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Original Contribution

Landscape Seroprevalence of Three Hemorrhagic Disease-Causing Viruses in a Wild Cervid

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Abstract: Disease plays a major role in shaping wildlife populations worldwide, and changes in landscape conditions can significantly influence risk of pathogen exposure, a threat to vulnerable wild species. Three viruses that cause hemorrhagic disease affect cervid populations in the USA (*Odocoileus hemionus* adenovirus, bluetongue virus, and epizootic hemorrhagic disease virus), but little is known of their distribution and prevalence in wild populations. We explored the distribution and co-occurrence of seroprevalence of these three pathogens in southern mule deer (*Odocoileus hemionus fuliginatus*), a subspecies of conservation concern and a harvested species native to southern California, to evaluate the distribution of exposure to these pathogens relative to landscape attributes. We found that habitat type, level of development, and proximity to livestock may affect hemorrhagic disease seroprevalence in southern mule deer. Continued monitoring of hemorrhagic disease-causing viruses in areas where deer are in proximity to cattle and human development is needed to better understand the implications of future outbreaks in wild populations and to identify opportunities to mitigate disease impacts in southern mule deer and other cervid species.

Keywords: Odocoileus adenovirus, Bluetongue virus, Epizootic hemorrhagic disease virus, Hemorrhagic disease, Epidemiology, Southern mule deer, Wild cervid

Introduction

Pathogens are a known stressor that can affect the persistence of wildlife populations and even cause extinction in at-risk populations (Daszak et al. 2000; Harvell et al. 2002; Atkinson and Lapointe 2009; Rohr and Raffel 2010). Patterns of pathogen exposure and transmission can be driven by landscape factors like elevation, topography, and vegetation (Collinge et al. 2005; Atkinson and Lapointe 2009; Lafferty 2009; Randolph and Rogers 2010; Rohr and Raffel 2010; Laaksonen et al. 2010; Becker and Zamudio 2011; Liu et al. 2013; Jacquot et al. 2017), yet the patterns of exposure and transmission of many wildlife disease agents are largely unexplored. Anthropogenic stressors, such as habitat loss due to agricultural and urban development, climate change, increased human–wildlife interfaces, and even human recreation, can dramatically impact the transmission and range of many vector-borne, fungal, and viral diseases throughout the globe (Lindgren et al. 2012; Brearley et al.

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2013; Reynolds and Barton 2014; Van Hemert et al. 2014; Gudex-Cross et al. 2015; Semenza and Suk 2018; Gibb et al. 2020). However, the effects of shifting conditions and landscape changes on patterns of exposure to disease agents are complex. Barriers such as roads and rivers in the Midwestern United States have been found to limit the exposure and transmission of chronic wasting disease in white-tailed deer (Robinson et al. 2013), but fragmented landscapes have also been associated with increased transmission of hantavirus among rodent hosts (Rubio et al. 2014). More recently, the impact of climate change on pathogen transmission is being considered (Rohr et al. 2011), and there is growing evidence suggesting that the impacts or range of occurrence of several diseases caused by various microorganisms and parasites may increase with climate change in terrestrial, aquatic, and marine ecosystems (Harvell et al. 2002; Marcogliese 2008).

Hemorrhagic disease-causing viruses are one class of pathogen that can cause deadly outbreaks in wildlife populations. There are three viruses known to cause hemorrhagic diseases in North American wild ruminant species: *Odocoileus hemionus* adenovirus (OdAdV), bluetongue virus (BTV), and epizootic hemorrhagic disease virus (EHDV). BTV and EHDV can cause severe outbreaks in both domestic and wild ruminants resulting in large population die-offs (Roughton 1975; Woods et al. 1996; Beringer et al. 2000; Gaydos et al. 2004; Roug et al. 2012; Stallknecht et al. 2015), which can be ecologically damaging by depleting populations, and have economic impacts when harvested and domestic populations are infected, causing a loss of profits to farmers and hunters (Temizel et al. 2009; Velthuis et al. 2011; Ruder et al. 2015).

