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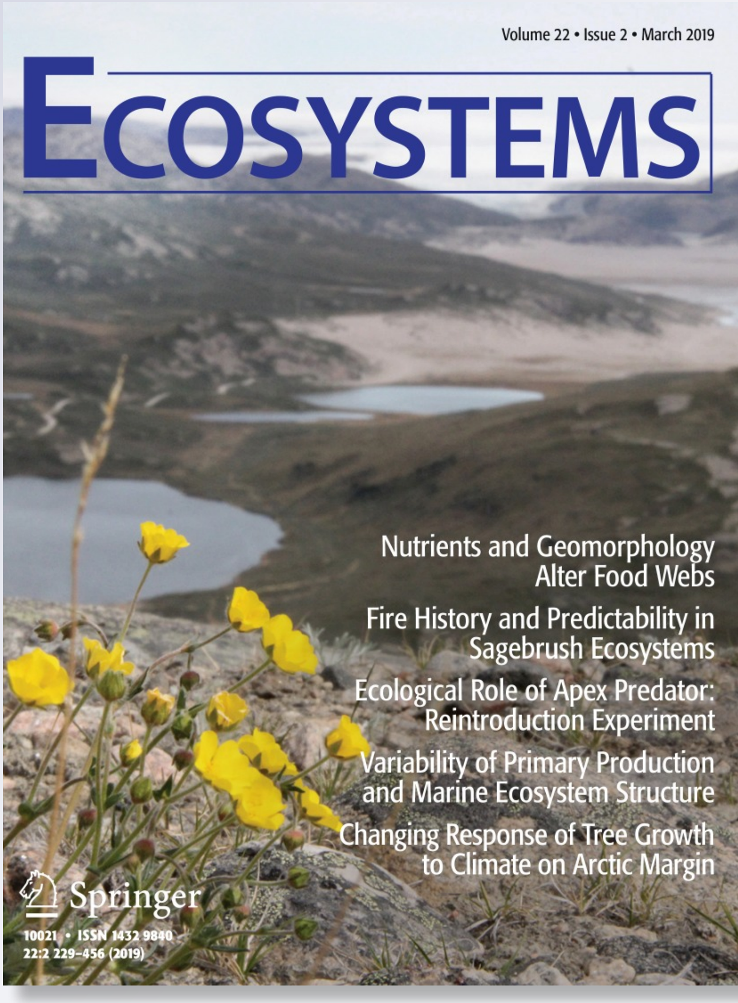

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Contributions of Hydrology to Vesicular Stomatitis Virus Emergence in the Western USA

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Abstract

Relationships between environmental variables associated with the spread of vector-borne pathogens, such as RNA viruses transmitted to humans and animals, remain poorly understood. Vesicular stomatitis (VS) is caused by a vector-borne, zoonotic RNA virus (VSV) and is the most common vesicular disease affecting livestock (domestic horses, cattle, pigs) throughout the Americas. This investigation focused on explaining patterns of more than 1500 VS-infected livestock premises in the western USA from 2004 to 2016 related to the ecology of the host-vector-virus-environment system. We investigated the relationship between VS incidents and habitat characteristics expected to be important to insect vectors: stream location, streamflow conditions, climate, and vegetation. Results show that VS incidents were distributed near the stream network with 72% located within 1 km of lotic habitat. Monthly incidents were closest to lotic habitat in April ($x = 525$ m) and furthest from lotic habitat in November, December and January (1843, 2141 and 4807 m) indicating that initial infection near streams may spread away from these locations. All first incidents ($n = 35$) occurred following peak annual streamflow, with 89% (31 of 35) of these occurring after streams returned to baseflow. This finding indicated that surveillance for VS could be targeted spatially in locally relevant geographic areas (that is, near streams) and temporally relative to local streamflow conditions which can be remotely monitored via existing web-accessible information networks. Habitat modeling of 11 subwatersheds revealed somewhat different models for each watershed with several factors important in multiple watersheds. In nine of the 11 watersheds, the highest model PC (31–71%) represented either higher-than-average long-term mean temperature or lower-than-average long-term mean precipitation. Approaching habitat modeling on a watershed basis reveals information to support additional research. These spatial and temporal relationships showcase the importance of hydrologic contributions to the

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emergence and distribution of an arthropod-borne disease in the western USA.

Key words: vesicular stomatitis; vector-borne disease; streamflow; western USA; livestock; horses; virus transmission; MAXENT.

Introduction

Ecosystem-disease research comprises less than 2% of disease ecology publications (Preston and others 2016). This may be because ecological change and disease emergence are often mediated through complex and large-scale processes that complicate causal inference (Parham and others 2015; Plowright and others 2008). As a consequence, relationships between environmental variables and spread of infectious disease remain poorly understood for many disease systems associated with vector-borne pathogens, such as West Nile, Dengue, and Zika (LaDeau and others 2011; Parham and others 2015; Racloz and others 2012). There has been a significant rise in the global number of disease events caused by vector-borne diseases, and this increase corresponds with climate anomalies (Jones and others 2008). Because vector-borne diseases account for more than 20% of emerging infectious diseases globally (Jones and others 2008), understanding their impacts on human and natural systems is vital. For example, transboundary animal diseases resulting from viruses transmitted to livestock can severely disrupt food security and international trade (Kompas and others 2015). One such disease, vesicular stomatitis (VS), is a common vesicular disease affecting livestock (domestic horses, cattle, pigs) throughout the Americas (Rodriguez and others 2002).

In cattle and swine, clinical signs of VS are indistinguishable from foot and mouth disease (FMD), one of the most devastating viral infections of livestock. VS leads to large economic losses associated with animal quarantines and trade embargoes (Timoney 2000) when it occurs in FMD-free areas (Goodger and others 1985), and the occurrence of VS greatly exacerbates the inherent difficulties involved in the control of FMD in endemic regions (Paton and others 2009). Therefore, VS is a reportable disease when it occurs in cattle and swine and the disease has been well studied in epidemic and endemic regions (Rodriguez and others 2002; Velazquez-Salinas and others 2014). Historical disease occurrence data are available throughout the geographic distribution of the disease in the USA (http://www.usda.aphis). The ecological associations of VS occurrence have been a subject of research for over four decades (Rodríguez and others 1996). However, remarkably little is known about the ecology of the disease system and the environmental variables related to spatial and temporal patterns in disease occurrence.

VS has occurred every decade since 1916 in the western USA with 1–3-year epidemic cycles. Although this disease has low mortality and morbidity rates, it can spread rapidly over large geographic areas in relatively short time periods (Rodriguez and others 2002). The disease seems to move northward from endemic areas in Mexico (Velazquez-Salinas and others 2014) to southern US States (Arizona, New Mexico or Texas) and then typically moves northward in the western USA (Perez and others 2010; Rainwater-Lovett and others 2007).

