuahuan deserts, Baja California, Cedro Island and Tiburon Island (Álvarez-Castañeda *et al.* 2017). Despite its widespread distribution, mule deer populations have declined across the United States over the past two decades (Bishop *et al.* 2009). In Mexico, its historic range has also contracted drastically (Álvarez-Castañeda *et al.* 2017) with drastic declines reported at the southern limit of the distribution, such as in San Luis Potosí. These patterns highlight the importance of monitoring *O. h. crooki* found at the southernmost extent of its range to guide effective

conservation and management actions. We acknowledge the ongoing debate regarding the validity of *O. h. crooki* as a subspecies (Heffelfinger 2000); however, within the ecological niche framework, recognizing *O. h. crooki* as inhabiting the Chihuahuan Desert—distinct from *O. h. eremicus* in the Sonoran Desert (Alminas *et al.* 2021)—is justified by their occupancy of different desert ecosystems.

Multiple factors may contribute to mule deer decline including habitat degradation, predator population expansion, recent virus outbreaks (Reeves *et al.* 2024) and other anthropogenic impacts (Schuyler *et al.* 2023). Climate and regional weather patterns have also been proposed as important factors in mule deer survival indirectly influencing habitat quality (Monteith *et al.* 2011). However, there is no consensus on the effects of climate change on deer populations. Some studies suggest that climate warming can increase forage biomass and quality, benefiting grass feeding ungulates such as mule deer (Belovsky and Slade 2024). In contrast, other research points to complex responses where changes in vegetation composition, phenology or trophic interactions might drive decreasing carrying capacities for herbivores (Stoner *et al.* 2018). Sustainable management of mule deer populations requires an understanding of the effects of climate change on its distribution. In northern Mexico and the southwestern United States, the desert mule deer is an economically and ecologically important resource, managed through regulated harvest and conservation programs in both countries to ensure sustainability. Identifying climate-change driven distribution changes is essential to establish suitable harvest quotas and conservation goals.

Mule deer are well adapted to environments with low-quality forage feeding on a wide variety of plants (Staudenmaier *et al.* 2022). Vegetation diversity is essential as it provides both a varied and seasonally reliable diet (Olivas-Sánchez *et al.* 2018) and cover from predators (Pierce *et al.* 2004). Habitat heterogeneity, combining forage availability with adequate concealment, is therefore a key factor influencing survival, reproduction, and population persistence (Pierce *et al.* 2004). In addition, mule deer prefer areas with moderate slopes and rough terrain features that allow them to detect predators and avoid human presence and roads (Coe *et al.* 2018). Climate also plays an important role in mule deer distribution; warmer winters might reduce energy expenditure, but hotter summers might pose a challenge to their physiological tolerance (Felton *et al.* 2024). For instance, fawn survival is influenced by climate conditions, with harsh conditions reducing fawn recruitment (Ciuti *et al.* 2015). Furthermore, vegetation is directly influenced by climate; changes in plant productivity due to climate change affect vegetation patterns and, in consequence, mule deer distribution (Stoner *et al.* 2018). Climate driven changes in plant phenology influence mule deer reproduction; specifically, timing of parturition and mean annual production vary depending on latitude and climate changing conditions (Stoner *et al.* 2016).

In addition, changes in land use and the introduction of non-native ungulates represent another challenge to desert mule deer persistence. For instance, the presence of free-ranging exotic ungulates such as the gemsbok (*Oryx gazella*) in parts of southwestern New Mexico represents direct competition to native deer (Hoenes and Bender 2010). Furthermore, regional conservation initiatives face the challenge of aligning protected area boundaries with rapidly shifting wildlife habitats under climate change (Alagador *et al.* 2014), as highlighted by recent adaptive planning efforts in northern Mexico (CONANP 2014). Incorporating human-elements into distributional assessments is therefore critical to ensure that theoretical bioclimatic suitability translates into viable, policy-driven conservation corridors.

In addition to these landscape pressures, projected warming temperatures will alter vegetation composition, water availability, and forage quality across desert ecosystems. For mule deer, particularly *O. h. crooki*, these changes may limit access to food, cover, and water, potentially modifying habitat suitability and distribution, thereby providing a unique opportunity to study the response of large herbivores to climate change in arid environments. Identifying these bioclimatic shifts provides an essential spatial baseline to inform transboundary land-use planning and long-term conservation strategies. This study aims to model the current potential distribution of desert mule deer and predict changes driven by bioclimatic factors for the period 2021 to 2040. We start by estimating the potential distribution of desert mule deer based on presence records and its relation to bioclimatic factors. We then use the obtained model to predict the 2021-2040 desert mule deer distribution.

Materials and methods

We modeled the potential distribution of *O. h. crooki* using a presence-only approach (MaxEnt implemented via the kuenm R package). Occurrence records were cleaned and filtered, and the accessible area ("M") was defined based on biogeographic criteria. Nineteen bioclimatic variables from WorldClim v2 were incorporated, from which a non-collinear subset was selected. Models were then calibrated and evaluated using omission rates and AUC, and final projections were generated under CMIP6 climate models with SSP1-2.6 (low emissions) and SSP5-8.5 (high emissions) scenarios.

Occurrence records. Occurrence data were compiled from field surveys and online databases. Field collected presence points were collected across central and northern Chihuahua, using standard non-invasive methods: night censuses (2009–2013) (Mayle *et al.* 1999), fecal pellet-group counts (2012–2013) (Mandujano and Gallina 1995), and trail camera traps (2019–2022) (Mandujano and Perez-Solano 2019). All field and institutional records were inspected to verify coordinates and eliminate duplicates, questionable entries, and spatial errors prior to modeling.