BTV and EHDV are related orbiviruses found in tropical and temperate regions around the world which are spread by a biting midge from the *Culicoides* genus. Rising temperatures have led to a northward expansion of *Culicoides* and thus have contributed to expansion of the ranges of BTV and EHDV (Ruder et al. 2015; Jewiss-Gaines et al. 2017; Jacquot et al. 2017; Allen et al. 2019). In the Western United States, BTV and EHDV transmission is attributed to *Culicoides sonorensis* Wirth and Jones (Gerry et al. 2009; Morales-Hojas et al. 2018; Mendiola et al. 2019). *C. sonorensis* is associated with polluted water and mud sources, often preferring water and mud contaminated with livestock manure for reproduction (Wong et al. 2018; Erram and Zurek 2018). Because of this, there is evidence that increased transmission and exposure rates of BTV occur in locations with greater livestock densities (Jacquot et al. 2017; Ma et al. 2019; Merrill et al. 2019; Chanda et al. 2019; Broennimann et al. 2020). Although it has not been empirically tested, it is assumed that EHDV has a similar risk of exposure (Roug et al. 2012).

Unlike BTV and EHDV, the virus that causes adenovirus hemorrhagic disease (AHD) in cervids is believed to be spread by direct transmission among infected individuals. AHD was first described in California after a major outbreak of the disease in 1993 within a Columbian black-tailed deer (*Odocoileus hemionus columbianus*) population (Woods et al. 1996). Since the 1993 outbreak, there have been numerous isolated outbreaks in other western states in non-migratory mule deer (Woods et al. 2018), elk (Fox et al. 2017), and moose (Shilton et al. 2002). Given its horizontal transmission, increased exposure is likely associated with aggregation of individuals (Woods et al. 1999, 2018) which may be linked to landscape changes that limit or reduce water and food sources, such as habitat loss or fragmentation.

The perceived expansion of hemorrhagic disease-causing viruses and their associated impacts on domestic and wild ruminants have spurred efforts to better understand their epidemiology (Purse et al. 2005; Wilson and Mellor 2008; Carpenter et al. 2009; Zuliani et al. 2015; Samy and Peterson 2016; Jones et al. 2019; Turner et al. 2019). One cervid subspecies that is susceptible to hemorrhagic diseases is the southern mule deer (*Odocoileus hemionus fulinginatus*), a non-migratory, harvested ungulate native to southern California and the Baja peninsula where populations are believed to be declining (Bohonak 2012). The objectives of this study were to assess the spatial pattern of seroprevalence-based evidence of three hemorrhagic disease-causing viruses in southern mule deer, identify patterns of co-occurrence among the three viruses, and determine whether exposure to these viruses is associated with landscape variables in San Diego County, CA, USA. Understanding how exposure to these viruses are influenced by landscape factors can provide important information needed to identify areas of disease risk and support the recovery of existing southern mule deer populations.

Methods

Study Area and Sample Collection

For this study, southern mule deer were captured within three study areas that represented the range of habitat types

available to deer in San Diego County; San Felipe Valley, Kitchen Creek, and Rancho Jamul (Fig. 1). San Felipe Valley is an open space wildlife area on the western border of the Anza-Borrego Desert State Park with a small scattering of private rural ranches and homes and two moderately used state route highways intersecting the study area. It consists of a transitional habitat ranging from oak woodland, interior sage scrub, chaparral, desert riparian woodland, and Sonoran Desert vegetation. San Felipe Valley is considered an important foraging and fawning habitat for the southern mule deer (CDFW 2020). Kitchen Creek is in the southwest corner of the Cleveland National Forest in the Kitchen Creek watershed. It is adjacent to a major Interstate, I-8, and is relatively remote aside from a nearby fire station, campground, and hiking trail. It has vegetation largely consisting of chamise chaparral, a favored plant of the southern mule deer (Colby 2008). The Rancho Jamul study site includes the Rancho Jamul Ecological Reserve and the Hollenbeck Canyon Wildlife Area. These two areas are separated by a heavily used highway and surrounded by private residential and agricultural land. The Ecological Reserve is used to pasture cattle and is adjacent to a large casino, a trailer park, and excessive traffic from US Customs and Border Patrol operations. The vegetation of Rancho Jamul is characterized as disturbed grassland, coastal sage scrub, and willow–sycamore riparian woodlands.

Animal capture and serological samples were conducted and collected from February 2018 to February 2019 (IACUC approval ID APF # 17-09-009L) by California Department of Fish and Wildlife personnel. Deer were captured using net guns deployed from helicopters. At capture, we recorded location (UTM coordinates) where the deer was captured, estimated age by tooth eruption and wear, fitted a Litetrack360 iridium GPS collar (Lotek Wireless, Inc., Ontario, Canada), and collected whole blood and serum samples. All collars were programmed to record GPS locations on a 7-h interval, and all unreliable locations (Dilution of Precision $>$ 5, Fix status $\leq$ 2-D) were removed before analysis. Collared deer were monitored for cause of death when a mortality occurred. To date, there has been no evidence of mortalities caused by hemorrhagic disease among the deer collared for this study.