VS transmission between individual premises may be mediated by certain insect species that serve as biological vectors of the disease, particularly black flies (*Simulium* spp.), sand flies (*Lutzomyia* spp.) and biting midges (*Culicoides* spp.) (Perez and others 2010). A premise is defined as the physical site or property where the subjects of an investigation are located. In this study, an infected premise could have one or more infected animals. Although black flies, midges, sand flies and other hematophagus insects are known vectors of VSV (Drolet and others 2005; Mead and others 1997, 1999, 2000a, b), unknown is the specific role of vectors in a given outbreak. Although black flies are the most likely vector in the southwestern USA, vector dominance may vary in different geographic regions. Midges may also play a role in transmission, in particular in the expansion across the region. It is very likely that the emergence of VS in each specific event and geographic region is dependent on a sufficiently dense and robust population of vectors. Black flies emerge from streams as water levels and velocities decline (Adler and others 2010).

Because flight distance ranges are limited (less than 8 km), proximity to a viable host and back to streams for oviposition indicate links between water source and vector lifecycle. Unclear, however, is the contribution of hydrology in terms of streamflow and soil moisture for VS occurrence as it relates to the vector lifecycles, particularly black flies. Because these insects spend a portion of their lifecycle in lotic (black flies) or moist (sand flies and biting midges) habitats (Rozendaal 1997), it follows that the prevalence of VS incidents in close spatial proximity to streams with flowing water suggests a

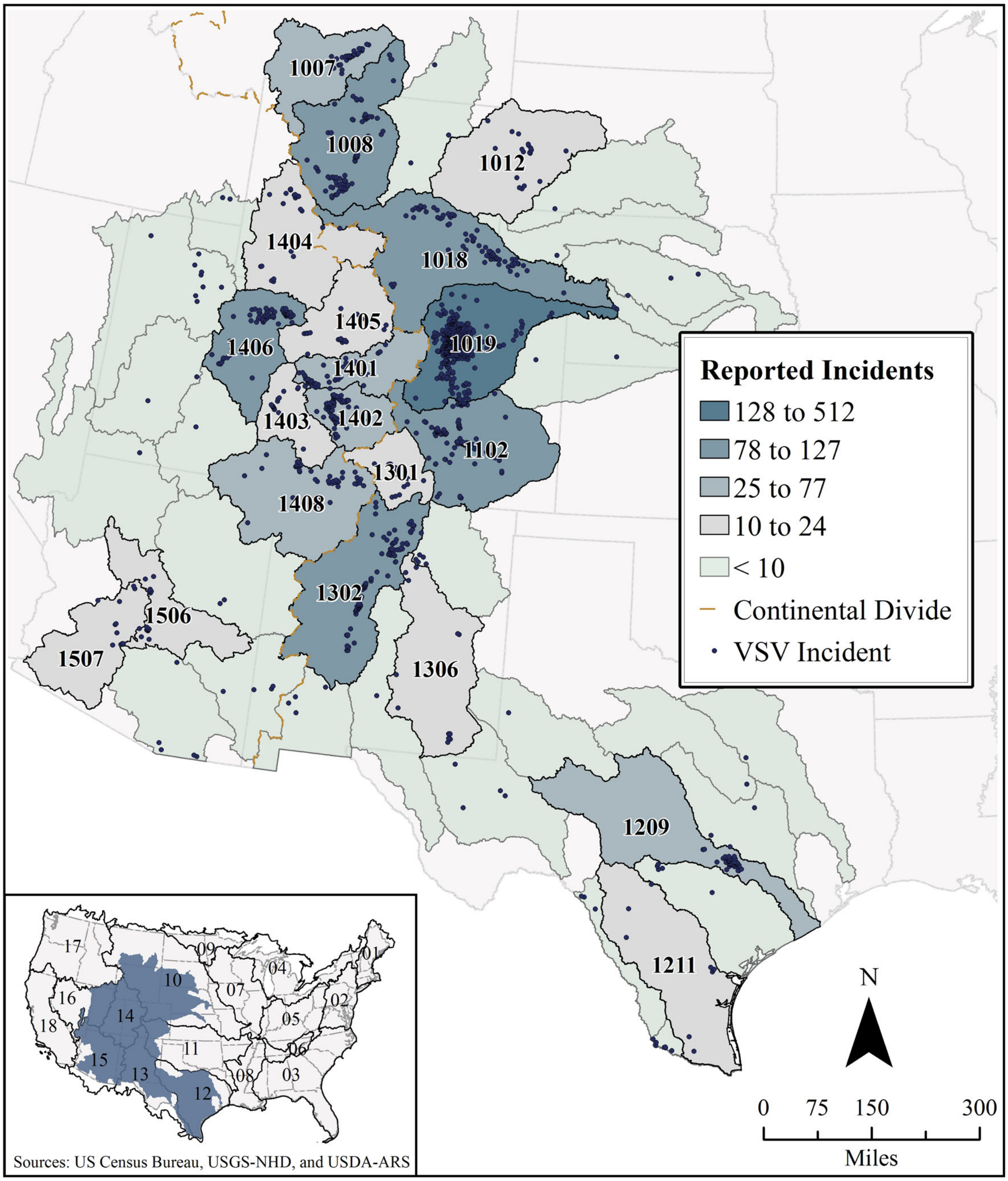


Figure 1. Major hydrologic boundary units associated with 2004–2016 VSV-affected premises in the western USA.

clear linkage of hydrology and insect ecology for VSV. Given habitat considerations, we expect black flies to be located and emerge from flowing water, whereas sand flies and biting midges are associated with moist soil. Vectors, particularly black flies, are organisms that move between systems of consideration, or 'mobile links' with the ability to transmit disease between systems (Lundberg and Moberg 2003). Hydrologic studies often focus on unidirectional aquatic-terrestrial interactions, such as the cascading impacts of terrestrial nutrient and sediment deposition to aquatic systems. However, research has shown that aquatic habitats provide important inputs to terrestrial systems via emergent aquatic insects (Bartrons and others 2013; Gratton and others 2008). Because insect ecology data are lacking for the spatial and temporal aspects of this analysis across the geographic extent of VS-infected

Table 1. Data Used in MAXENT Habitat Modeling by Hydrologic Region

Theme	Response variables (number of data layers)	Source of data	Spatial extent
VS case occurrence	Confirmed incident (1)	USDA-APHIS	Point
Livestock	Horse density (1)	USDA-NASS	County
Soil	Available water capacity (1)	USDA-NRCS	Polygon
Hydrology	Long-term annual mean streamflow (1)	USGS, NOAA, USEPA, and others NHDPlusV2	Flowline
	Seasonal mean soil moisture (4)	Variable Infiltration Capacity Model	12 km
Temperature	Seasonal mean maximum (4) Seasonal mean minimum (4)	PRISM Climate Group, OSU	4 km
Precipitation	Seasonal total (4)	PRISM Climate Group, OSU	4 km
Drought	Evaporative demand drought index Seasonal total (4)	NOAA	12 km
Vegetation	Normalized difference vegetation index Seasonal mean (4)	NASA MODIS	5.6 km

Seasons defined as winter (December, January, February), spring (March, April, May), summer (June, July, August) and Fall (September, October, November).

premises, we emphasize the hydrologic conditions in relation to confirmed VS premises.