Global Biodiversity Information Facility Occurrence data from GBIF were restricted exclusively to institutional providers (GBIF.org 2022) to prevent potential taxonomic misidentifications and georeferencing inaccuracies common in opportunistic records. The dataset was further filtered to remove duplicates, erroneous coordinates, and records lacking precise spatial information. We restricted our dataset to records from Arizona, New Mexico, Texas, Sonora, Chihuahua, and Coahuila de Zaragoza, as these regions encompass the Chihuahuan Desert (Morrone *et al.* 2017) and represent the ecological niche attributed to *O. h. crooki*.

Bioclimatic variables. Bioclimatic variables were obtained from WorldClim (http://www.worldclim.org/bioclim) at a 2.5-minute resolution. Distribution shapefiles (SHP) were obtained for Mexico (CONABIO 2023) and the United States of America corresponding to areas with *O. h. crooki* records.

Polygons representing the geographic extent of interest—accessible area "M" used for calibration—were generated in ArcGIS Pro for regions with reported occurrences, encompassing New Mexico, Arizona, Texas, Sonora, Chihuahua, Coahuila, northern Durango, and portions of Nuevo León and Zacatecas. The dataset of bioclimatic variables was clipped to these predefined state boundaries (Heffelfinger 2000; Alminas *et al.* 2021). The clipped bioclimatic data was then exported in TIFF format and subsequently converted to ASCII using QGIS. Each of the 19 bioclimatic variables was imported and processed individually via the raster conversion tool. Within ArcGIS Pro, values of these variables were assigned to presence points of the subspecies using the "Extract Multiple Values to Points" tool, yielding a comprehensive table containing the bioclimatic attributes for each recorded occurrence.

Bioclimatic variables correlation. To evaluate correlations among bioclimatic variables, minimize redundancy, and improve model robustness (Guisan *et al.* 2017), we used Pearson's correlation coefficient, a measure of the strength and direction of relationships between independent variables. The analysis was conducted in SPSS, using species presence records and their corresponding bioclimatic variables. To optimize model performance, highly correlated variables were removed (over 0.75), preventing over-representation and potential distortions in statistical results (Mota-Vargas *et al.* 2019).

For the 2021-2040 projection, two climate models were used: BCC-CSM2-MR, a high-resolution version of the Beijing Center climate model (Wu *et al.* 2019), and EC-Earth3-Veg, the third generation of the atmosphere-ocean configuration model (Döscher *et al.* 2022). These models were chosen for their high spatial resolution, performance in simulating climate variability in North America, and availability of bias-corrected outputs suitable for ecological niche modeling. Climate projections were based on Shared Socioeconomic Pathways (SSPs), which describe alternative socioeconomic futures and their interactions with climate change (Ebi *et al.* 2014). We focused on two contrasting scenarios: (1) SSP1-2.6 (EC-Earth3-Veg), representing a low-emissions, sustainability-focused trajectory with a projected temperature increase of 1.1–2.6 °C by 2081–2100; and (2) SSP5-8.5 (BCC-CSM2-MR), representing a high-emissions, fossil-fuel-intensive trajectory with a projected increase of 2.6–4.8 °C over the same period (IPCC 2014). Although using two models and contrasting SSPs does not allow us to account for uncertainties in climate projections we look to provide an initial insight into potential distribution variability under divergent emission pathways.

Model calibration and evaluation. Using presence data, kuenm an R statistical package (Cobos *et al.* 2019) that works through Maxent estimated the probability distribution of *O. h. crooki* based on the maximum entropy principle (Elith *et al.* 2011). This probability is represented by pixels, where Maxent determined values based on bioclimatic variables and presence records (Phillips and Dudík 2008). Model calibration identified the optimal combination of bioclimatic variables, ensuring statistically significant predictions while preventing over-parameterization using the AIC delta criterion.

To train the model, we used half of the dataset, reserving the remaining data for model performance evaluation (Muscarella *et al.* 2014). Once calibration was completed, the final models were generated and evaluated using all data points (Cobos *et al.* 2019). For dichotomous presence/absence maps, we chose not to extrapolate beyond the observed range, assigning a value of zero to areas outside the known distribution (Owens *et al.* 2013). Finally given that we might encounter multiple candidate models with similar behaviors, the final selection was performed with independent validations (Cobos *et al.* 2019).

Results

We identified 164 presence records within the species' historical distribution that met the selection criteria and were included in the analysis. Presence records were then correlated with bioclimatic variables BIO2, BIO8, BIO9, BIO15, and BIO19. These variables were selected because they exhibited the lowest intercorrelations (Pearson coefficient < 0.3) amongst all bioclimatic variables, thereby minimizing redundancy in the environmental predictors.

With the aid of Kuenm (parameters: algorithm MaxEnt, regularization β = 1.0, 800 replicates), we generated three candidate model sets. The first set 1_EC (AUC = 0.76) was selected for its equilibrium within omission (<10%) and optimal spatial specificity. Among the 10 individual models, O. hemionus_2, _4 y _7 stood out (Table 1) because of their high AUC values (0.768, 0.772 and 0.767, respectively) and optimal logistic thresholds (0.323, 0.323 and 0.329, respectively).

Evaluation of the calibration curve (Figure 1) confirms the expected diagnostic behavior of the model regarding the trade-off between predicted suitable area and omission rates. As cumulative thresholds increase, the predicted suitable area decreases systematically while the omission

Table 1. Relative estimation of the contributions of environmental variables in relation to ecological niche estimation for *O. h. crooki*, using the general model, O. hemionus_4, O. hemionus_2, O. hemionus_7.

Models	Variable	Percentage contribution	Permutation importance
General	Bio19	52	3.5
	Bio9	19.7	45.3
	Bio8	12.5	13.1
	Bio15	9.7	28.6
	Bio2	6.1	9.4
O. hemionus_2	Bio19	57.2	1.6
	Bio9	17.3	45.6
	Bio15	14	36
	Bio8	8.1	11.4
	Bio2	3.4	5.5
O. hemionus_4	Bio19	48.8	1.2
	Bio9	24.4	43.4
	Bio15	12.8	35.7
	Bio8	9.9	11.1
	Bio2	4.1	8.6
O. hemionus_7	Bio19	45.9	1.7
	Bio9	22.7	43
	Bio8	13.7	16.3
	Bio2	10.5	12
	Bio15	7.2	27

rate rises. The empirical omission curves closely match the theoretical expectation represented by the reference line, demonstrating acceptable model calibration without severe overfitting. Lower thresholds conserve a higher proportion of occurrence localities at the expense of greater spatial extent, whereas more restrictive thresholds narrow the predicted distribution while increasing omission. This functional response illustrates the empirical trade-off between sensitivity and specificity inherent in selecting a threshold for binary suitability classification.