Serological Testing

Blood samples were collected from 100 southern mule deer within the three study areas: 46 samples in San Felipe

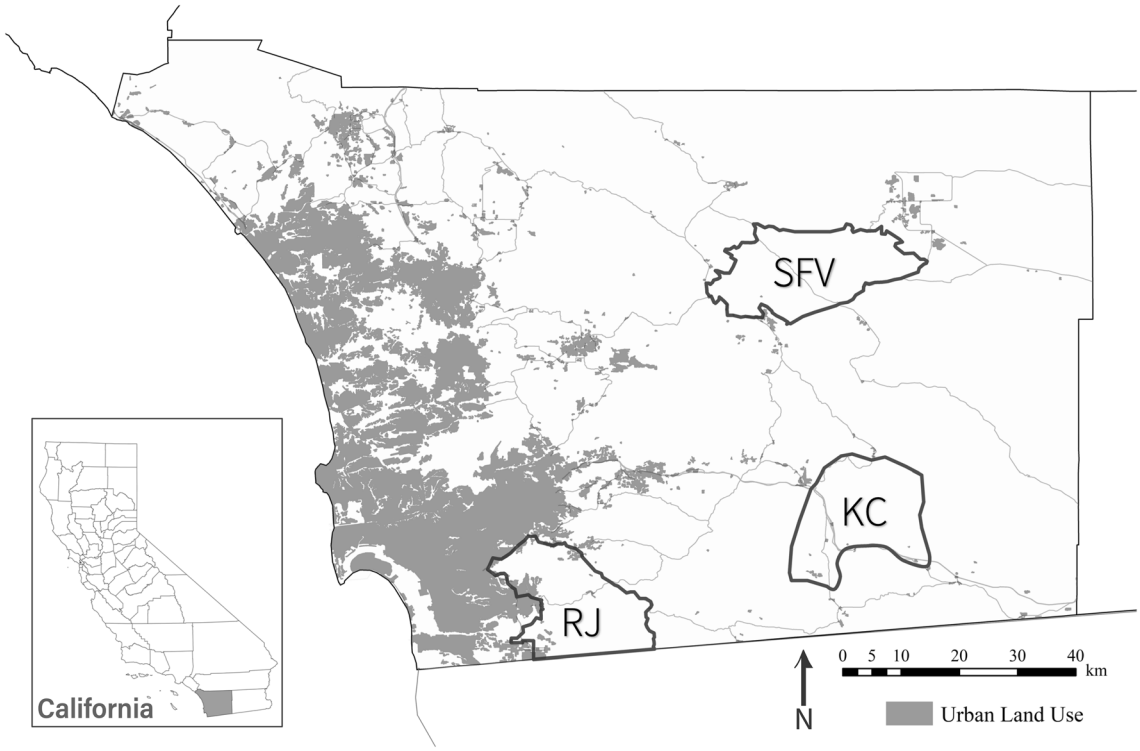


Figure 1. Map of Southern Mule Deer study area in San Diego County CA. The study sites include San Felipe Valley (SFV), Rancho Jamul (RJ), and Kitchen Creek (KC). Urban land use and roads are depicted to illustrate the degree of variation among the three study sites.

Valley, 11 in Kitchen Creek, and 43 in Rancho Jamul. Cervid adenovirus serology was tested by the Oregon Veterinary Diagnostic Laboratory at Oregon State University by serum virus neutralization assay measuring for the presence of *Odocoileus hemionus* adenovirus type 1 (OdAdV-1) neutralizing antibody, where a titer $\geq$ 1:4 was considered positive. EHDV and BTV were tested using standard methods set for livestock by California's National Animal Health Lab Network laboratory, the California Animal Health and Food Safety Laboratory at UC Davis. BTV serology was tested by capture enzyme-linked immunosorbent assay (cELISA) and EHDV serology was tested using an agar gel immunodiffusion (AGID) assay.

Statistical Analysis

To explore the patterns of seroprevalence and landscape features associated with exposure to these three viruses, we used the serological results for OdAdV, BTV, and EHDV as individual binomial attribute values (i.e., seropositive or seronegative) to investigate the spatial distribution of exposure, co-occurrence, and relationship with a suite of landscape variables. All analyses were conducted using R 3.5.0 (R Core Team 2019) and ArcGIS 10.6 (ESRI, Redlands, CA software), unless otherwise stated.