A recent comprehensive analysis of environmental variables for two incursion events led to the hypothesis that animals closer to flowing water have an increased probability of contracting VS and this might be due to effects of streamflow on the VS vector population (Peters and others 2017). These results are supported by previous studies showing that proximity to flowing water was associated with VS, with premises housing animals less than 400 meters from flowing water being more than twice as likely to have animals with clinical signs of VS (Hurd and others 1999). Moreover, individual premises covered with grassland or pasture or containing a body of water are at higher risk for VS infection (Duarte and others 2008). Here, our primary goal was to improve understanding of the complex host-vector-virus-environment system through examining the associations between hydrologic characteristics and patterns in VS emergence. We utilized existing fine spatial scale, yet large geographic extent hydrologic stream flow data from the NHD plus version 2 effort supported by the US Environmental Protection Agency and the US Geological Survey combined with other sources of environmental data to determine relationships between VS incidence and environmental variables across the geographic distribution of VS in the western USA.

Although prior studies have found evidence of a relationship between proximity to flowing water and VS incidents, no studies have investigated the relationship between streamflow timing, or changes throughout the year in the amount of water flowing through a river reach, and VS incident timing. In addition, few studies have quantified the proximity of VS incidents to flowing water throughout the year. Finally, few studies have applied a watershed approach, evaluating VS incidents within watershed boundaries, for ecological niche modeling comparisons. This research applies a decidedly hydrologic approach to evaluate these knowledge limitations: the spatial relationship between VS-infected premises and flowing water throughout the year, the temporal relationship between VS-infected premises and streamflow timing, and ecological niche modeling on a watershed basis to better understand the important environmental variables impacting VS occurrence in western watersheds. We used a dataset of 1550 VS-infected premises occurring from 2004 to 2016 across the western USA, an area greater than 1.1 M km^2. We expand upon the hydrologic analysis to include watershed-scale habitat modeling with remotely determined vegetation, soils and weather/climatic environmental variables to investigate the relationships between VS incidents and habitat characteristics expected to be important to vectors of VS.

Methods

VS Incidence Data

VS incidents occurred in portions of seven of the 21 major water resources regions (2-digit hydrologic units) in the USA (Figure 1).

In the USA, accredited veterinarians are required to report cases of any vesicular-lesioned, VS-apparent livestock they encounter. Follow-up is conducted by local state/federal regulatory officials which includes a visit to the premises, physical examination of the animal(s), and collection of diagnostic samples for confirmatory testing. A premise with a confirmed positive case is maintained under state quarantine for a period of at least 14 days past the onset of lesions in the last affected animal on the premises. Data from positive premises including location, animal inventory, species affected, estimated lesion onset date, quarantine start and release dates, and diagnostic test results are available online (U. S. Department of Agriculture 2016) as are VS Situation Reports and maps from previous outbreaks. The data in this analysis include premises with both equine and bovine cases; however, equine-infected premises represent a majority (84%) of the total infected premises (Supplementary Material).

Environmental Data

Data to Evaluate Incident Location Relative to the Nearest Stream with Water

We used the NHDPlusV2 geospatial hydrologic framework dataset built by the US EPA Office of Water and the US Geological Survey to define the active stream network on a monthly basis. The NHDPlusV2 produces a reliable stream network based upon the National Hydrography Dataset, the Watershed Boundary Dataset and the National Elevation Dataset (Moore and Dewald 2016). The data are provided online (http://www.horizon-systems.com/NHDPlus/NHDPlusV2_home.php), distributed by major hydrologic region (2-digit hydrologic unit code (HUC)). We downloaded data for seven 2-digit HUCs to process for use (described in ''Objective 1: VSV Incident Distance from Stream Network'' section).

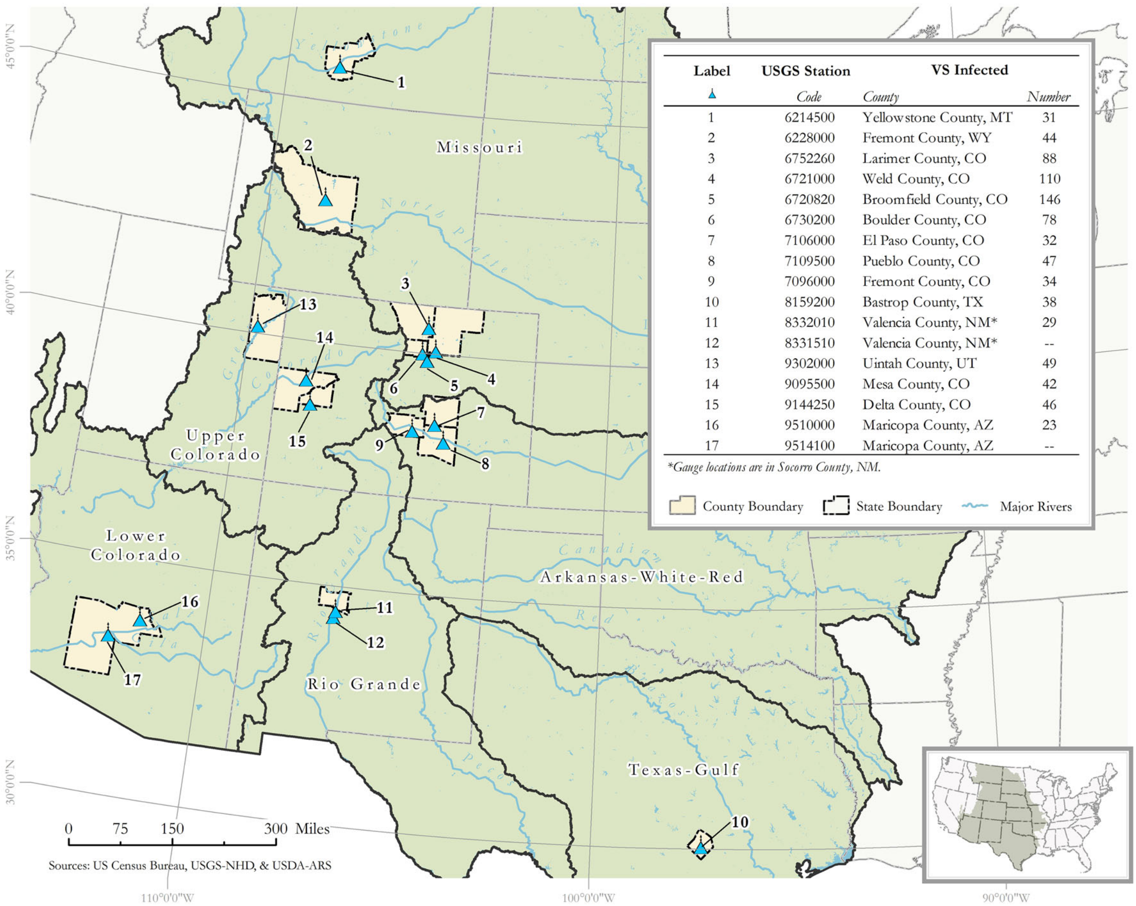
Data to Evaluate Incident Timing Relative to Streamflow

To evaluate VS incidents in relation to typical hydrologic conditions through time, we selected areas within the region with an elevated number of confirmed infected premises. Typically, when one premise in a county is confirmed positive for VS, public health officials assume the entire county may contain infected animals, making the county a valid unit of analysis. Of the counties selected for streamflow analyses, most had more than 30 confirmed premises over the 2004–2016 study period; however, Maricopa County, Arizona (n = 23) and Valencia County, New Mexico (n = 29) were also included in the analyses as these counties contained the most VS-infected premises in Arizona and New Mexico, respectively. Daily streamflow data for the January 1, 2004 to December 31, 2016, timeframe were downloaded from the National Water Information System stream gauges near VS-confirmed premises (US Geological Survey 2001).

