Socio-ecology of the marsh rice rat (*Oryzomys palustris*) and the spatio-temporal distribution of Bayou virus in coastal Texas

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Abstract. Along the southeastern coast of the United States of America (USA), the marsh rice rat (*Oryzomys palustris*) is the primary host for the hantavirus genotype Bayou. According to the socio-ecological model for a territorial, polygamous species, females should be distributed across space and time by habitat resources and predation risks, whereas males should space themselves according to the degree of female aggregation and reproductive synchrony. To investigate how females affect the male-male transmission paradigm of Bayou virus, rodents were captured, marked, released, and re-captured in two macrohabitat types across a 30-month period. Microhabitat cover variables were quantified around the individual trap stations. A geodatabase was created from habitat and rodent capture data and analysed in a geographical information system. The ratio of breeding to non-breeding females was ~1:1, with breeding females overly dispersed and non-breeding females randomly dispersed. Spatial analyses revealed both macro- and microhabitat preferences in females. Compared to sero-negatives, higher proportions of seropositive adult males were found consistently within closer proximities to breeding females but not to non-breeding females, indicating that male locations were not driven simply by habitat selection. Activities to acquire dispersed receptive females could be an important driver of Bayou virus transmission among male hosts. To date, socio-ecological theory has received little attention as an investigative framework for studying pathogen dynamics in small, solitary mammals. Herein, we describe an interdisciplinary effort providing a novel approach to elucidate the complexity of hantavirus trafficking and maintenance in rodent populations of a coastal marsh ecosystem.

Keywords: *Oryzomys palustris*, Bayou virus, socio-ecological model, geographical information systems, coastal marsh ecosystem, marsh rice rat, USA.

Introduction

Hantaviruses constitute a distinct genus (*Hantavirus*) of currently 39 antigenically and phylogenetically related viruses of the family Bunyaviridae (Klein and Calisher, 2007). At least 21 hantaviral species are known to cause fatal outcomes in humans, ranging from pulmonary edema manifested in hantavirus pulmonary syndrome (HPS) to massive desanguination resulting from hemorrhagic fever with renal syndrome (HFRS). Unique within the Bunyaviridae, hantaviruses frequently exploit species-specific male rodents (order Rodentia: family Cricetidae) rather than arthropod vectors. For many of the known hantavirus-rodent associations, complete characterizations are still lacking with respect to the ecological and biological processes and spatial scales that determine viability and variability in transmission potentials.

Rodents of the tribe Oryzomyini (family Cricetidae; subfamily Sigmodontinae) are endemic to the Western Hemisphere, ranging from the Argentine Patagonia through the Galápagos and Central America, throughout Mexico and the Gulf and Atlantic coasts of the southeastern U.S. Oryzomyine rodents display an array of morphological adaptations (Carleton and Olson, 1999) that enable them to thrive across a spectrum of vegetation types (Eisenberg, 1999), including mixed forests and fresh and salt water marshes to sedge-shrub habitats (Wolfe, 1985). Recent work has clarified the structure of this tribe (Weksler 2006, Hanson et al. 2010), but issues still remain at the species level, hampering identification of other potential reservoirs in epidemiologic and phylogeographic studies, among others (La Salle et al. 2009).

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In the United States of America (USA), the oryzomyine rodent known as the marsh rice rat (*Oryzomys palustris* Harlan, 1837) is the primary host for the hantavirus genotype Bayou, the second-leading strain responsible for HPS in the USA (Torrez-Martinez et al., 1998). The marsh rice rat occurs from southern New Jersey southwestwardly to Kansas-Missouri-Illinois, through coastal Texas and down into peninsular Florida. It favours riparian and wetland habitats, is strictly nocturnal and prefers a carnivorous diet of fish, crustaceans, insects and the eggs and young of marsh birds and turtles, but will supplement its dietary needs with omnivory based on seasonal conspecific densities and plant phenologies. Empirical support for both macrohabitat and microhabitat selection in *O. palustris* has been described previously (Kincaid et al., 1983; McIntyre et al., 2005, 2009). Although little is known of the social relationships and behaviours of the marsh rice rat, it is believed to be solitary, aggressive and territorial, contingent upon population density and resource availability.