To explore the spatial distribution of each virus agent within our study area, we applied a global spatial autocorrelation analysis using Global Moran's I (Cliff and Ord 1973) implemented in the lctools package in R (Kalogirou 2012). Global Moran's I is a metric that uses a feature's location and value to categorize distribution patterns as either clustered, dispersed, or random (Cliff and Ord 1973).

We considered co-exposure to the three viruses for each individual animal using the Checkerboard score, or "C-score" index (Stone and Roberts 1990) implemented in the EcoSimR package (Gotelli et al. 2015). We calculated the C-score as an index of occurrence based on checkerboard units in a pairwise matrix of exposed individuals within our sampled population, measured as an average for all pairs of the three viruses (Gotelli 2000). A C-score that is larger than what is expected by chance indicates that evidence of exposure was segregated, i.e., no co-occurrence, whereas a small C-score indicates that exposure to any of the three viruses was aggregated, indicating likely co-occurrence (Gotelli 2000). We compared matrix C-score values with 1000 null simulated expectations calculated using the simulation 9 (SIM 9) algorithm, which is known for its performance and low frequency of type I errors (Gotelli et al. 2015). This algorithm treats the number of rows and columns in the matrix as fixed, meaning that each random simulation preserves the number of pathogens, and the frequency in which they occur. To further explore the relationship between each pathogen we also calculated individual pairwise C-scores, along with the skew and variance of the matrix C-score. The skewness of the C-score identifies the presence of outlier pairs whereas the variance of the C-score quantifies the degree of heterogeneity. We calculated pairwise C-scores for each pathogen pair in the ecospat package (Broennimann et al. 2020).

To assess the influence of landscape variables on southern mule deer exposure to the cervid adenovirus, BTV, and EHDV, we extracted habitat, topographic, and climatic variables (Table 1) from each animal's minimum convex polygon (MCP) home range, calculated as a 100% isopleth for simplicity of calculation and full coverage of an animal's habitat use. MCP home ranges were calculated from GPS locations collected from collars affixed at capture. Vegetation type, agriculture, and human development delineations were calculated as a percentage of each individual's home range. Distances to water and cattle pastures were measured from the center of each home range. Cattle density data are not available in San Diego County, so home range distance to cattle pastures, derived from the Farmland Mapping and Monitoring Project (DOC 2019), was used as a proxy. We did not get a sufficient number of GPS locations to calculate home ranges for 12 of the 100 deer sampled, due to either death or collar malfunction. For these 12 individuals we calculated the average male and female MCP home range sizes from all other deer, 15.13 and 7.52 km^2, respectively, and buffered that area around the deer's capture location as a proxy for home range. To confirm our results were not influenced by the deer with buffered home ranges, we ran a subset of our regression analysis with the buffered home ranges removed to certify that the trends remained consistent.

We investigated the effect of the landscape attributes on the risk of exposure to each hemorrhagic disease-causing virus using generalized linear models (GLM) in the lme4 package (Bates et al. 2019) with a binomial distribution based on serostatus using the landscape variables described in Table 1. We initially implemented generalized linear mixed-effect models where each study site was considered as a random effect, but further calculations estimated the random effect variance at zero for each virus, indicating that the models could be simplified by elimi-

Table 1. Table of Variables used in Regression Analysis.

