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ARTICLE
Disease Ecology

Sex and habitat drive hantavirus prevalence in marsh rice rat populations impacted by the Deepwater Horizon oil spill

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Abstract

Bayou orthohantavirus (BAYV) is one of several hantaviruses in the United States that cause hantavirus pulmonary syndrome in humans. Its host reservoir, the marsh rice rat (*Oryzomys palustris*), inhabits coastal saltmarshes of Louisiana, a region extensively impacted by anthropogenic disturbances, such as the 2010 Deepwater Horizon (DWH) oil spill. The oil spill presents an opportunity to investigate how a large-scale ecological disturbance can influence the hantavirus host–pathogen dynamic by examining BAYV presence in its reservoir host species in areas with different oiling histories. Here, we: (1) quantify BAYV prevalence in the rice rat in coastal saltmarshes of Louisiana; (2) assess whether prevalence is driven by rice rat demographics, seasonality, or association with habitat characteristics; and (3) determine whether these factors differ by marsh oiling history. We collected mark–recapture data and blood and tissue samples over 5 years (2013–2017) at oiled, unoiled, and reference sites. Testing of the samples for BAYV revealed an antibody and RNA prevalence of 13.7%. Logistic regression analysis found that prevalence varied seasonally and inter-annually, and in July of 2016 reached 30.8%. Sex (male) and increasing cover of *Sporobolus alterniflorus* and open water compared to *Juncus roemerianus* and bare ground were the strongest predictors of hantavirus prevalence. Abundance estimates derived from Huggins closed-capture models were greatest at oiled sites, but oiling treatment had no residual influence on BAYV prevalence, and abundance and prevalence were not correlated. This study supports the hypothesis that habitat is a main driver of hantavirus prevalence in the host and implies that continued and future disturbances in the region will likely impact the rice rat–BAYV dynamic by altering plant communities and landscape structure.

KEYWORDS
Bayou virus, coastal saltmarsh, Deepwater Horizon oil spill, demographics, hantavirus, Louisiana, marsh rice rat, prevalence

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INTRODUCTION

Host–pathogen interactions do not occur in isolation but, rather, within a broader ecological context, and researchers must consider community composition, landscape structure, and ecosystems in their understanding of infectious disease systems (Keesing et al., 2008; McCallum, 2008). Likewise, disturbances that impact these ecological factors should be included in assessments of host–pathogen dynamics. In 2010, the Deepwater Horizon (DWH) oil rig blowout resulted in the largest accidental marine oil spill in history (Crone & Tolstoy, 2010) and severely oiled coastal saltmarshes of the United States Gulf of Mexico (Michel et al., 2013). This included habitat occupied by the marsh rice rat (*Oryzomys palustris*), a wetland-obligate, semi-aquatic rodent, and endemic host of *Bayou orthohantavirus* (BAYV), which produces hantavirus pulmonary syndrome (HPS), an often-fatal illness, in humans (Ksiazek et al., 1997; Wolfe, 1985). This overlap of the DWH oil spill and a hantavirus host reservoir species presents a unique opportunity to investigate how a significant ecological disturbance influences a viral host–pathogen dynamic.

Human illness from viral zoonoses has emerged at an accelerated rate in recent decades, with particular concern given to the emergence of highly mutable RNA viruses (Jones et al., 2008; Rosenberg, 2015; WHO, 2007). These viruses originate from wild animal hosts and infect human populations following contact in what is commonly referred to as "spillover." Probable causes for the increased rate of zoonotic spillover are various but include reservoir host species habitat disturbance, fragmentation, and land use changes (Allan et al., 2003; Goodin et al., 2006; Plowright et al., 2011). These emerging pathogens highlight the need to include host species ecology in assessments of host–pathogen relationships to better understand and predict the circumstances leading to spillover events and how anthropogenic disturbances may influence them (Keesing et al., 2008). Zoonoses of importance include many RNA viruses (Rosenberg, 2015), such as West Nile virus, Ebolavirus, severe acute respiratory syndrome coronaviruses (including the current COVID-19 outbreak), avian influenza viruses, and hantaviruses.

Hantaviridae are a worldwide group of negative-sense, single-stranded RNA viruses (Jonsson et al., 2010). In human disease, the genus of hantaviruses (*Orthohantavirus*) associated with illness is exclusively carried by rodents and is likely transmitted through inhalation of contaminated rodent excreta (Armstrong et al., 1995). Infection in the reservoir host is chronic (lifelong) with no clinical manifestation of disease, and each strain is highly specific to its host (Jonsson et al., 2010). *Bayou orthohantavirus* is one of three North American hantaviruses that cause HPS in humans, a disease that has a case fatality rate of ~40% (Lednicky, 2003). Its endemic host is the semi-aquatic marsh rice rat (*O. palustris*; the subject of this study), which ranges across the eastern United States (Reid, 2006; Torrez-Martinez et al., 1998). The large majority of HPS cases in North America are due to *Sin nombre orthohantavirus* (SNV) carried by *Peromyscus maniculatus* and *P. leucopus* (Childs et al., 1994; Knust & Rollin, 2013), but HPS cases and fatalities attributable to BAYV have been documented in Texas and Louisiana (Khan et al., 1995; Morzunov et al., 1995; Torrez-Martinez et al., 1998).