VS Data Used to Evaluate Incident-Habitat Associations: Ecological Niche Modeling

VS premises, horse density, and soils were each represented by a static data layer for the 2004–2016 study period (Table 1). Latitude and longitude coordinates of the location of every confirmed VS premises were recorded and imported into a geographic information system along with data layers representing environmental and climatic themes. Animal density contributes to the spread of infectious disease. In this study, we used the mean horse density within a county reported from 2002, 2007 and 2012 by the National Agricultural Statistics Service (NASS 2013). County areas for density calculations were downloaded from the National Atlas as the geodatabase at one-million scale (USGS 2014). Some of the vectors associated with VS spread, particularly *culicoides*, prefer mud, animal waste or shallow standing water as habitat (Pfannenstiel and others 2015). Areas suitable for standing water can be transient and intermittent, emerging following rains or during monsoonal conditions. To capture the potential for this habitat, the available water capacity (AWC) from STATSGO2 was used (Soil Survey Staff 2016).

Mean seasonal [Winter (December, January, February), Spring (March, April, May), Summer (June, July, August), Fall (September, October, November)] data were generated to represent hydrologic, climatic and vegetation themes. The distance to flowing water from each VSV occurrence was included in analyses. The distance to streamflow was defined using the mean annual normal streamflow (1970–2000) from the NHDplusV2 dataset described previously. Hydrologic conditions were also represented by mean soil moisture from the Variable Infiltration Capacity model (Liang 1994). Mean seasonal PRISM data at a 4 km resolution provide a continuous surface of



Label	USGS Station Code	VS Infected County	Number
1	6214500	Yellowstone County, MT	31
2	6228000	Fremont County, WY	44
3	6752260	Larimer County, CO	88
4	6721000	Weld County, CO	110
5	6720820	Broomfield County, CO	146
6	6730200	Boulder County, CO	78
7	7106000	El Paso County, CO	32
8	7109500	Pueblo County, CO	47
9	7096000	Fremont County, CO	34
10	8159200	Bastrop County, TX	38
11	8332010	Valencia County, NM*	29
12	8331510	Valencia County, NM*	--
13	9302000	Uintah County, UT	49
14	9095500	Mesa County, CO	42
15	9144250	Delta County, CO	46
16	9510000	Maricopa County, AZ	23
17	9514100	Maricopa County, AZ	--

*Gauge locations are in Socorro County, NM.

Figure 2. Vesicular stomatitis-confirmed premises by county (2004–2016).

minimum and maximum temperature and precipitation (Daly and others 2008). The evaporative demand drought index (EDDI) (McEvoy and others 2016) and the normalized difference vegetation index (Tucker 1979) data layers for seasonal time periods were used to represent drought conditions and vegetation greenness, respectively.

Maxent requires spatial standardization among all datasets by geometrically aligning the dataspace to ensure all data pixels represent the same object at the same scale and extent. Spatial data co-registration is the process of transforming multiple datasets into one common coordinate system, one common pixel origin as well as identical scale and area. This process was completed to spatially align data of varying pixel sizes, such as PRISM (4 km grid), NDVI data (5.6 km grid) and EDDI (12 km grid).

Analysis

VSV-infected premises between 2004 and 2016 represent two independent events of emergence. The viral strains responsible for each incursion are of distinct genetic lineage, and in each case their ancestry is closely related to viral strains circulating in endemic areas of Mexico (Rainwater-Lovett and others 2007; Velazquez-Salinas and others 2014). Despite the different phylogeographic origin of the etiological agents, the pattern of case distribution was remarkably similar, suggesting that underlying ecological factors, rather than solely intrinsic viral characteristics, mediated the case distribution and outbreak dynamics. In a related paper, we examined two of the largest events (2004–2006, 2012–2015) and found similar environmental variables were important in explaining patterns of spread (Peters and others 2018). It is well established that different viral phenotypes can mediate or dramatically influence the initiation and spread of disease. Such is the case of the Venezuelan equine encephalitis virus, where endemic low-virulence strains can give rise to epidemic and highly transmissible strains. However, such clear distinction of endemic versus epidemic strains has not yet been established for VSV. Thus, we elected to group the 2004–2016 data.

Incident Location Relative to the Nearest Stream with Water

In the western USA, water often flows intermittently and streams can be dry for much of the year. Hence, we mapped the distance from each VS incident to the mean monthly streamflow, for the month in which the incident occurred, of the National Hydrography Dataset Plus Version 2 (Moore and Dewald 2016; NHDPlus Team 2016). For this dataset, the monthly average streamflow for each stream segment was estimated using the extended unit runoff method (EROM). We used the recommended gage-adjusted streamflow (Q0001E) values for each line of the National Hydrography Dataset (NHD) flowline feature. For each month, we removed streams with no monthly average flow using the 'select by attributes' feature using GIS software. Streams in the 2-digit hydrologic regions composing the VS incident extent were merged to create a stream network with likely streamflow. Next, we created shapefiles of VS incidents by month and calculated distance between the location of reported incidents and the nearest flowing water on a monthly basis, the number of VS incidents within 1 km of flowing water and summary statistics by hydrologic region. The ArcGIS 'generate near table' tool using the geodesic method was used to generate distance metrics.

Incident Timing Relative to Streamflow

Each VS incident was plotted against the daily streamflow of the nearest gauge (Figure 2). Daily streamflow results were separated into baseflow and runoff components using the recursive digital filter for perennial streams with porous aquifers within the web-based hydrograph analysis tool (Lim and others 2005). The return to baseflow conditions following snowmelt runoff was defined as the five consecutive days where baseflow represented 90% of total daily streamflow volume. Peak streamflow dates for each stream and year were obtained from the USGS NWIS database (US Geological Survey 2012). Days between return to baseflow conditions and first confirmed VS incident for each outbreak were recorded.

VS Incident–Habitat Associations: Ecological Niche Modeling

The maximum entropy algorithm implemented in Maxent version 3.3.3 was used on a watershed basis [subregion; 4-digit hydrologic unit codes (HUC-4)] to compare the spatial distribution of VS infection using long-term environmental conditions (Phillips and others 2006). Data layers representing eight variables (infected premises, horse density, soil properties, hydrology, temperature, precipitation, drought, vegetation) were initially used as input data (Table 1). A model for each hydrologic region was based upon all principal components contributing 5% or more of the percent contribution (PC) or the permutation importance (PI).