Variable BIO9 (mean temperature of the driest quarter) showed the highest permutation importance (43–45.3%), indicating its critical role in defining the niche. BIO19 (precipitation of the coldest quarter) also had substantial influence, with permutation importance values ranging from 19.7–24.4%.

The model for present distribution (Figure 2) partially overlaps with the historical distribution described by Taylor (1956), projecting expansions in New México and Texas (+43.8–48.5% for 2040). These projected expansions are associated to increases in BIO9 (RCP 4.5: +1.2°C; RCP 8.5: +2.1°C), which may reduce winter seasonality and facilitate the colonization of high latitudes.

The projection model for the 2021-2040 period indicates range expansion under both emission scenarios (SSP 126 and SSP 585) (Figure 3). In the United States of America, the potential distribution of *O. hemionus crooki* is projected to increase by 43.83% under the low-emission SSP1.2-6

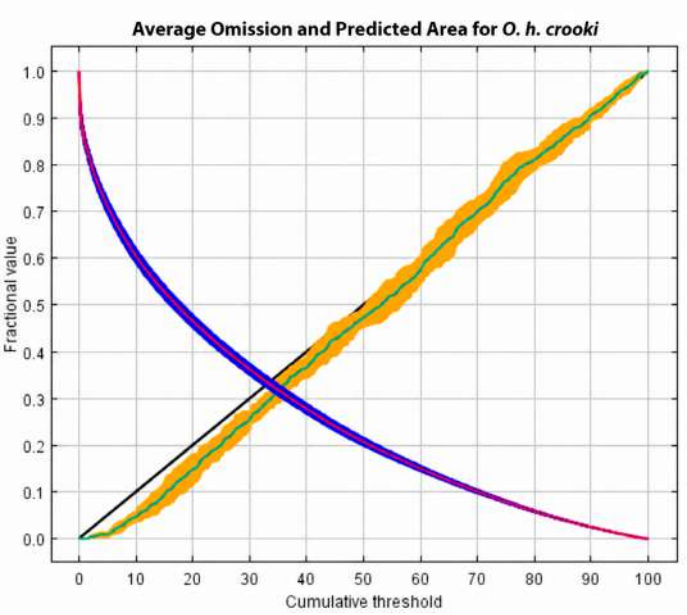


Figure 1. Omission average rate and predicted suitable area for *O. h. crooki* actual distribution. The curves represent the top-performing candidate model set (1_EC: environmental dataset 1 under optimal calibration parameters selected via kuenm). Red line average area, blue line, average area +- Standard deviation; Green line, average omission, orange line average omission area +- Standard deviation; Black line, predicted omission.

scenario and by 48.51% under the high-emission SSP5-8.5 scenario. Similarly, in Mexico, we observe a range expansion of 42.80% and 45.52% under the respective scenarios. Overall, we observe that both projections indicate that climatic conditions will be more suitable for an expansion at the northern range.

Discussion

The apparent climatic resilience of *O. h. crooki* observed in these results reflects its physiological adaptation to arid environments, where BIO9 (average temperature of the driest quarter) acts as a primary abiotic filter defining its fundamental niche. However, the discrepancy between historical records and broader modeled projections highlights the gaps between fundamental and realized niches. While thermal conditions may permit range expansion, actual establishment is probably constrained by dispersal barriers and biotic interactions such as interspecific competition and emerging diseases. Because changes and overlaps in distribution of cervids can increase opportunities for pathogen transmission as well as novel host-pathogen interactions (Conner *et al.* 2008; Wiethoelter *et al.* 2015), future health surveillance will be critical in areas of potential range expansion.

The range expansion reported here contrasts with declines reported in boreal ungulates (e.g., *Rangifer tarandus*, (Boyce *et al.* 2017), underscoring the heterogeneity of responses to climate change within the family Cervidae. This pattern could be explained by the trophic plasticity of *O. h. crooki*, which allows it to exploit diversified resources in altered environments (Hofmann 1989). This trophic plasticity may enable *O. h. crooki* to adapt to dietary changes associated with rising temperatures, similar to that reported for