The hantavirus host–pathogen dynamic is largely driven by multiple, and often interacting, ecological factors, such as seasonality (Abbott et al., 1999; McIntyre et al., 2005), climate (Kallio et al., 2006), resource availability (Tersago et al., 2009), small mammal community composition (Suzán et al., 2009), habitat/vegetation characteristics (Abbott et al., 1999; Camp et al., 2021), landscape structure (Goodin et al., 2006; Langlois et al., 2001), and predation on small mammal hosts (Khalil et al., 2016; Orrock et al., 2011). These ecological factors can influence host species' inter- and intraspecific competition (Clay et al., 2009; Langlois et al., 2001), movements (Amman et al., 2013; Douglass et al., 2006; Owen et al., 2010), population dynamics and demographic structure (Abbott et al., 1999; McIntyre et al., 2005; Voutilainen et al., 2012), and the stability of the virus in the environment (Kallio et al., 2006), which subsequently influences contact rates and transmission efficiency. However, hantaviruses have complex spatiotemporal dynamics that cannot be easily generalized across different host species, and the significance and directionality of the relationship between environmental variables and hantavirus prevalence depends on the unique ecology of the host species (Khalil et al., 2014; Tian & Stenseth, 2019). Likewise, it can be difficult to predict how anthropogenic disturbances will influence that relationship.

The marsh rice rat (rice rat, hereafter) occupies the coastal saltmarshes of Louisiana, one of the most threatened ecosystems in the United States due to ever-accelerating land loss (Kennish, 2001) and the accidental release of oil from drilling operations in the Gulf of Mexico (Rangoonwala et al., 2016). In 2010, the DWH released an unprecedented ~4.4 million barrels of crude oil into the Gulf of Mexico (Crone & Tolstoy, 2010; Rabalais & Turner, 2016; Silliman et al., 2012). Louisiana coastal saltmarshes were heavily impacted by the spill (Michel et al., 2013), and oiling extended into the interior of the marsh (Ramsey et al., 2014). Terrestrial species living in these nearshore environments experienced acute exposure to freshly spilled oil (USFWS, 2011), chronic exposure to periodically resuspended oil deposits (Perez-Umphrey et al., 2018; Turner et al., 2014), significant habitat disturbance in the form of vegetation loss and subsequent erosion (Hester et al., 2016; McClenachan et al., 2013), and food

web alterations caused by changes in prey availability (Bam, 2015; Husseneder et al., 2016; Moyo et al., 2021; Zengel et al., 2016; but see Olin et al., 2017).

Consequently, environmental damages may influence BAYV prevalence by impacting rice rat population dynamics, movements, and resource availability (Holsomback et al., 2013; McIntyre et al., 2005). Unlike deer mice, rice rats are not peridomestic (Ksiazek et al., 1997), which significantly reduces the risk of viral spillover into human populations. However, as saltmarshes are lost, rice rats might seek habitat nearer to human habitation and compete for remnants of habitat and the risk of BAYV spillover may increase (Holsomback et al., 2013). Our objectives were to: (1) quantify BAYV prevalence in coastal saltmarshes of Louisiana; (2) assess whether BAYV prevalence is driven by rice rat demographics, seasonality, and association with specific habitat characteristics; and (3) determine whether these factors differ depending on historical oiling of the different sites.

METHODS

Field data collection

Rice rats were trapped at nine sites located in Plaquemines Parish, LA (Figure 1), all of which were only accessible by boat. Seven of these were west of the Mississippi River in Barataria Bay and were designated as "oiled" ($n = 4$) or "unoiled" ($n = 3$) using NOAA's Shoreline Cleanup Assessment Technique (SCAT) (NOAA, 2013; Santner et al., 2011). Two "reference" sites were located on the eastern side of the river (see also Perez-Umphrey et al., 2018), where oil from the DWH spill did not come ashore. One grid per site was established, and two sampling sessions of three consecutive trap nights were conducted per year, the first from 28 March to 31 May and the second from 1 June to 2 July, a time period that captures peak rice rat reproductive activity (Wolfe, 1985). A minimum of 30 days passed between the end of the first trapping session and the beginning of the second at that same site. Sites were trapped in the same order (O6; O4 and U1; O3 and U4; U2 and O2; D1 and D2) in both sessions, except for in 2017 when O3 was trapped last due to weather. A pilot study began in 2013, and rice rat trapping continued from 2014 to 2017. Mark–recapture datasets were considered complete when three consecutive trapping days occurred during a session. Not all sites had complete BAYV prevalence (see Appendix S1: Table S1) and mark–recapture (Appendix S1: Table S2) datasets for both sessions in every year.

Rice rats were trapped using Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, FL) baited with oatmeal–peanut butter balls and set in 30 m × 130 m grids. Grids consisted of 3 rows of 14 traps placed 10 m apart, for a total of 42 traps. Each row was separated by 15 m. Trapping grids were set along the shoreline, and traps were placed on a Styrofoam float with a hole to accommodate a pin flag, which allowed the trap assembly to float with the tide. Grid and trap locations were kept consistent across years and trapping sessions, with some adjustments due to shoreline erosion. Rice rats were weighed to the nearest gram with a Pesola scale and aged by weight class based on the criteria outlined in Wolfe (1982, 1985) with some modifications: juvenile <30 g; subadult 30–44 g; and adult ≥45 g. Sex was determined by anogenital distance and the presence/absence of primary sexual characteristics. Untagged individuals received either 1 cm ear tags (National Band and Tag, Co., Newport, KY) or, if the animal weighed over 30 g, a 12.5 mm PIT tag (Biomark, Inc., Boise, ID). The tagging method changed over the course of the study in an effort to minimize tag loss: In 2013, only the right ear was tagged; from 2014 to 2016, both ears were tagged; and in 2017, animals received either two ear tags or a PIT tag implanted between the shoulder blades. Blood was collected from the retro-orbital venous complex of all animals over 30 g (either subadults or adults), and rice rats were anesthetized with isoflurane prior to drawing blood. A subset of rice rats >30 g was collected on the final day of the second trapping session (up to $n = 48$ total per season across all sites). Rice rats were euthanized with isoflurane, then decapitated. All tissues and whole blood samples were flash-frozen in liquid nitrogen and later stored at −80°C.