Evaluation of VS habitat was conducted on a hydrologic subregion basis (HUC-4). Nationally, the lower 48 states contain 204 HUC-4 level watersheds. Since river networks are associated with VS, we evaluated all HUC-4 watersheds containing VS between 2004 and 2016. While 45 HUC-4 watersheds had at least one VS incident between 2004 and 2016, only 11 watersheds contained more than 40 incidents, which were selected for Maxent ecological niche modeling. More than one-third of all VS-confirmed premises occurred in a single HUC-4 watershed, the South Platte ($n = 512$). The area evaluated was defined as the hydrologic subregions (HUC-4) containing higher numbers of confirmed VS incidents between 2004 and 2016. A total of 11 watersheds were analyzed (Figure 1).

The bootstrap function in Maxent was used to produce 10 replicate analyses. Because correlated values have been shown to falsely increase model performance, Maxent simulation was conducted in two phases. First, Maxent was executed with all variables for each watershed. Maxent variables contributing at least 3 PC or PI were analyzed for correlation on a watershed basis using ArcGIS multivariate statistics to identify correlated variables that can cause over fit models (Merow and others 2013). Correlations near 1 or − 1 indicated highly correlated variables, whereas correlations closer to 0 indicated little correlation. Second, Maxent was executed a second time after variables considered highly correlated ($|r| \geq 0.7$) (Olea and others 2010) were removed by omitting the correlate with the lowest PC or PI to the watershed model. Model robustness was evaluated by the area under the recovered operating characteristic curve (AUC). The AUC is the probability that a randomly chosen presence site is ranked above a random background site, with a random ranking having AUC of 0.5 and the best possible AUC being 1.0 (Phillips and others 2006). For the 11 watersheds analyzed, AUC reports good model performance, ranging from 0.93 to 0.99. Ultimately, confirmed

Table 2. Vesicular Stomatitis-Positive Premises: Distance from Flowing Water by Hydrologic Region and Month in the USA, 2004–2016 (*n* = 1,550 incidents)

Hydrologic region	Incidence within 1 km of stream Count	Total incidents Count	Percent %	Mean distance Meters	Maximum distance Meters	Minimum distance Meters
Lower Missouri	360	611	59%	1192	14,141	2
Upper Missouri	135	166	81%	790	18,370	8
Arkansas	96	132	73%	841	5046	4
Texas	58	70	83%	998	25,132	43
Rio Grande	129	170	76%	738	5371	12
Upper Colorado	296	341	87%	505	3153	1
Lower Colorado	39	47	83%	610	2855	10
Great Basin	8	13	62%	1300	6665	36
Total	1121	1550	72%			

Month	Incidents within 1 km of river Count	Total incidents Count	Percent %	mean distance Meters	maximum distance Meters	minimum distance Meters
April	15	17	88%	525	2678	10
May	30	46	65%	1636	24,600	25
June	39	66	59%	1156	7634	16
July	292	381	77%	718	6665	6
August	383	532	72%	847	9209	1
September	166	238	70%	997	7943	1
October	142	199	71%	920	8695	4
November	39	59	66%	1843	18,370	4
December	3	8	38%	2141	6508	186
January	2	3	67%	4807	14,141	62
February	1	1	–	110	–	–
March	0	0	–	–	–	–
Total	1112	1550	72%			

Total incidents within 1 km of river differs because hydrologic region calculations were based upon mean annual streamflow, whereas monthly calculations were based on monthly long-term streamflow.

premises–habitat associations on a watershed basis provide an analysis of factors important in describing VS occurrence. This analysis allows us to estimate factors important in all watersheds as well as those factors specific to certain watersheds to better understand VS-habitat conditions by hydrologic region.

Results

Objective 1: VSV Incident Distance from Stream Network

Between 2004 and 2016, only 17 of 1550 total confirmed infected premises were reported in April; however, this month had the highest percentage (88%) of incidents that occurred within 1 km (mean—525 m) of flowing water. April VS incidents generally occurred in years following a year with VSV outbreak, suggesting emergence following overwintering (Perez and others 2010), and these VS incidents generally occurred in the southern part of the western USA. VS incidents reported remained low through June, but peaked in July and August, with greater than 50% of the total incidents occurring in these 2 months (Table 2).

Overall, 72% of the VS-confirmed premises (*n* = 1,112) occurred within 1 km of a flowing stream, with only 19 incidents (1.2% of total) occurring beyond 5 km. Of the seven major 2-digit hydrologic regions containing VS-infected premises, nearly 40% of the total premises occurred in the Lower Missouri, which drains the South Platte (512 premises), Big Horn (101 premises), North Platte (94 premises) and Upper Yellowstone (41 premises) HUC-4 regions. Although the Lower Missouri had the highest total of VS-confirmed premises, this watershed had the lowest percent of premises (5%) within 1 km of flowing water,

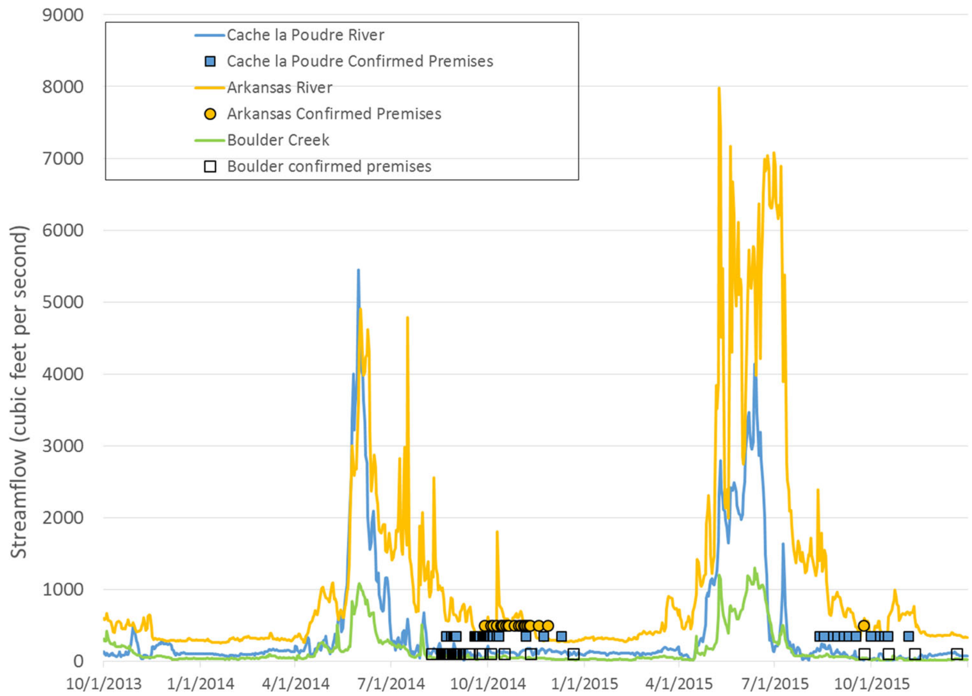


Figure 3. Streamflow, VS incidence of confirmed premises for the Cache la Poudre River, Larimer County, Colorado (USGS gauge number 6752260), Arkansas River near Avondale, Pueblo County, Colorado (USGS gauge number 7109500) and Boulder Creek, Boulder County, Colorado (USGS gauge number 6730200).

resulting in a high mean distance of VS incident occurrence from water (1.2 km). The Upper Colorado Basin watershed contained the second most total VS incidents (n = 341; 22%), but the largest percentage (87%) of VS incidents that occurred within 1 km of a flowing stream, causing in a low mean distance (0.5 km) from VS-infected premises to flowing water.