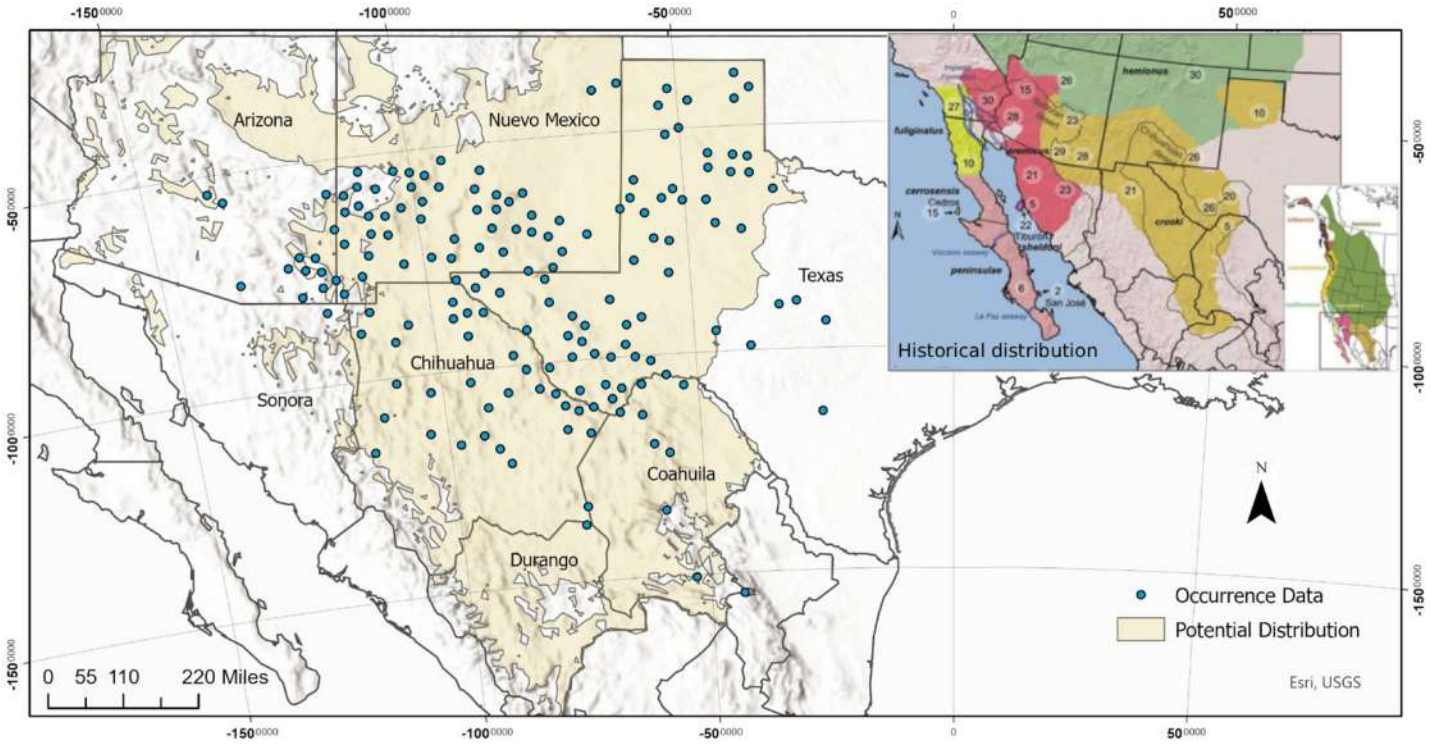


Figure 2. Current potential distribution of *O. h. crooki* estimated using the five least correlated bioclimatic variables. The inset in the top right corner shows the geographic distribution of the subspecies according to Alminas *et al.* (2021).

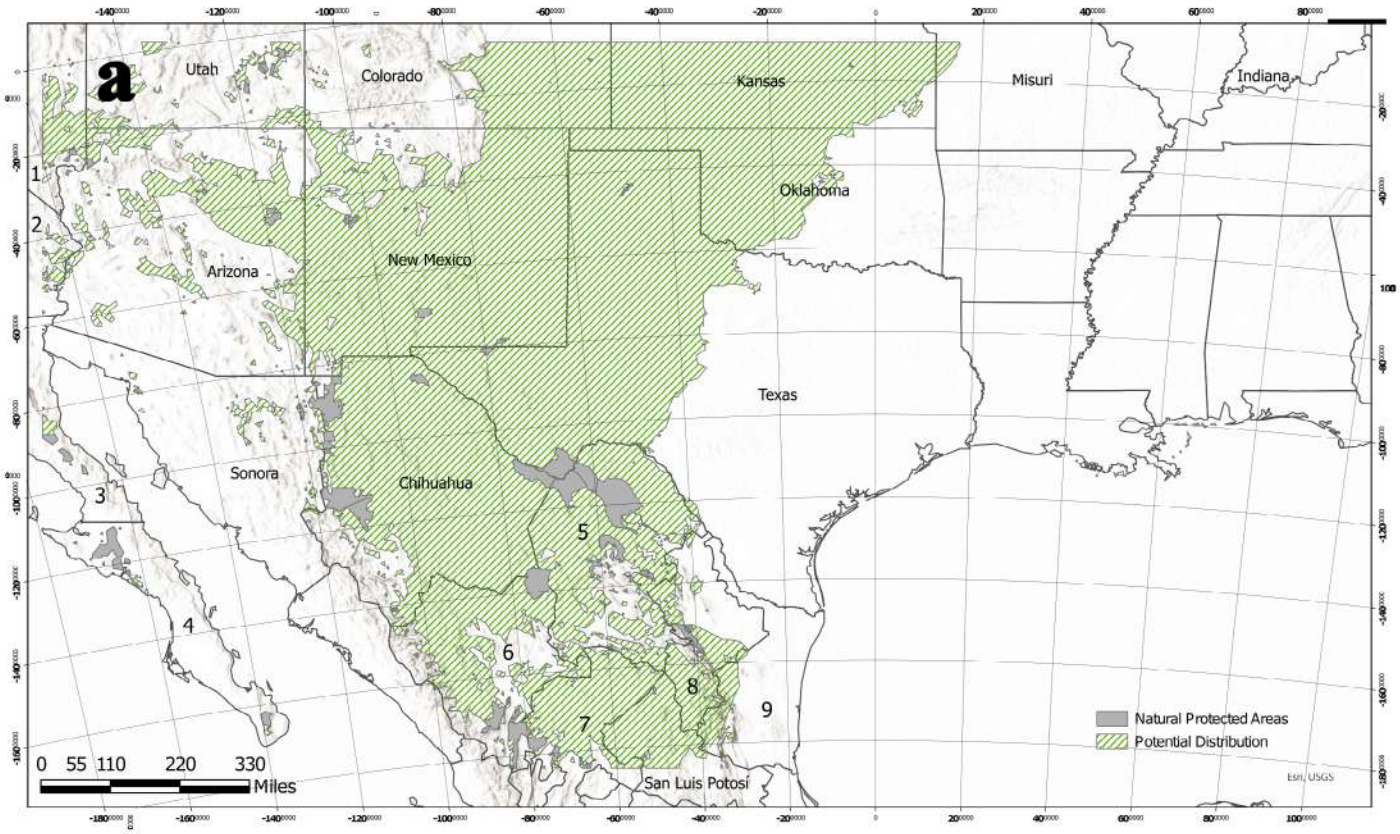
O. virginianus (Dawe and Boutin 2016). However, northward expansion will increase spatial overlap with *O. h. hemionus* and *O. virginianus,* leading to greater interspecific competition (Apollonio and Chirichella 2023) as well as greater exposure to novel pathogens and parasites.