Bayou virus infection screening

Blood and tissue samples were screened for BAYV antibodies and RNA, respectively. A total of $n = 314$ blood samples (serum, $n = 293$; whole blood, $n = 21$) collected over the course of the study were screened. Only blood was screened for individuals captured in session 1 ($n = 148$), whereas both blood and tissue were screened for rice rats captured and dissected in session 2 ($n = 166$).

Immunofluorescent assays

Blood samples were screened for the presence of BAYV antibodies (Ab) by indirect immunofluorescent antibody (IFA) assays, following Chu et al. (2003). Briefly, antigen slides were prepared with Vero E6 cells infected with Andes virus on which samples were incubated with FITC-labeled anti-mouse IgG secondary antibody (Kirkegaard and Perry Laboratories, Inc., Gaithersburg,

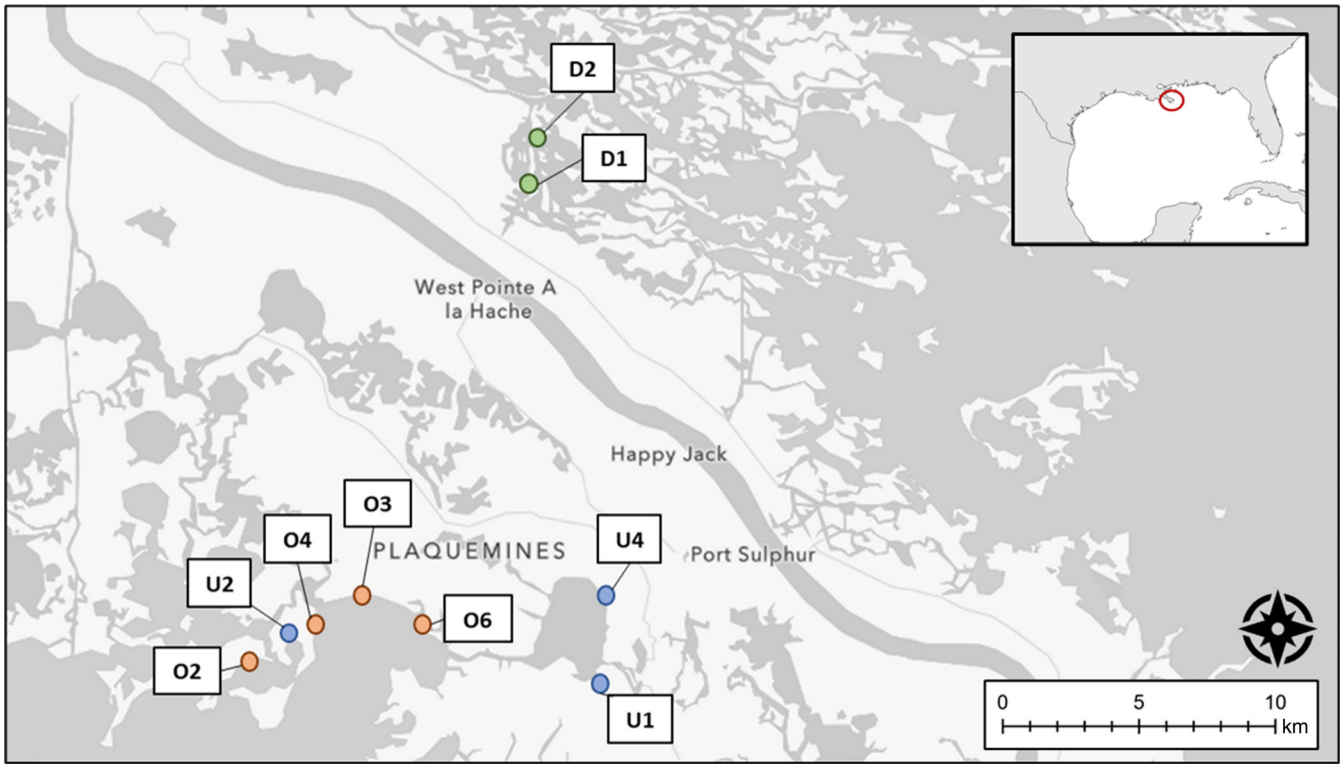


FIGURE 1 Map of study area. Field sites are shown in their respective bays within Plaquemines Parish, LA. Oiled ("O"; yellow) and unoiled ("U"; blue) sites were located in Bays Jimmy, Batiste, and Sansbois, on the western side of the Mississippi River in Barataria Bay, Louisiana. Reference sites ("D"; green) were located ~13 km away on the eastern side of the Mississippi River