Category	Explanatory variable	Description	Mean and range
Random	Site	San Felipe Valley, Rancho Jamul or Kitchen Creek	N/A
Terrain	Elevation[a]	Average elevation within deer HR (m)	666
			207–1620
	Slope[a]	Average slope within HR (%)	24.9
			6.9–41.7
Intrinsic	MCP HR size	MCP calculated from all verified deer GPS locations (km^2)	8.7
			1.8–54.2
	Group size	Average group size within deer HR, based on deer aerial surveys	1.9
			1.2–2.8
	Age	Age of deer at capture	4.8
			0.5–9.0
Land use	Cattle Grazing Proximity[b]	Distance HR centroid to nearest grazable land (m)	1071.50
			0–4692.5
	Water proximity[c]	Distance from HR centroid to nearest water source (m)	1227.00
			4.7–4616.2
	Human Development[d]	Percent of HR in human development areas (%)	0.9
			0–12.5
	Agriculture[d]	Percent of HR in agriculture (%)	3.6
			0–29.5
Vegetation	Coastal Sage scrub[d]	Percent of HR with coastal sage scrub (%)	30.7
			0–90.1
	Inland Sage scrub[d]	Percent of HR with inland sage scrub (%)	12.5
			0–74.0
	Chaparral[d]	Percent of HR with chaparral (%)	23.3
			0–82.2
	Chamise Chaparral[d]	Percent of HR with chamise chaparral (%)	16.1
			0–92.1
	Grassland[d]	Percent of HR in Grassland (%)	3.7
			0–28.9
	Riparian[d]	Percent of HR in riparian habitats (%)	3.4
			0–34.5
	Woodland[d]	Percent of HR in woodland and forest habitats (%)	5.4
			0–48.0
Climate	Annual precipitation[e]	Precipitation average from 1970 to 2000 (mm)	449
			334–678
	Precipitation seasonality[e]	Coefficient of variation of precipitation	87
			77.6–94.7
	Annual temperature[e]	Temperature average from 1970 to 2000 (°C)	16.2
			12.6–17.7
	Temperature seasonality[e]	Temperature standard deviation *100	540
			433–637

Variables considered in GLMs with seroprevalence as response variable.

[a]Derived from USGS DEM (2013).

[b]Farmland Mapping and Monitoring Program (2016).

[c]SanDag GIS Database Hydro lines (2017) and CDFW Wildlife Drinkers (2016).

[d]SanDag GIS Database Vegetation Layer (2017).

[e]WorldClim Global Climate Data (2020).

nating the mixed effects component (Bolker et al. 2009). We ran each variable in a univariate GLM for OdAdV, BTV, and EHDV. Continuous variables that we found to be significant for exposure to each virus were then compared in a Pearson's autocorrelation test and all possible model combinations were considered, with correlated variables ($r > |0.60|$) excluded (Kirch 2008). Final models for exposure to each disease agent were evaluated using model averaging in the MuMIn R package (Barton 2020) using models with delta AICc values of less than 1.5. To visualize variable effects, we calculated odds ratios and confidence intervals by exponentiating the coefficient for each variable in the final GLMs in the Mass package (Ripley et al. 2019). To quantify the importance of individual variables within each model, we used hierarchical partitioning in the package "hier.part" (Walsh and Mac Nally 2020). Hierarchical partitioning calculates the independent effect of each variable to the variance in the response variable across all combinations to provide a visualization and evaluation of the relative importance of predictor variables.

Results

Pathogen Exposure Prevalence

Of the 100 southern mule deer serology samples collected across sites within San Diego County, 31 were seropositive for OdAdV, 37 seropositive for BTV, and 50 seropositive for EHDV. The majority of deer sampled were adults (age > 2, $n = 86$), with 13 yearlings (1–2 years), and 1 fawn (< 1). Prevalence of exposure to each pathogen varied among sites (Table 2). Of the 100 deer tested, 42 were exposed to more than one of the hemorrhagic viruses for which we tested.

EHDV had a Moran's Index of 0.173 (z-score = 3.48, $p < 0.005$), indicating that EHDV seropositive deer were significantly clustered. Exposure to OdAdV and BTV, however, was found to be randomly distributed in the deer population that was sampled (Table 3).

Co-exposure among OdAdV, BTV, and EHDV was significantly higher than the range calculated for all 1,000 random null models, indicating a pattern of segregation among the three viruses (Table S1). Further analysis of the pairwise interactions among exposure to the three pathogens revealed that the OdAdV was significantly less likely to be present in deer with either BTV or EHDV, whereas deer exposed to BTV were significantly likely to also be exposed to EHDV (Table 4).

Landscape Predictors of Pathogen Exposure

The landscape variables associated with seropositive individuals differed among the three pathogens. In regression analysis, exposure to OdAdV had a significant negative relationship with the percent of chamise vegetation within a deer's home range, which also accounted for the greatest variance to OdADV seroprevalence (Table S2, Fig. 2a, b). Deer seropositivity to BTV had a significant negative relationship with home range distance to cattle pastures, and this distance also contributed to the greatest percentage of variance in BTV seroprevalence (Table S2, Fig. 2c, d). Finally, EHDV exposure had a significant negative associa-

Table 2. Deer Pathogen Exposure Status by Site.