Chronic wasting disease has been reported extensively across northern ranges in both white-tailed deer (Thompson *et al.* 2023) and mule deer (Miller and Conner 2005). Furthermore, expanding into areas with higher vegetation cover could expose *O. h. crooki* to important tick vectors of the genera *Amblyoma* and *Dermacentor*, along with other emerging vectors (Rochlin *et al.* 2025). As a result, northern range expansion may ultimately expose naïve *O. h. crooki* populations to novel disease transmission vectors that could outweigh the potential benefits of range expansion. In addition to abiotic factors, actual northward expansion could be constrained by physical barriers along the USA-Mexico border and interactions with novel introduced exotic species. The border wall might act as an impermeable barrier fragmenting connectivity corridor for large mammals such as *O. h. crooki* (Harrity *et al.* 2024). Moreover, sympatry with introduced exotic ungulates such as the oryx is likely to intensify competition for already limited resources, potentially restricting niche realization despite favorable future climatic conditions.

Although physiological parameters were not measured in this study, published thermal constraints in deer help explain how climate warming could drive this northward expansion facilitating the projected expansion. Research suggests that low temperatures and snow cover impose severe energetic constraints on ungulate survival, increasing energy expenditure and reducing food availability (Giroux *et al.* 2014). For instance, prolonged exposure to temperatures below -7 °C has been shown to impose high metabolic costs (DelGuidice 2005; Garroway and Broders 2005), while harsh winters have a negative impact on the survival rate of offspring (Dawe *et al.* 2014). In this context, climate change is reducing the length of cold seasons, which could favor population growth of the subspecies due to an increase in reproductive rates associated with warmer temperatures (Simard *et al.* 2010). Although *O. h. crooki* currently occupies warmer arid landscapes, continued warming could facilitate its northward expansion, potentially leading to competition with species less adapted to rapid environmental changes, altering ecosystem dynamics (Apollonio and Chirichella 2023).

Conversely, excessive warming temperatures will also bring significant challenges for the desert mule deer that could counteract habitat suitability gains. The strong contribution of BIO 9 in our models identifies the driest period as a primary bioclimatic bottleneck for *O. h. crooki*. Although physiological responses were not measured here, established metabolic models show that once the maximum heat dissipation capacity is reached, mammals undergo behavioral changes to mitigate heat stress (Speakman and Król 2010; Sejian *et al.* 2018). While macroclimatic warming may suggest broader theoretical suitability, localized persistence will remain constrained by microclimatic thermal refugia and reliable water sources (Apollonio and Chirichella 2023).

Our results highlight the complex interaction between climate change and the ecology of desert mule