MD), and visualized with a Leica DM6B fluorescent microscope at Louisiana State University's Shared Instrumentation Facility. Positive samples had a characteristic punctate fluorescence in the cytoplasm visible at 10 or 20 × (Jonsson et al., 2011).

qRT-PCR

Total RNA was extracted from 5 mg of either frozen lung (n = 117; 2015–2017 samples) or kidney tissue when lung tissue was not available (n = 49; 2013–2014 samples) using a TRIzol/chloroform method (Invitrogen, Carlsbad, CA; Chu et al., 2003; Jonsson et al., 2011). Although lung tissue is the preferred organ for hantavirus screening in rodents (Ermonval et al., 2016), virus is detectable in kidney tissue (Korva et al., 2009). Tissues were homogenized in a Fisherbrand Bead Mill Homogenizer and then transferred to a Phasemaker tube (Invitrogen, Carlsbad, CA) prior to centrifugation (see Jonsson et al., 2011).

The presence of BAYV RNA was detected by quantitative reverse transcription-PCR (qRT-PCR; Jiang et al., 2014) using a *Power* SYBR Green RNA-to-CT 1-Step Kit (Thermo Fisher Scientific, Waltham, MA) on a QuantStudio 6 Flex Real-Time PCR System. Standard curves were generated using 10-fold dilutions of a pUC57 plasmid (GenWay Biotech, San Diego, CA) with a 1028-bp insert of the BAYV nucleocapsid protein sequence available in GenBank (L36929.1; Morzunov et al., 1995). Primers were designed in Geneious Prime 2018.11.1 (https://www.geneious.com) to amplify a 147 bp of the insert region (157F: 5′-CCCT CTGCTTCTGCTGTGTAAT C-3′; 303R: 5′-TGAGTGCCC TTTCCTCCCAAAG-3′), and all standards and samples were run in triplicate. Cycling conditions were those recommended by the manufacturer. Samples were considered positive if the cycle threshold was consistent across the sample triplicates and lower than 35 cycles.

Statistical analyses

Multiple datasets (mark–recapture, infection screening, and habitat characteristics) were used, although data types were not equally available across years. Data analyses were as follows: (1) prevalence versus abundance (2015—1 session; 2016 and 2017—two sessions per year); and (2) prevalence versus treatment, site-specific habitat, year, session, age, and sex (2013—1 session; and 2014–2017—two sessions per year).

Demographics

Estimates of rice rat abundance (N) were derived from Huggins closed-capture models (Huggins, 1989; Otis et al., 1978) run in program MARK v 6.2 (White & Burnham, 1999) using mark–recapture datasets (https://doi.org/10.7266/n7-c7zj-xe50). In closed-capture models, the population is assumed to be geographically and demographically "closed" over a short period of time, which allows the estimation of N as a function of the probability of first capture (p) and recapture (c). Each time period (i.e., session and year) was considered separately in order to meet these assumptions of closure. Candidate model sets (Table 1) included Otis et al. (1978) models where p and c are constant (M_0), vary by time (M_t), or response to trapping (M_b). Additional candidate models were considered where parameter estimation varied by site, the three treatment groups (oiled, unoiled, and reference), and where sites were grouped by a hierarchical series of "bays" (two bays: Western and Eastern Mississippi River; three bays: Bay Batiste, Bay Sansbois, and Eastern Mississippi River; Figure 1). Corrected Akaike's information criterion (AIC_c) was used to inform model selection, and model averaging was performed for those models with a $\Delta AIC_c \leq 6$ (Appendix S1: Table S3) to derive estimates of abundance (N) (Burnham & Anderson, 2002; Richards, 2005; Symons & Mousalli, 2011).

All statistical analyses were performed in R 4.0.1 (R Core Team, 2020). Kruskal–Wallis tests were used to determine whether rice rat abundance differed by treatment type, year, or site, followed by a Dunn's post hoc test with a Bonferroni correction (*FSA* v.0.8.32; Ogle et al., 2021). The 2016 and 2017 datasets were used to assess whether the number of captured individuals in each age class changed between the first and second sessions (Pearson's chi-squared test). A one-tailed Wilcoxon signed-rank exact test (*exactRankTests*, v.0.8.32; Hothorn & Hornick, 2021) was used to determine whether rice rat abundance (N) differed between sessions (2016, 2017), and an exact binomial test was used to assess whether the sex ratio was even.

TABLE 1 Candidate model set

Model number	Candidate models
1	M_0
2	M_t
3	M_b
4	$g \times M_0$
5	Treat $\times M_0$
6	2bay $\times M_0$
7	3bay $\times M_0$

Note: Huggins closed-capture models were those described by Otis et al. (1978): where capture probabilities are constant (M_0; $p(.) = c(.)$), vary by trapping day (M_t; $p(t) = c(t)$), or where capture and recapture probabilities differ (M_b; $p(.)$, $c(.)$). Additionally, models were considered where capture probabilities varied by site (g), treatment "Treat," Eastern v. Western Mississippi River "2bay," or between Bay Batiste, Bay Sansbois, and the Eastern Mississippi River "3bay."