Virus	San Felipe Valley ($n = 46$) (%)	Kitchen creek ($n = 11$) (%)	Rancho Jamul ($n = 43$) (%)	Total ($n = 100$) (%)
No exposure detected	41.3	36.4	14.0	29
OdAdV only	19.5	9.0	14.0	16
BTV only	2.2	0	2.3	2
EHDV only	10.9	18.2	9.3	11
OdAdV and BTV	0	0	7.0	3
OdAdV and EHDV	2.2	0	14.0	7
BTV and EHDV	21.7	36.4	30.2	27
OdAdV, BTV and EHDV	2.2	0	9.3	5

The percentage of deer at each site with a specific seropositive status for the hemorrhagic pathogens tested. From a total of 100 deer sampled between all sites, a total of 50 deer tested positive for exposure to EHDV, 37 tested positive for exposure to BTV and 31 tested positive for exposure to OdAdV.

Table 3. Results from Global Moran's I Analysis.

Disease	Moran's index	*z*-Score	*p*-Value
AHD	0.063	1.39	0.165
BTV	0.041	0.98	0.327
EHDV	0.173	3.48	< **0.005**

Global Moran's I values of seropositive southern mule deer for each hemorrhagic disease agent. AHD and BTV have no significant distribution, while EHDV is significantly clustered. Significant *p*-values < 0.05 are in bold.

tion with the percent of woodland vegetation and percent slope within deer home ranges, and a significant positive association with the percent of human development within deer home ranges, where human development had the largest percent contribution to EHDV seroprevalence variance (Table S2, Fig. 2e, f). Subsetted regression analysis using only MCP calculated home ranges showed consistent trends with the combined MCP and buffered home range results, indicating that buffered deer home ranges did not overly influence regression results.

Discussion

This study provides the first large-scale evaluation and testing of exposure to hemorrhagic disease-causing viruses within a southern mule deer population. Our results show that these viruses are collectively present in more than 50% of the deer we tested, though there were no recorded hemorrhagic disease outbreaks in the area leading up to and during this study. Our analyses revealed differing patterns of distribution, co-occurrence, and association with landscape variables among individuals exposed to each of these relatively prevalent viruses, indicating potentially complex transmission pathways for these pathogens.

Contrary to our expectations, OdAdV was not significantly clustered in the southern mule deer population we sampled which we had anticipated because OdAdV is horizontally transmitted (Woods et al. 2018). However, because our sampling design limited the number of deer captured from a single group, it is possible that the lack of clustering for OdAdV seroprevalence is an artifact of our sampling design. Future OdAdV testing should include group sampling of deer across the landscape to obtain a clearer picture of transmission and hot spots. Our study suggests that animals exposed to OdAdV did not co-occur with animals exposed to the other two hemorrhagic viruses tested, a finding consistent with those in other wildlife studies in which OdAdV, BTV, and EHDV serology were tested concurrently (Mathieu et al. 2018; Woods et al. 2018; Ferguson and Lee 2020). Whether this pattern of segregation between OdAdV and BTV or EHDV is a result of differences in transmission pathways, the timing of exposure (Hoverman et al. 2013; Devevey et al. 2015), or some other form of interaction among these pathogens (Cobey and Lipsitch 2013; Rogers et al. 2015) is currently unknown.