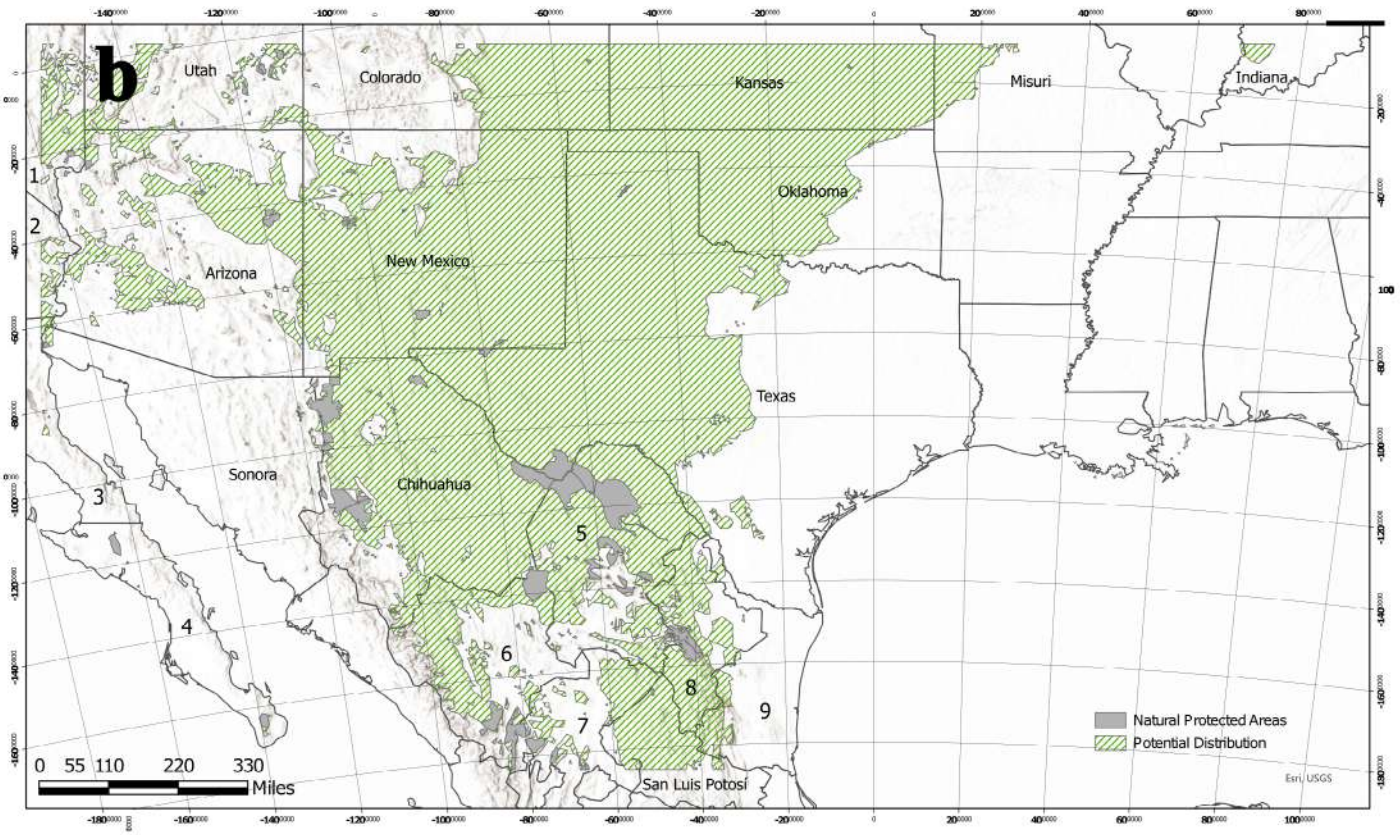


Figure 3. Layout of the potential distribution estimates for *O. h. crooki* (2021–2040) based on the five least correlated bioclimatic variables. (a) Projections using the EC-Earth3-Veg model under the SSP1-2.6 scenario; (b) Projections using the BCC-CSM2-MR model under the SSP5-8.5 scenario. Numbers indicate geographic regions: 1 = Nevada, 2 = California, 3 = Baja California, 4 = Baja California Sur, 5 = Coahuila, 6 = Durango, 7 = Zacatecas, 8 = Nuevo León, and 9 = Tamaulipas.

deer, particularly in arid environments. Consequently, monitoring seasonal temperature changes, which directly influence habitat suitability, and population dynamics must be prioritized. Nevertheless, the discrepancy between modeled suitability and historical ranges suggests that future distribution models must incorporate biotic interactions, such as interspecific competition and emerging pathogens. Despite the statistical rigor, macroclimatic models have inherent uncertainties; projections can vary considerably among alternative general circulation models and emissions trajectories (Araújo and New 2007; Diniz-Filho *et al.* 2009); while assuming static biotic interactions during climate-driven range shifts. Additionally, our models might neglect some ecological constraints, such as seasonal water availability and anthropogenic disturbance, both limiting factors in arid ecosystems (Briggs *et al.* 2020). Furthermore, expanding urban areas across the projected northward range drive continuous habitat loss and infrastructure development that our bioclimatic models do not consider. Integrating these land-use changes with regional policy instruments (e.g. CONANP 2014) will be essential to translate bioclimatic projections into effective conservation efforts and adaptive management strategies.

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Declaration of Artificial Intelligence use

The authors used Google Gemini exclusively to improve English grammar and improve the writing style. The authors reviewed all suggested changes.

Author contributions

Alberto García-Álvarez: Writing – original draft, Investigation, Methodology, Formal analysis, Data curation, Conceptualization, Funding acquisition, Visualization. Cuauhcihuatl Vital-García: Writing – review and editing, Project administration, Investigation, Methodology, Resources, Data curation, Conceptualization, Visualization, Supervision. María E. Torres-Olave: Writing – review and editing, Project administration, Investigation, Methodology, Resources, Data curation, Conceptualization, Visualization, Supervision. John F. Aristizabal: Writing – review and editing, Project administration, Investigation, Methodology, Conceptualization, Visualization. Martha P. Olivas-Sánchez: Writing – review and editing, Investigation, Methodology, Conceptualization, Visualization. Ana B. Gatica-Colima: Writing – review and editing, Investigation, Methodology, Conceptualization, Visualization.

Literature cited

Alagador D, Cerdeira JO, and Araújo MB. 2014. Shifting protected areas: scheduling spatial priorities under climate change. *Journal of Applied Ecology* 51:703–713. https://doi.org/10.1111/1365-2664.12230

Alminas OSV, Heffelfinger JR, Statham MJ, and Latch EK. 2021. Phylogeography of Cedros and Tiburón Island mule deer in North America's desert southwest. *Journal of Heredity* 112:260–275. https://doi.org/10.1093/jhered/esab013

Álvarez-Castañeda ST, Álvarez Solórzano T, and González-Ruiz N. 2017. *Guía para la identificación de los mamíferos de México*. Baltimore (USA): Johns Hopkins University Press.

Apollonio M, and Chirichella R. 2023. Deer and climate change: impacts and perspectives. *Animal Production Science* 63:1573–1582. https://doi.org/10.1071/AN22296

Araújo MB, and New M. 2007. Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* 22:42–47. https//10.1016/j.tree.2006.09.010

Belovsky GE, and Slade JB. 2024. Climate change and herbivores: forty years in a bunchgrass prairie. *Animals* 14:18. https://doi.org/10.3390/ani14182647

Bishop CJ, White GC, Freddy DJ, Watkins BE, and Stephenson TR. 2009. Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs* 172:1–28. https://doi.org/10.2193/2008-107

Boyce MS, Mallory CD, Morehouse AT, Prokopenko CM, Scrafford MA, and Warbington CH. 2017. Defining landscapes and scales to model landscape–organism interactions. *Current Landscape Ecology Reports* 2:89–95. https://doi.org/10.1007/s40823-017-0027-z

Briggs MK, Lozano-Cavazos EA, Mills Poulos H, Ochoa-Espinoza J, and Rodriguez-Pineda JA. 2020. The Chihuahuan Desert: a binational conservation response to protect a global treasure. In: DellaSala DA, and Goldstein MI, editors. *Encyclopedia of the World's Biomes*. Vol. 2, *Deserts: life in the extremes*. Amsterdam (NLD): Elsevier; p. 126–138.