Habitat data

Site-level vegetation data were collected as part of another, concurrent study (Hart et al., 2021); GoMRI https://doi.org/10.7266/n7-w5g6-e664). Ground cover was quantified for a 5 m radius around randomly selected points ($n = 200$; total). Seven mutually exclusive categories were used to describe ground cover: percent cover of saltgrass (*Distichlis spicata*), black needlerush (*Juncus roemerianus*), saltmarsh cordgrass (*Sporobolus alterniflorus*, formerly *Spartina alterniflora*), bare ground, detritus, water, and other vegetation. "Water" did not indicate bay water, but rather ponds in the interior of the marsh. "Other vegetation" included woody vegetation and freshwater plants. Because data points were selected randomly, direct comparisons of ground cover composition over time were not possible and data were compiled across all years to derive a broad description of the habitat characteristics of each site. A principal component analysis (PCA) was first used to evaluate structure in ground cover characteristics (*ggbiplot*; Vu, 2011). Based on the results of the PCA (Figure 2) and Hart et al. (2021), which found substantial overlap in PCA space for vegetation $\times$ treatment, it was more informative to investigate the site-specific relationship between ground cover characteristics and prevalence rather than group data points by treatment. The mean plot scores of PC1 and PC2 (Fischer et al., 2018; Kitagawa et al., 2020) for each site were used in analyses (described below) to evaluate whether prevalence was related to a site's ground cover characteristics.

Bayou virus prevalence

Data were excluded from analyses if IFA and/or qRT-PCR results for an individual were inconclusive ($n = 7$), resulting in a total of 307 screened individuals. Logistic regressions were used to model BAYV prevalence as a function of experimental and demographic factors. Logistic regressions are appropriate for proportional data (e.g., prevalence) when a binomial, rather than a Bernoulli, distribution is used, which allows for multiple binary

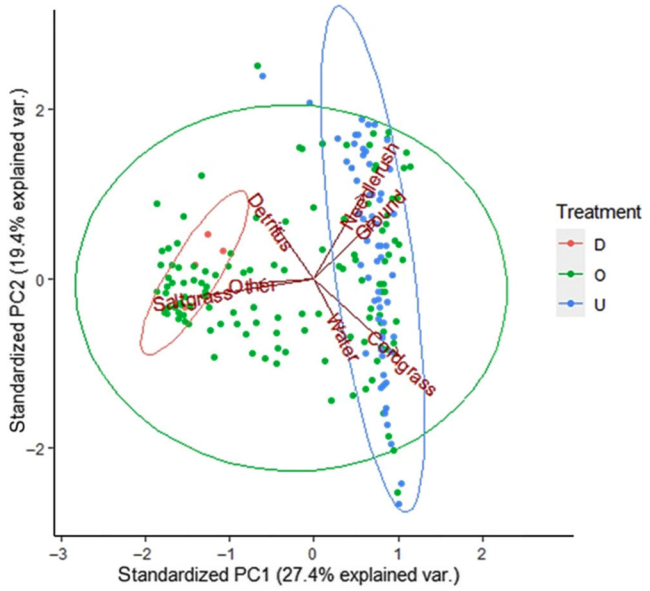


FIGURE 2 PCA of ground cover characteristics. Ground cover characteristics: saltgrass (*Distichlis spicata*), black needlerush (*Juncus roemerianus*), saltmarsh cordgrass (*Sporobolus alterniflorus*), bare ground, detritus, water, and other vegetation, with 95% CI ellipses projected for each treatment across all years. Treatment types are denoted as "D" (reference), "O" (oiled), and "U" (unoiled)

responses per independent variable (Crawley, 2013; King & Zeng, 2001; Warton & Hui, 2011). First, for those years/sessions where data were available (2015—session 1; 2016/2017—sessions 1 and 2), we tested whether estimates of rice rat abundance (N) were a significant predictor of BAYV prevalence (family = quasibinomial). Because it was not statistically significant ($\alpha = 0.05$; odds ratio: 1.01 [0.99–1.03]; $p = 0.387$), N was excluded from further analyses. Then, a second model was used to predict BAYV prevalence as a function of age, sex, treatment, session, year, and mean plot scores of PC1 and PC2 of ground cover characteristics at each site (family = quasibinomial). A quasibinomial distribution was used in this model to account for overdispersion in the dataset due to the large number of Ab/RNA-negative individuals. Saturated and simplified models were compared using F tests to test the statistical significance of each factor (Crawley, 2013). All models were weighted by sample sizes (King & Zeng, 2001).

RESULTS

Over 5 years of trapping and 8904 trap nights, 1031 individual rice rats were caught over 2087 capture events. No species besides *O. palustris* was captured during our entire 5-year trapping effort. Three rice rats, all male, survived and were captured across subsequent years: one individual from 2014 to 2015 and two individuals from 2016 to 2017. No individual was caught in more than 2 years. One of these three rice rats was screened and was negative for BAYV. Two of the rice rats remained at the same site across years; however, one changed sites between field seasons (2014 and 2015) and moved ~1.24 km (from U2 to O4; Figure 1).

Best-supported Huggins closed-capture models were consistently those where capture and recapture probabilities varied, and where capture probabilities varied by trap day (Appendix S1: Table S3). Recapture probabilities were consistently higher than initial capture probabilities (M_b models), and capture probabilities also increased with each trap day (M_t models). Together, these indicated a general "trap happy" response by the rice rats (Appendix S1: Table S5). However, in 2017, top models also included those where capture probabilities varied by treatment type and bay (Appendix S1: Table S3). Kruskal–Wallis tests of derived abundance estimates demonstrated a statistically significant effect of site ($H = 23.44$; df = 8; $p = 0.0028$) and treatment ($H = 13.56$; df = 2; $p = 0.0011$), but not year ($H = 1.47$; df = 2; $p = 0.480$). Post hoc Dunn's tests revealed that rice rat abundance was significantly lower at site D1 relative to sites O2 ($z = -3.31$; $p = 0.033$) and O3 ($z = -3.62$; $p = 0.010$). Abundance was greater at oiled sites relative to reference sites ($z = 3.61$, $p = 0.0009$) but not unoiled ones ($z = 2.06$; $p = 0.118$). Reference and unoiled sites also did not differ from each other ($z = -1.72$, $p = 0.258$).