Objective 2: Incidence Relative to Streamflow Conditions

All first incidents of VS-confirmed infection of a premises (n = 35) occurred following peak annual streamflow, with 89% (31 of 35) of these occurring after streams returned to baseflow conditions (Figure 3). Figure 3 depicts incidents occurring following peak streamflow conditions during an isolated time window (2013–2015); however, this pattern was consistent during other time windows. Two-thirds of the streams near VS-infected premises exhibited a rapid return to baseflow conditions within 2 weeks of peak flow. The range of days from baseflow onset to the date of first VS-confirmed premises spanned from 62 days prior to baseflow to 165 days following baseflow onset across all stream/year combinations. However, VS-confirmed premises in 19 of the 35 stream/year combinations occurred between 31 and 90 days of return to baseflow conditions.

Objective 3: Ecological Niche Modeling by Watershed

In nine of the 11 watersheds, the highest model PC (31–71%) represented either higher-than-average long-term mean temperature or lower-than-average long-term mean precipitation at infected premises as compared to background conditions across the watersheds (Table 3). Horse density occurred most often (six of 11 watersheds) in watershed models, but represented a relatively low PC (9–29%) compared with other variables. Each of the 11 watersheds had unique variables associated with confirmed VS-infected premises. But only the Upper Arkansas watershed (average horse density; PC of 29%) and the San Juan watershed (average water content, AWC; PC of 27%) had variables other than temperature or precipitation as the variable of highest PC to the overall model.

Watersheds west of the continental divide (Lower Green and San Juan) had models associated with a higher AWC PC (24–27%), whereas the models for watersheds east of the continental divide had a lower AWC PC (16%), but on both sides of the continental divide VS-infected premises were

Table 3. Maxent Results by Subwatershed Percent Contribution (Permutation Importance)

Watershed name	Upper Yellowstone	Big Horn	North Platte	South Platte	Upper Arkansas	Texas	Rio Grande	Colorado Headwaters	Gunnison	Lower Green	San Juan	Total
HUC-4	1007	1008	1018	1019	1102	1209	1302	1401	1402	1406	1408	Of 11
Premises	41	101	94	512	127	49	115	61	77	89	51	
AUC	0.99	0.98	0.96	0.93	0.96	0.99	0.97	0.93	0.95	0.96	0.94	
Median elevation	1591	1695	1877	1592	1633	536	2092	2600	2690	1941	1925	
Available water content		16 (6)								24 (7)	27 (32)	3
EDDI winter[1]							10 (6)				13 (15)	2
EDDI summer[1]	12 (11)				11 (15)			5 (12)			5 (16)	4
EDDI spring[1]											9 (16)	1
EDDI fall[1]						12 (5)						1
Average horse density				10 (8)	29 (16)	22 (1)	9 (11)		10 (4)		10 (3)	6
Soil moisture winter					9 (14)							1
NDVI winter[2]					17 (18)						5 (10)	2
NDVI summer[2]								13 (20)	17 (25)		24 (7)	3
NDVI spring[2]			14 (13)				20 (26)	12 (3)				3
NDVI fall[2]		17 (16)		28 (35)						30 (37)		3
Precipitation winter[3]										37 (11)		1
Precipitation summer[3]		33 (23)	13 (34)	33 (12)			42 (45)					4
Precipitation spring[3]			23 (8)		15 (15)							2
Precipitation fall[3]										6 (42)		1
Maximum temp winter[4]	71 (81)	9 (20)		19 (26)	14 (19)				53 (52)			5
Maximum temp summer[4]						56 (87)						1
Maximum temp spring[4]								61 (62)				1
Minimum temp winter[5]		18 (30)										1
Minimum temp spring[5]			31 (39)									1

[1]30-year evaporative demand drought index; [2]30-year normalized difference vegetation index; [3]30-year mean precipitation; [4]30-year mean maximum temperature; [5]30-year mean minimum temperature. Seasons defined as winter (December, January, February), spring (March, April, May), summer (June, July, August) and fall (September, October, November).

Table 4. Mean and Standard Deviation for Background and VSV Associated Environmental Variables by Watershed

HUC Watershed name	1007 Upper Yellowstone	1008 Big Horn	1018 North Platte	1019 South Platte	1102 Upper Arkansas	1209 Texas	1302 Rio Grande	1401 Colorado Headwaters	1402 Gunnison	1406 Lower Green	1408 San Juan
Available water content background		9.3 (5.0)								8.3 (6.3)	8.7 (6.9)
Available water content VSV		12.3 (1.9)								12.2 (2.6)	19.4 (24.0)
EDDI[1] winter background							0.06 (0.12)				− 0.06 (0.08)
EDDI[1] winter VSV							− 0.02 (0.09)				− 0.10 (0.07)
EDDI[1] summer background	0.18 (0.05)				0.20 (0.12)			− 0.13 (0.09)			0.05 (0.08)
EDDI[1] summer VSV	0.23 (0.02)				0.14 (0.07)			− 0.16 (0.03)			0.009 (0.06)
EDDI[1] spring background											0.24 (0.11)
EDDI[1] spring VSV											0.15 (0.11)
EDDI[1] fall background						0.34 (0.09)					
EDDI[1] fall VSV						0.46 (0.02)					
Average horse density background				0.68 (0.52)	0.36 (0.3)	0.45 (0.37)	0.22 (0.18)		0.42 (0.43)		0.35 (0.25)
Average horse density VSV				1.1 (0.45)	0.67 (0.28)	1.37 (0.25)	0.46 (0.30)		0.98 (0.43)		0.57 (0.35)
Winter soil moisture background					42.9 (8.1)						
Winter soil moisture VSV					44.4 (7.2)						
Winter NDVI[2] background					0.21 (0.08)						0.18 (0.07)
Winter NDVI[2] VSV					0.23 (0.07)						0.21 (0.04)
Summer NDVI[2] background								0.54 (0.15)	0.52 (0.16)		0.28 (0.16)
Summer NDVI[2] VSV								0.46 (0.11)	0.46 (0.09)		0.41 (0.15)
Spring NDVI[2] background			0.27 (0.06)				0.24 (0.10)	0.27 (0.09)			
Spring NDVI[2] VSV			0.30 (0.04)				0.26 (0.07)	0.36 (0.07)			
Fall NDVI[2] background		0.25 (0.09)		0.35 (0.09)						0.28 (0.11)	
Fall NDVI[2] VSV		0.29 (0.08)		0.40 (0.05)						0.35 (0.09)	
Winter precipitation[3] background										29.7 (22.1)	
Winter precipitation[3] VSV										13.3 (3.5)	
Summer precipitation[3] background		33.2 (11.2)	42.8 (13.7)	57.8 (8.8)			47.0 (12.8)				
Summer precipitation[3] VSV		21.0 (4.2)	44.0 (10.7)	46.7 (9.1)			35.9 (7.6)				
Spring precipitation[3] background			45.9 (15.5)		40.2 (11.7)						
Spring precipitation[3] VSV			42.1 (4.2)		36.0 (8.4)						
Fall precipitation[3] background										36.3 (16.5)	
Fall precipitation[3] VSV										24.0 (3.5)	