Ciuti S, Jensen WF, Nielsen SE, and Boyce MS. 2015. Predicting mule deer recruitment from climate oscillations for harvest management on the northern Great Plains. *The Journal of Wildlife Management* 79:1226–1238. https://doi.org/10.1002/jwmg.956

Cobos ME, Peterson AT, Barve N, and Osorio-Olvera L. 2019. kuenm: an R package for detailed development of ecological niche models using MaxEnt. *PeerJ* 7:e6281. https://doi.org/10.7717/peerj.6281

Coe PK, Clark DA, Nielson RM, Gregory SC, Cupples JB, Hedrick MJ, *et al*. 2018. Multiscale models of habitat use by mule deer in winter. *The Journal of Wildlife Management* 82:1285–1299. https://doi.org/10.1002/jwmg.21484

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad [CONABIO]. 2023. Portal de información geográfica. Ciudad de México (MEX): CONABIO; March 2023. [Accessed March 23rd, 2023]. http://www.conabio.gob.mx/informacion/gis/

Comisión Nacional de Áreas Naturales Protegidas [CONANP]. 2014. Programa de Adaptación al Cambio Climático del Complejo Mapimí. Ciudad de México

(MEX): CONANP. [Accessed October 2nd, 2026]. https://www.gob.mx/cms/uploads/attachment/file/247260/PACC_Mapimi.pdf

Conner MM, Ebinger MR, Blanchong JA, and Cross PC. 2008. Infectious disease in cervids of North America: data, models, and management challenges. *Annals of the New York Academy of Sciences* 1134:146–172. https://doi.org/10.1196/annals.1439.005

Dawe KL, Bayne EM, and Boutin S. 2014. Influence of climate and human land use on the distribution of white-tailed deer (*Odocoileus virginianus*) in the western boreal forest. *Canadian Journal of Zoology* 92:353–363. https://doi.org/10.1139/cjz-2013-0262

Dawe KL, and Boutin S. 2016. Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. *Ecology and Evolution* 6:6435–6451. https://doi.org/10.1002/ece3.2316

DelGuidice GD. 2005. Assessing the relationship of conifer thermal cover to winter distribution, movements, and survival of female white-tailed deer in north central Minnesota. In: Wingate PJ, Kimmel RO, Lawrence JS, and Lenarz MS, editors. *Summaries of Wildlife Research Findings*. Minnesota (USA): Minnesota Department of Natural Resources; p. 69–85.

Diniz-Filho JAF, Bini LM, Rangel TF, Loyola RD, Hof C, Nogués-Bravo D, *et al*. 2009. Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography* 32:897–906. https://doi.org/10.1111/j.1600-0587.2009.06196.x

Döscher R, Acosta M, Alessandri A, Anthoni P, Arsouze T, Bergman T, *et al*. 2022. The EC-Earth3 earth system model for the Coupled Model Intercomparison Project 6. *Geoscientific Model Development* 15:2973–3020. https://doi.org/10.5194/gmd-15-2973-2022

Ebi KL, Hallegatte S, Kram T, Arnell NW, Carter TR, Edmonds J, *et al*. 2014. A new scenario framework for climate change research: background, process, and future directions. *Climatic Change* 122:363–372. https://doi.org/10.1007/s10584-013-0912-3

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, and Yates CJ. 2011. A statistical explanation of MaxEnt for ecologists: statistical explanation of MaxEnt. *Diversity and Distributions* 17:43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Felton AM, Wam HK, Borowski Z, Granhus A, Juvany L, Matala J, *et al*. 2024. Climate change and deer in boreal and temperate regions: from physiology to population dynamics and species distributions. *Global Change Biology* 30:e17505. https://doi.org/10.1111/gcb.17505

Garroway CJ, and Broders HG. 2005. The quantitative effects of population density and winter weather on the body condition of white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada. *Canadian Journal of Zoology* 83:1246–1256. https://doi.org/10.1139/z05-118

Global Biodiversity Information Facility [GBIF.Org]. 2022. GBIF Occurrence Download. Copenhagen (DNK): The Global Biodiversity Information Facility; 2022. [Accessed May 23rd, 2023]. https://doi.org/10.15468/DL.VXQCZ9

Giroux M-A, Tremblay J-P, Simard MA, Yoccoz NG, and Côté SD. 2014. Forage-mediated density and climate effects on body mass in a temperate herbivore: a mechanistic approach. *Ecology* 95:1332–1340. https://doi.org/10.1890/13-0956.1

Guisan A, Thuiller W, and Zimmermann NE. 2017. *Habitat suitability and distribution models: with applications in R*. Cambridge (UK): Cambridge University Press.

Harrity EJ, Traphagen M, Bethel M, Facka AN, Dax M, and Burns E. 2024. USA-Mexico border wall impedes wildlife movement. *Frontiers in Ecology and Evolution* 12:1487911. https://doi.org/10.3389/fevo.2024.1487911

Heffelfinger JR. 2000. Status of the name *Odocoileus hemionus crooki* (Mammalia: Cervidae). *Proceedings of the Biological Society of Washington* 113:319–333.

Hoenes BD, and Bender LC. 2010. Relative habitat- and browse-use of native desert mule deer and exotic oryx in the greater San Andres Mountains, New Mexico. *Human-Wildlife Interactions* 4:12–24.

Hofmann RR. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443–457. https://doi.org/10.1007/BF00378733

Intergovernmental Panel on Climate Change [IPCC]. 2014. Cambio climático 2014: informe de síntesis. Contribución de los grupos de trabajo I, II y III al Quinto informe de Evaluación del Grupo Intergubernamental de Expertos sobre el Cambio Climático. Ginebra (CHE): Grupo Intergubernamental de Expertos sobre el Cambio Climático. https://www.ipcc.ch/site/assets/uploads/2018/02/SYR_AR5_FINAL_full_es.pdf

Mayle BA, and Peace AJ, Gill MRA. 1999. *How many deer? a field guide to estimating deer population size. Field Book 18*. Edinburgh (SCT): Forestry Commission.

Mandujano S, and Gallina S. 1995. Comparison of deer censusing methods in tropical dry forest. *Wildlife Society Bulletin* 23:180–186.