Rice rat abundance was significantly higher in the second session ($V = 114$, $p = 0.0398$; one-sided; Figure 3), an increase driven by the appearance of a significantly greater number of juveniles relative to those in other age classes ($\chi^2 = 8.83$; df = 1; $p = 0.0030$). There was no change in the male-to-female ratio of reproductive-age (subadult and adult) captures across sessions ($\chi^2 = 2.18$; df = 1; $p = 0.140$); however, an exact binomial test indicated that overall, the proportion of males (0.63) was greater than the expected value of 0.5 ($p < 0.0001$; two-sided).

Of the 307 individuals screened by IFA and/or qRT-PCR, 42 were BAYV-positive, for an overall prevalence of 13.7% (Appendix S1: Table S4). For rice rats that were screened by both IFA and qRT-PCR, 10 of 28 seropositive individuals had no detectable BAYV RNA. Seventeen rice rats were positive for BAYV RNA, of which all but one was also seropositive. Prevalence was significantly greater in males (odds ratio: 4.83 [3.99–5.67]; $p < 0.0001$), which represented 83.3% of infected individuals (35/42). Age was not a statistically significant predictor ($p = 0.470$), although prevalence was more than twice as high in adult males (30/144; 20.8%) than in subadult males (5/51;

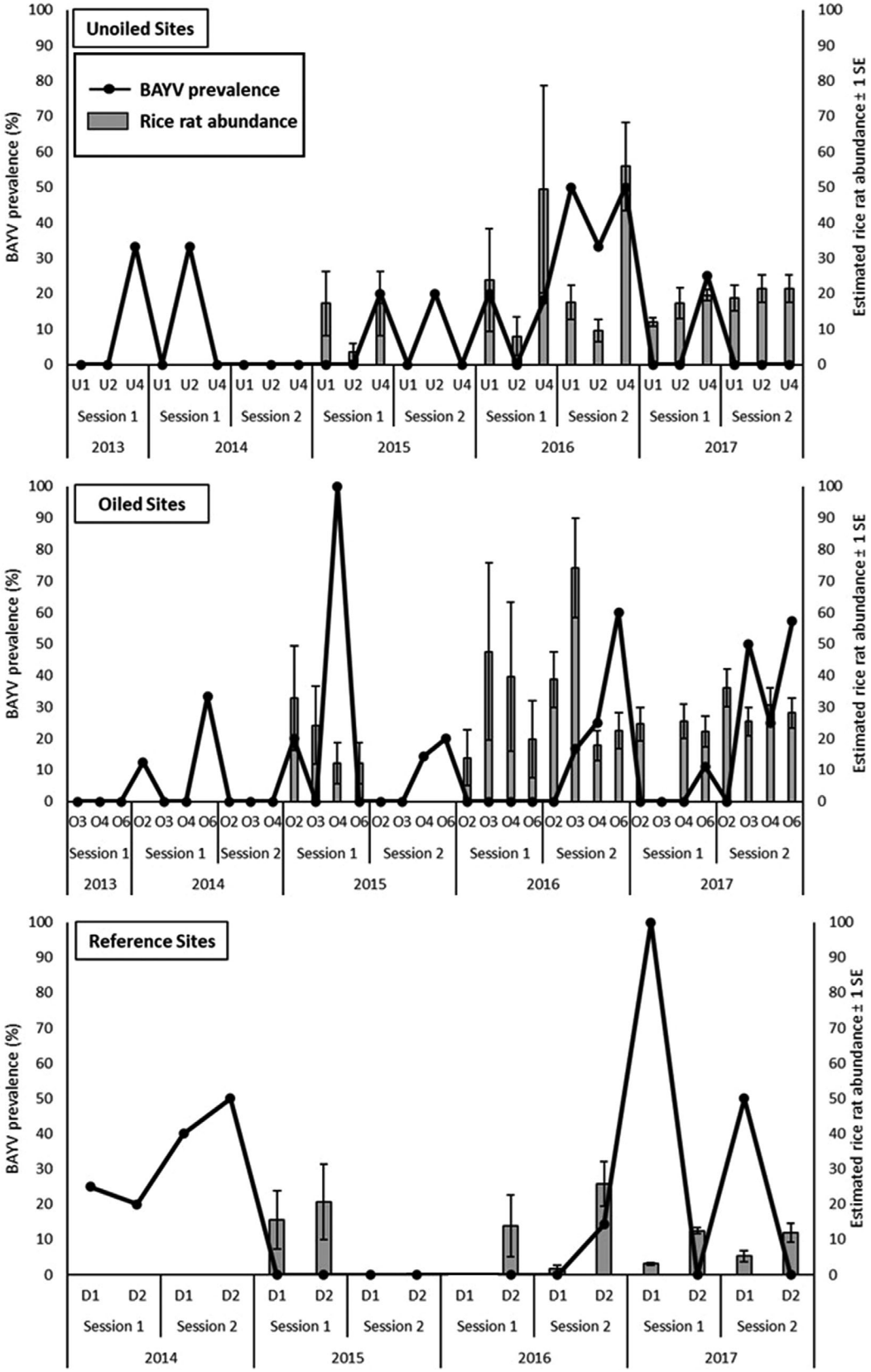


FIGURE 3 Estimated abundance and prevalence. Rice rat abundance estimates (±1 SE) derived from closed-capture models in program MARK (bars) and BAYV prevalence (lines) at unoiled (first panel), oiled (second panel), and reference (third panel) sites. Abundance estimates were available for all sites trapped in 2015 (session 1) and 2016 and 2017 (sessions 1 and 2), except for site O3 (2017, session 1)