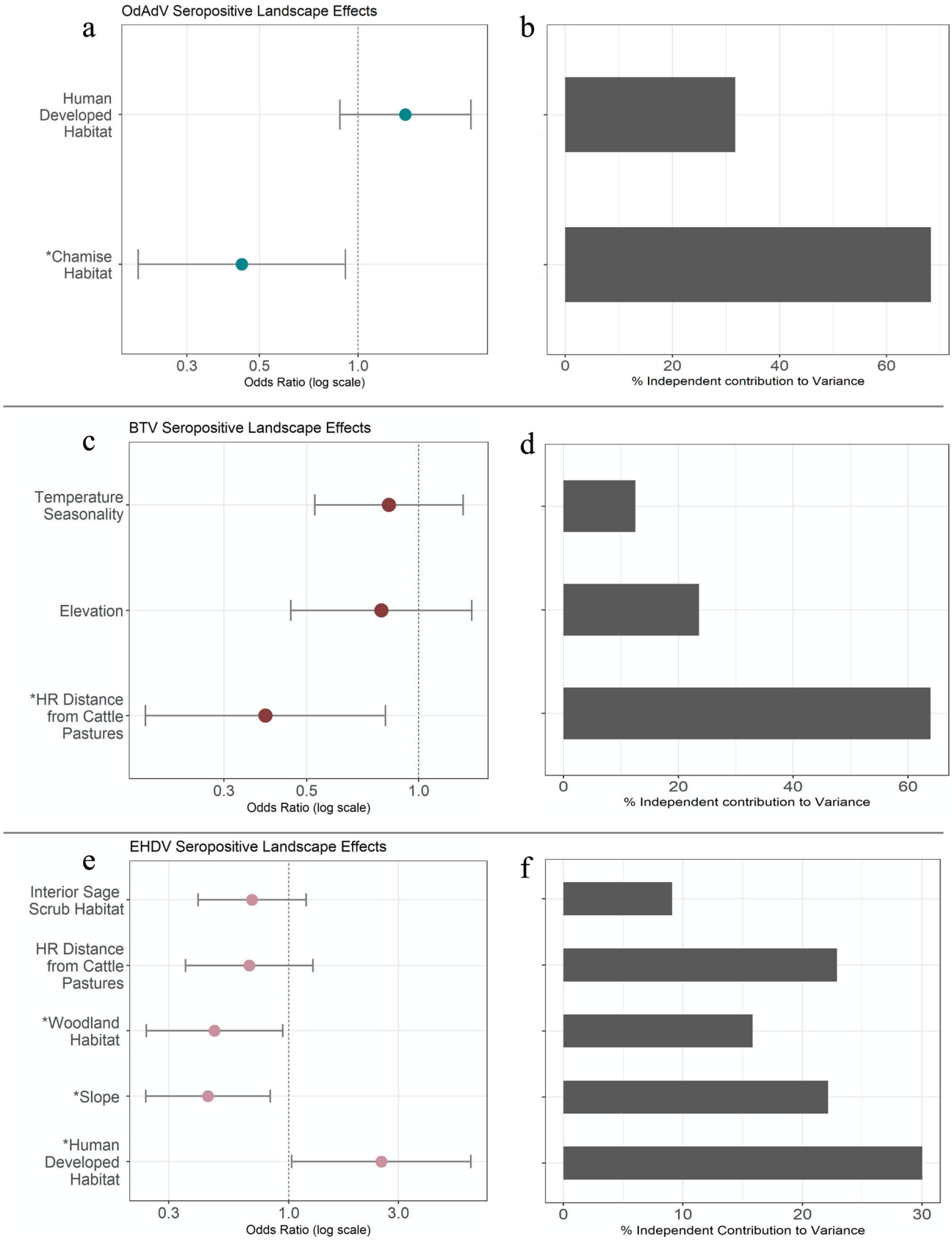
We found OdAdV seropositivity to be inversely related to the percent of chamise vegetation within a home range, which is a preferred food source of southern mule deer in this area (Colby 2008). When food resources are scarce, animals are more likely to congregate in areas where limited food sources are present, which can lead to an increase in virus transmission (Bradley and Altizer 2007; Murray et al. 2016). In the case of the southern mule deer in San Diego County, it is possible that areas with limited chamise vegetation may lead to increased aggregation of deer, which could potentially facilitate the spread of OdAdV in this area, a finding that is confirmed by other OdAdV research (Woods et al. 2018).

While OdAdV is a relatively newly recognized disease agent (Woods et al. 1996), BTV and EHDV likely emerged in wild ruminants long before BTV was first described in 1905 (Verwoerd and Erasmus 2004; Coetzee et al. 2012; Maclachlan et al. 2019). Yet despite their historical presence

Table 4. Pairwise Co-occurrence Results.

Pair	Observed *C*-score	Expected *C*-score	Standard effect size	*p*-Value less	*p*-Value greater
AHD–BTV	667	567	2.38	0.996	**0.021**
AHD–EHDV	722	416	3.72	1.000	< **0.001**
BTV–EDHV	90	338	− 4.37	< **0.001**	1.000

Pairwise *C*-scores among AHD, BTV, and EHDV. AHD pairs are significantly segregated, while BTV and EHDV are significantly aggregated. Significant *p*-values < 0.05 are in bold.


a
OdAdV Seropositive Landscape Effects
Human Developed Habitat
*Chamise Habitat
0.3
0.5
1.0
Odds Ratio (log scale)
b
0
20
40
60
% Independent contribution to Variance
c
BTV Seropositive Landscape Effects
Temperature Seasonality
Elevation
*HR Distance from Cattle Pastures
0.3
0.5
1.0
Odds Ratio (log scale)
d
0
20
40
60
% Independent contribution to Variance
e
EHDV Seropositive Landscape Effects
Interior Sage Scrub Habitat
HR Distance from Cattle Pastures
*Woodland Habitat
*Slope
*Human Developed Habitat
0.3
1.0
3.0
Odds Ratio (log scale)
f
0
10
20
30
% Independent Contribution to Variance