Table 4. continued

HUC Watershed name	1007 Upper Yellowstone	1008 Big Horn	1018 North Platte	1019 South Platte	1102 Upper Arkansas	1209 Texas	1302 Rio Grande	1401 Colorado Headwaters	1402 Gunnison	1406 Lower Green	1408 San Juan
Winter Tmax[4] background	0.60 (3.15)	0.84 (2.4)		4.7 (2.5)	6.7 (2.97)				1.3 (2.6)		
Winter Tmax[4] VSV	3.9 (0.18)	1.6 (0.6)		6.5 (1.0)	8.1 (1.6)				5.0 (0.91)		
Summer Tmax[4] background						34.0 (0.6)					
Summer Tmax[4] VSV						34.8 (0.05)					
Spring Tmax[4] background								10.8 (4.0)			
Spring Tmax[4] VSV								17.3 (2.8)			
Winter Tmin[5] background		− 11.6 (1.6)									
Winter Tmin[5] VSV		− 12.7 (0.7)									
Spring Tmin[5] background			− 1.8 (2.0)								
Spring Tmin[5] VSV			− 0.42 (0.93)								

[1]30-year evaporative demand drought index; [2]30-year normalized difference vegetation index; [3]30-year mean precipitation; [4]30-year mean maximum temperature; [5]30-year mean minimum temperature.

associated with higher AWC than background conditions (Table 3). AWC was selected to represent soils where water may pool supporting vectors favoring moist, standing water habitat. VS-infected premises were associated with higher AWC than background conditions in the three watersheds where AWC contributed to the habitat model indicating that slightly wetter soils were associated with VS-confirmed premises (Table 4).

Results indicate that EDDI contributes to six of 11 watershed models, but in varying seasons and with relatively low PC (5–13%). 30-year mean summer EDDI appears the most frequently with four of 11 watershed models including this factor (PC = 5–12%). Most of the watershed models (three of four) indicating long-term summer EDDI associated with VSV-infected premises were typically wetter areas, based on the 30-year average, as compared to background conditions.

In addition to AWC and EDDI, the hydrologic factors important in habitat models were precipitation and soil moisture. Mean 30-year seasonal precipitation values appeared in six of the 11 watershed models, most often in the summer. For the six watersheds, VS-infected premises were often associated with mean 30-year precipitation at least 10 mm less than background seasonal precipitation within the watershed (Table 4). Seasonal precipitation comprised more than 30% PC for the Lower Green River (37%, winter), Rio Grande (42%, summer), South Platte (33%, summer) and Big Horn (33%, summer) watersheds. Soil moisture was included only the Upper Arkansas watershed, with a 9% PC to the overall model. VS-infected premises in the Upper Arkansas watershed were associated with wetter winter soils.

NDVI was an important variable in nine of the 11 watershed models (Texas and Upper Yellowstone were the exceptions) with varying seasons important for each watershed (Table 4). NDVI values associated with VS were typically higher than background NDVI values and no single season stood out as the most important across most watersheds. In the highest median elevation basins (Colorado Headwaters and Gunnison) summer NDVI associated with VSV-infected premises was lower than background conditions. NDVI PC ranged from 5 to 30%, with highest contributions for the Rio Grande (20%, spring), South Platte (28%, autumn) and the Lower Green (30%, autumn) watersheds.

Temperature contributed to habitat models of eight of 11 watersheds with higher mean 30-year temperatures within each watershed typically associated with more VS-infected premises. Warmer-than-average winter daytime temperatures were important in five watersheds (Upper Yellowstone, Big Horn, South Platte, Upper Arkansas and Gunnison), with the PC ranging from 14% (Upper Arkansas) to 71% (Upper Yellowstone).

Discussion

Previous studies have suggested that incidence of VS in the Western USA occurs in proximity to flowing water and that this might be related to favorable habitat for black flies (*Simulium* spp.), known biological vectors for VSV. The objectives of this study were to analyze the proximity of VS-infected premises to flowing water, the VS timing related to streamflow conditions and ecological niche by watershed.

VSV incidents were spatially and temporally related to the stream network with most incidents occurring near flowing water and during baseflow conditions. The findings of this study show that more than 72% of VS-infected premises were within 1 km of lotic habitat and that most infections occur during a specific phase of the hydrologic cycle, indicating a likely relationship between streamflow conditions, vector lifecycles and VS infection. Moreover, habitat niche modeling supports the importance of a viable host population, specific hydrologic conditions and greenness characteristics related to the prevalence of VS incidents in the western USA.

We found first incidents occurring after peak streamflow and generally during baseflow conditions. Streamflow can impact the numbers of surviving larva because floods affect different species in different ways, impacting larval distribution and cross-seasonal survival. A given species may adapt to survive but optimal (blood feeding) gonadotrophic cycles, and disease transmission may only occur under very specific environmental conditions. This is especially true where environmental conditions can vary from season to season and year to year. This has been demonstrated in several black fly populations in different global geographic regions where there are known climatic ecological variations in vectorial capacity and diseases prevalence in Africa and South America. (Cross and others 2011; Docile and others 2015; Figueiro and others 2014; Millest and others 1999; Opara and Fagbemi 2005; Pachon and Walton 2011; Ya'cob and others 2016a, b; Zarroug and others 2014, 2016). It is likely that regional subpopulations of a given *Simulium* species vary with respect to vector competence for VSV transmission. With many vector-borne diseases, the number of infected insects is very low and increasing vector population density and fluctuations in the age distribution of the vector population may have a paradoxical, negative impact on the actual vectorial capacity as reviewed by Black and Moore (2005). Although the specific causes are unknown, regional and temporal variances in vectorial capacity have been observed in multiple species of black flies (as referenced above). Prior research indicated peak black fly emergence occurs early in the spring, with *Simulium vittatum* adults being among the first black flies to emerge as streams return to baseflow and water temperatures begin to increase (Abdelnur 1968). In the regions of VSV emergence, there are likely five to seven populations spikes (emergence cycle cohorts) in a typical year (Jessen 1977). It is known that later season females are refractory to VSV infection and are therefore less likely to transmit infection (Howerth and others 2002). Sand fly and midge larval development and adult emergence are far less synchronized than black flies. In general, as temperatures increase and moisture and nutrients (blood meals and wildflower nectar) are available, reproductive activity and efficiency increase. Cold weather, such as the first hard frost, generally brings a halt to species activity.