9.8%). For females, 6.5% (5/77) of adults and 5.7% (2/35) of subadults were infected. Prevalence varied among years, with the lowest total percentage in 2013 (7.1%) and the highest in 2016 (19%; 7.5% in session 1 and 30.8% in session 2). Across all years, prevalence was highest at site O6 (27.03%) and lowest at O2 (5.26%). However, neither year ($p = 0.092$), session ($p = 0.211$), nor oiling status ($p = 0.192$) were significant predictors of prevalence.

In a PCA of ground cover characteristics, 46.8% of the total variation was accounted for by two axes, where PC1 explained 27.4% of the variance and PC2 explained 19.4% (Figure 2). In the logistic regression analysis, mean plot scores of PC1 were non-significant ($p = 0.137$), but PC2, which discriminated between sites with high percentages of saltmarsh cordgrass/water versus black needlerush/bare ground, was a significant predictor of prevalence (odds ratio: 0.14 [−0.82–1.11]; $p < 0.0001$). For every unit increase in PC2, the log odds of prevalence decreased by −1.96 ($t = -3.95$, $p = 0.0001$). In descending order, sites O2 (0.91), U2 (0.88), U1 (0.53), D2 (0.50), and O4 (0.33) had positive PC2 mean plot values. D1 (−0.20), U4 (−0.23), O6 (−0.43), and O3 (−0.44) had negative values.

DISCUSSION

Sex and site-level ground cover characteristics were the strongest predictors of BAYV prevalence. The proportion of infected males (18%) was significantly greater than that of females (6%), and prevalence was more than twice as high in adult males as subadult males, which is consistent with most other studies of hantavirus host species (Khalil et al., 2014). One plausible explanation for this trend is the frequency with which heavier (i.e., older) males come into contact with conspecifics' excreta or are wounded during aggressive and competitive interactions (Glass et al., 1988). Prevalence also appeared to be higher at sites with greater proportions of saltmarsh cordgrass and water (e.g., O3, O6, and U4). Conversely, sites, such as O2, U2, and U1, with greater proportions of black needlerush and bare ground had a negative association. Bare ground, in particular, is likely an undesirable attribute for rice rats, which are frequently depredated by aerial predators (Jemison & Chabreck, 1962). Saltmarsh cordgrass, however, is an especially important component of rice rat habitat. Although rice rats are primarily carnivorous and rely heavily on fiddler crab populations for food (*Uca* spp.; Martin et al., 1991), saltmarsh cordgrass is a seasonally important part of the diet (Kruchek, 2004; Sharp, 1967). Rice rats also build nests from saltmarsh cordgrass (Sharp, 1967, personal observation). The ground cover characteristic of "water," which was defined as areas with consistent (i.e., not due to flooding/tides), distinctive, and deep pockets of water within the interior of the marsh, was also associated with higher prevalence.

As other studies have demonstrated, the relationship between landscape structure/habitat use and hantavirus prevalence may be more complex than simple density dependence and instead involves territoriality, inter- and intraspecific interactions, and movements of the host species. For example, Holsomback et al. (2009) detected more frequent BAYV spillover from rice rats to other sympatric rodent species in areas with higher proportions of grass/shrub cover and that were nearer to sources of freshwater. The importance of freshwater was especially pronounced during dry periods, which suggested that because higher quality habitat patches are occupied by dominant males, their aggressive territorial defense against either sympatric species or conspecifics transmits the virus. Goodin et al. (2009) noted microhabitat differences according to serostatus of *Akodon montensis* in Paraguay, postulating that this pattern was derived from dominant males occupying preferred patches. Langlois et al. (2001) modeled SNV prevalence as a function of habitat quality and found that prevalence was lowest in areas with intermediate levels of preferred habitat. They suggested that this was due to the interacting factors of habitat preferences, habitat connectivity, deer mouse movements, and density. Habitat preferences and their influence on hantavirus prevalence appear to be host species-specific (Camp et al., 2021; Eastwood et al., 2018), but overall, habitat is a consistently important factor across hantavirus–host systems. For instance, Khalil et al. (2014) found that 27 of 30 studies of hantavirus prevalence found some association with habitat features. Whatever the exact mechanism, saltmarsh cordgrass and water appear to be important drivers of BAYV prevalence, which may be due to rice rat competition for those preferred resources. We might also expect sites with preferred resources to have greater population densities and therefore higher transmission rates and prevalence, but we found no relationship between abundance and prevalence. This may largely be due to the duration and continuity of our study. As Calisher et al. (2007) note, hantavirus prevalence is highly temporally and spatially variable, and it may be that longer-term, more continuous datasets (such as their own 10-year study) are necessary to detect any underlying patterns (see also Douglass & Vadell, 2016). Furthermore, hantavirus prevalence can have a delayed density-dependent relationship (Adler et al., 2007; Mills et al., 1999), a relationship our sampling strategy precluded testing for. Both hantavirus prevalence and rice rat abundance were consistently greater in the second session, and the shift in abundance was driven by juvenile recruitment. Because juveniles

can maintain maternal antibodies to hantaviruses for ~80 days (Kallio et al., 2006), an influx of some unsusceptible individuals can also produce a delayed density-dependent relationship (Adler et al., 2007; Mills et al., 1999). Had we continued sampling and screened these populations after the recruited juveniles aged into susceptible subadults, perhaps a delayed density-dependent effect would have become apparent.