Mandujano S, and Pérez-Solano LA. 2019. *Fototrampeo en R: organización y análisis de datos. Volumen I*. Xalapa (MEX): Instituto de Ecología A. C.

Miller MW, and Conner MM. 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: spatial, temporal, and demographic influences on observed prevalence patterns. *The Journal of Wildlife Diseases* 41:275–290. https://doi.org/10.7589/0090-3558-41.2.275

Monteith KL, Bleich VC, Stephenson TR, Pierce BM, Conner MM, Klaver RW, *et al*. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere* 2:art47. https://doi.org/10.1890/ES10-00096.1

Morrone JJ, Escalante T, and Rodríguez-Tapia G. 2017. Mexican biogeographic provinces: Map and shapefiles. *Zootaxa* 4277:277–279. https://doi.org/10.11646/

zootaxa.4277.2.8

Mota-Vargas C, Encarnación-Luevano A, Ortega-Andrade M, Prieto-Torres D, Peña-Peniche A, and Rojas-Soto O. 2019. Una breve introducción a los modelos de nicho ecológico. In: *La biodiversidad en un mundo cambiante: fundamentos teóricos y metodológicos para su estudio*. Ciudad de México (MEX): Editorial Libermex; p. 39–63.

Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, *et al*. 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for MaxEnt ecological niche models. *Methods in Ecology and Evolution* 5:1198–1205. https://doi.org/10.1111/2041-210X.12261

Olivas-Sánchez MP, Vital-García C, Flores-Margez JP, Mora-Covarrubias ADL, and Clemente-Sánchez F. 2018. Mule deer forage availability and quality at the Chihuahuan Desert rangelands, Mexico after a severe 3-year drought. *Cogent Biology* 4:1536315. https://doi.org/10.1080/23312025.2018.1536315

Owens HL, Campbell LP, Dornak LL, Saupe EE, Barve N, Soberón J, *et al*. 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling* 263:10–18. https://doi.org/10.1016/j.ecolmodel.2013.04.011

Phillips SJ, and Dudík M. 2008. Modeling of species distributions with MaxEnt: new extensions and a comprehensive evaluation. *Ecography* 31:161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Pierce BM, Bowyer RT, and Bleich VC. 2004. Habitat selection by mule deer: forage benefits or risk of predation? *Journal of Wildlife Management* 68:533–541. https://doi.org/10.2193/0022-541X(2004)068%255B0533:HSBMDF%255D2.0.CO;2

Reeves AM, Gray SS, Campbell JC, Harveson LA, Hilton CD, Heffelfinger LJ, *et al*. 2024. Hematology and biochemical reference intervals and seroprevalence of hemorrhagic diseases for free-ranging mule deer (*Odocoileus hemionus*) in West Texas. *Journal of Zoo and Wildlife Medicine* 55:1019–1031. https://doi.org/10.1638/2023-0118

Rochlin I, Kenney J, Little E, and Molaei G. 2025. Public health significance of the white-tailed deer (*Odocoileus virginianus*) and its role in the eco-epidemiology of tick- and mosquito-borne diseases in North America. *Parasites & Vectors* 18:43. https://doi.org/10.1186/s13071-025-06674-6

Schuyler EM, Ellsworth LM, Sanchez DM, and Whittaker DG. 2023. Effects of anthropogenic and climate-induced habitat changes on adult female mule deer survival. *Rangeland Ecology and Management* 91:73–81. https://doi.org/10.1016/j.rama.2023.08.003

Sejian V, Bhatta R, Gaughan JB, Dunshea FR, and Lacetera N. 2018. Review: adaptation of animals to heat stress. *Animal* 12:s431–s444. https://doi.org/10.1017/S1751731118001945

Simard MA, Coulson T, Gingras A, and Coţé SD. 2010. Influence of density and climate on population dynamics of a large herbivore under harsh environmental conditions. *The Journal of Wildlife Management* 74:1671–1685. https://doi.org/10.2193/2009-258

Speakman JR, and Król E. 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology* 79:726–746. https://doi.org/10.1111/j.1365-2656.2010.01689.x

Staudenmaier AR, Shipley LA, Camp MJ, Forbey JS, Hagerman AE, Brandt AE, *et al*. 2022. Mule deer do more with less: comparing their nutritional requirements and tolerances with white-tailed deer. *Journal of Mammalogy* 103:178–195. https://doi.org/10.1093/jmammal/gyab116

Stoner DC, Sexton JO, Nagol J, Bernales HH, and Edwards TC. 2016. Ungulate reproductive parameters track satellite observations of plant phenology across latitude and climatological regimes. *PLoS ONE* 11:e0148780. https://doi.org/10.1371/journal.pone.0148780

Stoner DC, Sexton JO, Choate DM, Nagol J, Bernales HH, Sims SA, *et al*. 2018. Climatically driven changes in primary production propagate through trophic levels. *Global Change Biology* 24:4453–4463. https://doi.org/10.1111/gcb.14364

Taylor W. 1956. The deer of North America: the white-tailed, mule and black-tailed deer, genus *Odocoileus*, their history and management. Harrisburg (USA): Stackpole Company.

Thompson NE, Huang MHJ, Christensen SA, and Demarais S. 2023. Wildlife agency responses to chronic wasting disease in free-ranging cervids. *Wildlife Society Bulletin* 47:e1435. https://doi.org/10.1002/wsb.1435

Wiethoelter AK, Beltrán-Alcrudo D, Kock R, and Mor SM. 2015. Global trends in infectious diseases at the wildlife–livestock interface. *Proceedings of the National Academy of Sciences* 112:9662–9667. https://doi.org/10.1073/pnas.1422741112

Wu T, Lu Y, Fang Y, Xin X, Li L, Li W, *et al.* 2019. The Beijing climate center climate system model (BCC-CSM): the main progress from CMIP5 to CMIP6. *Geoscientific Model Development* 12:1573-1600. https://doi.org/10.5194/gmd-12-1573-2019

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