The general association of black fly emergence following streamflow decline is based on stream dynamics that affect larval feeding efficiency and lower dispersion, with slower water being better (Adler and others 2010). Water temperature is also important, and a thermal constant has been calculated for some species of black flies (Adler and others 2010; Bernotiene and Bartkeviciene 2013; Brannin and others 2014; Cheke 1995, 2012; Cid and others 2016; Hadi and Takaoka 1995; Ivkovic and others 2014; Thomson and others 2004). For black flies, the distance between lotic habitat and feeding sites is important. Travel to teneral feeding sites, blood meal sources and oviposition sites are limited and generally less than 8 km. The usual flight distances are less than 5 km under still conditions (Adler and others 2010).

The observation that all first incidents of infected premises that occurred follow peak annual streamflow may prove helpful in disease management and future research by limiting the anticipated time of year when VS infection may occur on a local basis. For example, local streamflow conditions could be monitored via existing networks (that is, USGS NWIS) to identify peak streamflow prior to surveying for common VS vectors or infected animals. Although helpful in narrowing the anticipated infection window, other environmental factors, beyond peak flow timing, appear important in anticipating VS infection.

VSV ecological niche modeling revealed that different variables were important in describing VS incidence in each watershed. Horse density was consistently important, with more animals associated with more VS-infected premises. The VS association with higher temperatures and lower precipitation may be an artifact of temperature and precipitation relationships with elevation since often mean temperatures decline and precipitation increases with increased elevation. We found that some hydrologic factors, such as AWC and EDDI, indicated VS was associated with wetter than average conditions, whereas precipitation indicated that VS was associated with drier than average long-term precipitation across the watershed. These seemingly inconsistent findings can be explained by considering which component of the hydrologic cycle the variables represent. For example, AWC represents soil water, indicating VS-infected premises are more prevalent near wet soils. Such conditions might favor midges. Midges require small patches of shallow water for successful larval development. Development of *Culicoides* spp. larvae occurs in waste-enhanced mud along the edges of standing water. Therefore, soil properties that favor holding moisture could be an important factor contributing to vector abundance. The number of vector competent females peaks in late summer and early fall (Mullens and Rodriguez 1988; Mullens 1989; Pfannenstiel and Ruder 2015). Adding to the complexity of differing VSV insect vectors (black flies, sand flies and midges) is that climatic factors impact vector efficacy and life stages in different ways. For example, low precipitation might increase vector feeding rates, whereas high moisture might favor conditions for larval vectors. Hence, changes in the sequence of climatic conditions throughout the year in relation to vector life stage and VSV infection should be considered.

The emergence of VSV in specific regions indicates that certain conditions may be necessary for VS in isolated geographic areas that are not important for other areas. For example, VS was associated with greener vegetation in nearly all watershed/season combinations. However, the high elevation basins, which contained the highest NDVI (Colorado Headwaters and Gunnison), had VS incidents associated with lower NDVI in summer. There may be an optimal greenness range, possibly linked to specific vegetation types, related to VS prevalence, and future field research to test this may be necessary. There are known examples of environmental influences on the blood-feeding and gonadotrophic cycles of the flies that affect the relative susceptibility of the flies to viral infection and to vectorial capacity. Under drier/warmer conditions fly physiology, host-seeking, biting frequency and periodicity, and reproductive efficiency may change considerably (wet dry phenotypes). Plant growth and type of riparian plant species are important factors in providing as energy sources, resting and oviposition locations for vectors (Botto and others 2005; Eyo and others 2014; Grillet and others 2005; McCall 1995; McCall and others 1998; McCall and Trees 1993; Murdock and others 2013).

Although black flies, midges, sand flies and other hematophagus insects are competent, biological or mechanical vectors of VSV (Drolet and others 2005; Mead and others 1997, 1999, 2000a, b), it is difficult to know the specific role of vectors in a given outbreak setting. The observation that outbreaks tend to occur and spread along waterways in the initial outbreak and then spread to proximal premises during expansion across the region supports the hypothesis that different vectors may be operating in different years or different times of a given emergence year (Peters and others 2017). The observed climatic associations with times of peak incidence also support the primary role of arthropod vectors in viral transmission (Hurd and others 1999; McCluskey and others 1999; Vanleeuwen and others 1995). Experimental demonstration of VSV infections in multiple insect species also supports the accepted understanding that VS is a vector-borne disease. Further, black flies are the most likely vector in many regions of the southwestern USA, but it is not clear what species of the *Simulium* genus is the dominant vector. Vector dominance may vary in different geographic regions. Midges may also play a role in transmission, in particular in the expansion across the region (Peters and others 2017). It is very likely that the emergence of VS in each specific event and geographic region is dependent on a sufficiently dense and robust population of vectors.

Although this study offers important information on the relationship between VSV infection and hydrology, other factors should be considered in future research. The impact of both stream velocity and temperature is related to streamflow and could be more directly evaluated. In addition, water quality, particularly available nutrients, may be an important factor related to vectors. Vector data were limited, leaving critical uncertainties in this analysis. A clearer understanding of the relationship between environmental conditions and assumed vectors of VSV could prove helpful in understanding and potentially minimizing VSV infection. The impact of changes in the sequence of climatic conditions throughout the year in relation to vector life stage and VSV infection should be considered.

Conclusions

In most watersheds, infected premises were associated with warmer temperatures, less precipitation, greener vegetation, wetter soils and higher animal density than the long-term background watershed. However, important exceptions, such as the lower greenness in high-mountain infected premises and drier summer EDDI in the Upper Yellowstone watershed, indicate regional differences in environmental factors that may impact VS transmission. The watershed approach to evaluating environmental variables associated with VS infection proved efficacious in that results indicated commonalities (horse density, warm temperature, lower precipitation) within watersheds that held across most watersheds, but also highlighted important differences for future investigation (that is, greenness differences).

VS incidents were spatially associated with the stream network and temporally associated with baseflow conditions. Additionally, only 11 of 45 HUC-4 watersheds had more than 40 VS-confirmed premises during the study period, indicating likely hot spots for future VS infections. These findings provide for future targeted sampling based upon streamflow, proximity to flowing water and prior highly impacted watersheds as a means of targeted surveillance research. For example, livestock managers and biologists could first select watersheds with historically high VS infection, such as the 11 HUC-4 watersheds analyzed here. They could then identify gauging stations within each watershed near areas of infected premises and monitor daily streamflow conditions on-line to identify peak streamflow and transition to the recession limb of the hydrograph. Biologists could utilize this streamflow decline to commence vector surveillance and sampling. Such investigations could establish predictive relationships between streamflow dynamics, vectors and confirmed VS premises. In turn, these relationships could support effective targeted surveillance related to both vector ecology and VS emergence and re-emergence. Livestock managers could use the return to baseflow conditions as an indicator to more diligently evaluate livestock for legions and other physical signs of VS infection. Return to baseflow conditions could also initiate management strategies such as moving animals away from flowing water or providing shelter and other actions to minimize potential infection.

Our findings demonstrate a substantial increase in the understanding of the relationship between VS-infected premises, spatial proximity to flowing water and temporal streamflow dynamics. This knowledge helps minimize some of the complexity of the environment–host interactions for this vector-borne virus with the potential to significantly affect livestock.

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