The number of spatial and temporal replicates we were able to achieve was smaller than what might be possible in a typical small mammal mark–recapture study. This was largely due to the difficulty of accessing sites, which was only possible by boat and therefore highly weather-dependent. While we had 5 years of prevalence and habitat data, only three of those years had sufficient data for abundance x prevalence comparisons, and as mentioned above, more continuous sampling would have allowed us to better address the dynamic spatiotemporal nature of the hantavirus–host relationship. Finally, habitat data were limited to only a broad description of the characteristics of each site, and we were not able to quantify changes in those characteristics over time. While the general characterization of each site appeared highly stable over time, subtle shifts in ground cover composition could play a role in explaining temporal variation in BAYV prevalence.

Hantavirus prevalence in hosts frequently exhibits substantial seasonal and inter-annual variation (Douglass & Vadell, 2016). Climatic conditions play an important role, through driving host behavior and population dynamics (Abbott et al., 1999; Davis et al., 2005; McIntyre et al., 2005), as well as factors (i.e., humidity, temperature) that influence the stability and longevity of shed virus in the environment (Kallio et al., 2006). Across our sites, prevalence varied up to 10.5% between subsequent years across all sites (10% in 2015 and 19% in 2016) and 66.7% between subsequent years within a single site (D1, from 2016 to 2017). Seasonally the data were more consistent, with prevalence typically higher in the second session (July) relative to the first (March–May), although this pattern varied by site. Prevalence also varied more in the second trapping session across all 5 years (between 6.8% and 30.8%) relative to the first session (between 7.1% and 14.6%). Much of this variation was driven by the second session in 2016, which had a 4.5-fold increase in prevalence (30.8%) from the previous year's July sampling.

Only one species, the marsh rice rat, was caught over 5 years of trapping. This is not atypical in the southern, coastal portion of the rice rat's range (Wolfe, 1985), and saltmarshes in general are characterized by low species diversity (Odum, 1988). This result is relevant to the "dilution effect," where pathogen persistence is negatively correlated with host species diversity. While certainly not a universal phenomenon (Salked et al., 2013), it can be a mechanism driving transmission dynamics and hantavirus prevalence in other systems (e.g., Clay et al., 2009; Suzán et al., 2009). However, given that there is only one small mammal species present at our study sites, what can be an influential driver in other hantavirus–host systems is fundamentally incompatible in the coastal saltmarshes of Louisiana. Here, any changes in hantavirus prevalence and transmission rates cannot be due to changes in small mammal community composition, and instead must be due to either intrinsic shifts in population dynamics, behavior, or external environmental factors.

Despite the major ecological disturbance of the 2010 DWH oil spill, we found no apparent residual influence of the spill on BAYV prevalence. It is possible that by 2013 (the start of this study), any oiling effects of significance to the hantavirus–host dynamic had since attenuated. For instance, because the most heavily oiled vegetation eroded away first, some oiled areas appeared recovered only 3 years after the spill (Hester et al., 2016), which, given the importance of habitat in hantavirus–host systems, could neutralize any observable effect on hantavirus prevalence. The attenuation of oiling effects is also observable in another terrestrial vertebrate, the Seaside Sparrow (*Ammospiza maritima*). Studies of the Seaside Sparrow benefited from data collection immediately after the spill (i.e., in 2011 and 2012) and showed significant responses to oiling (Bonisoli-Alquati et al., 2016, 2020) that lessened with time (Perez-Umphrey et al., 2018). However, these studies describe individual effects; it has been difficult to detect population-level effects of the oil spill on Seaside Sparrows, an issue potentially shared by rice rats. Our estimates of rice rat abundance derived from mark–recapture data did show statistically significant differences between oiled and reference sites, but not between oiled and unoiled ones, with the greatest abundance of rice rats at oiled sites. The only other oiling effect detected in rice rats, thus far, has been in stable isotope analyses, which show wider trophic niche width in rice rats at oiled vs. unoiled sites (Moyo et al., 2021). Regardless, this reservoir of pathogenic hantavirus, ~40 km from suburbs of New Orleans, a major port and a metropolitan area of more than 1 million people, merits continued surveillance, especially given the current forecasts of continued disturbance in the forms of land loss, climate change, and offshore oil drilling in this region. Because habitat characteristics appear to be one of the best predictors of hantavirus prevalence in this area, continued disturbance will likely influence the rice rat–BAYV dynamic.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC): mark–recapture dataset, https://doi.org/10.7266/n7-c7zj-xe50; infection screening dataset, https://doi.org/10.7266/n7-383p-6k11; and habitat dataset, https://doi.org/10.7266/n7-w5g6-e664.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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