◀**Figure 2.** Corresponding odds ratio visualizations and percent influence based on hierarchical partitioning models for each variable from the best fitting regression models for hemorrhagic seroprevalence response in southern mule deer (*Odocoileus h. fuliginiatus*) to landscape variables. Variables listed on the y-axis are the same for each pair of plots. Significant variables are indicated with an ***: **a**, **b** OdADV seroprevalence had a positive but nonsignificant relationship with human development and a significant negative relationship with the percent of chamise vegetation within a deer's home range, where the percentage of chamise habitat accounted for 68% of the variance for the final model; **c**, **d** BTV seroprevalence had a significant negative relationship with home range distance to cattle pastures and a negative but nonsignificant relationship with seasonal temperature and elevation, where distance to cattle pastures contributed for 64% of the variance for the final model; **e**, **f** EHDV seropositivity had a significant negative relationship with the percent of woodland vegetation and percent slope within deer home ranges, a significant positive relationship with the percent of human development within deer home ranges, and a negative but nonsignificant relationship with home range distance to cattle pastures and percent of interior sage scrub habitat within a deer's home range, where human developed habitat accounted for 30% of the variance for the final model.

in wild populations, these two highly related orbiviruses are re-emerging global pathogens whose ranges are expanding in response to changing climate conditions for their vector (Maclachlan et al. 2019). The differences in exposure between these two pathogens was demonstrated by the distribution and degree of seroprevalence among individuals within our study areas. Our analyses revealed that EHDV exposure was more prevalent than BTV exposure (50 and 37%, respectively), and EHDV exposure was significantly clustered, whereas BTV was not. However, our findings show that co-exposure to BTV and EHDV was relatively common in the southern mule deer populations we sampled, an outcome consistent with the previous research (Sailleau et al. 2012), and expected considering that these pathogens are closely related and are transmitted by the same *Culicoides* vector.

Landscape variables associated with pathogen exposure in southern mule deer varied for the two vector-borne hemorrhagic viruses. While we found co-occurrence of EHDV and BTV, there were differences in the features associated with their seroprevalence across the landscape. BTV seroprevalence was highest in deer with home ranges closer to cattle pastures. This broadly aligns with previous studies that have also found BTV prevalence is highest in areas with high levels of livestock–wildlife interactions (Ruiz-Fons et al. 2008; Rossi et al. 2014; Rajeev et al. 2017; Merrill et al. 2019). In contrast to BTV, EHDV seroprevalence was not related to cattle; rather, we found EHDV seroprevalence was positively associated with home range proximity to development and negatively related to proportion of woodland vegetation and slope. These factors associated with increased EHDV seroprevalence may be indicative of other cumulative factors influencing transmission, such as habitat fragmentation. In other study areas, reductions in patch area and increased patchiness due to habitat fragmentation have been associated with increased reservoir host density, disease outbreaks, and disease persistence (Brownstein et al. 2005; Rubio et al. 2014; Gao et al. 2019). These differences in landscape factors associated with BTV and EHDV may also be related to vector–host dynamics among different reservoir populations. Although both diseases agents can affect wild and domestic populations, BTV is more common in domestic livestock, whereas EHDV predominantly affects wild ungulates (Mcvey and Maclachlan 2015), which likely affects transmission dynamics and patterns of prevalence for these two related orbiviruses. While not available for our research, further testing of both the *Culicoides* vector as well as cervid and domestic hosts might help tease apart the differences in the factors affecting seroprevalence of these pathogens.

Our study provides further evidence that human disturbances, including livestock presence, urban and built development, and resource limitation, influence the transmission of hemorrhagic disease-causing viruses, an important family of pathogens that are prevalent in cervids and other ungulates. For southern mule deer, a subspecies of conservation concern, systematic and continued virus screening will be needed to better understand the impacts of these pathogens on the health and persistence of the population. Understanding these viruses, including vector, host, and landscape dynamics, will provide needed information about their distribution, transmission, and prevalence. This is especially important in human-dominated landscapes where these pathogens can cause significant losses to both domestic and wild populations (Stevens et al. 2015; Spickler 2019), and have the potential to be devastating to sensitive populations like the southern mule deer.

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