Hantaviruses are transmitted among hosts chiefly via antagonistic male-male interactions (Glass et al., 1988). Factors controlling the frequency of such interactions are poorly understood, however. Moreover, the nature of transmission between the sexes is also unclear. Our understanding of the factors that maintain the virus in wild populations thus hinges upon a better understanding of the social and environmental forces that drive potential hosts together or apart. The socio-ecological model (SEM; Crook and Gartlan, 1966) provides a theoretical link between environmental factors and characteristics of social systems (Emlen and Oring, 1977), allowing for predictions about associations as functions of resource distributions, types of competition and social organizations, relationships and structure (van Schaik and Kappeler, 2006; Dammhahn and Kappeler, 2009). Sex-specific features limit the fitness of females and males resulting from intersexual differences in parental investment (Trivers, 1972). An assumption of the SEM is that the spatio-temporal scattering of females is determined predominately by the distribution of habitat resources and risks (Dammhahn and Kappeler, 2009). As the dispersive sex in mammals, males seek out reproductively receptive females (Altmann, 1990), so their juxtaposition should be based primarily on the spatial arrangement of those females (Clutton-Brock, 1989).

Socio-ecological thought has been invoked to comprehend and minimise effects of cyclic patterns of pathogens transmitted indirectly and directly among humans (Parkes et al., 2003) and other social primates

(Wlasiuk and Nachman, 2010), but mainly for sexually transmitted diseases. Within the constructs of the SEM, no thorough attempt has been made to explain variation in general regarding the social systems of solitary species (Dammhahn and Kappeler, 2009); furthermore, it has gone unnoticed as an applied framework for studying direct disease transmission in small mammals, like hantaviruses in rodents. Hantavirus researchers also have overlooked the importance of females and their impact on male movements and virus dissemination. Application of the SEM to the host-hantavirus system may reveal previously unknown aspects of transmission and hence human disease risk.

Geographical information systems (GIS) are used in hantavirus studies mainly from a human epidemiological perspective: (i) in retrospective, public health reports; and (ii) for surveillance, to forecast outbreaks by spatial mapping of various risk criteria, including rodent host densities, conversion of landscape characteristics, and climatic variables (Ostfeld et al., 2005; Glass et al., 2006). However, we are unaware of other studies where GIS and the SEM have been converged and applied at the scales and towards the goals we have set forth here.

Therefore, our objectives were to investigate the socio-ecology of adult *O. palustris* at multiple spatial scales, using a GIS to evaluate the spatial relationships of females and males as a function of habitat as well as intraspecific attraction. Moreover, we specifically wanted to explore the role of females as potential infection drivers/mediators between males, based on spatial receptivity patterns. Thus, we assessed habitat selection in adult breeding and non-breeding females (which was then associated with the distribution of adult males), to investigate specifically how females affect the male-male transmission paradigm of Bayou virus (BAYV).

Materials and methods

Study site

Seasonal characterization of habitat and rodents was conducted at the Justin Hurst Wildlife Management Area (JHWMA) (UTM: 15-3202562-262435), formerly Peach Point WMA, in Brazoria County, Texas from March 2002 through May 2004. Situated ~ 60 km south of Houston, JHWMA comprises 4174.5 ha and southeasterly is bordered by the Gulf Coast Intracoastal Waterway. Clay soils describe the landscape which is fairly low and flat (0-5 m ASL), and is composed of low-lying assemblages of brackish

to saline coastal marshlands that grade farther inland to freshwater marshes and mixed uplands with trees. Precipitation occurs year round (60% falls from April to September), and average precipitation is 1,334 mm (from the National Oceanic and Atmospheric Administration Freeport 2NW weather station, located ~10 km from JHWMA; http://www.noaa.gov/). High temperature averages range from 18 °C (winter) to 33 °C (summer); even in winter, average annual lows are well above freezing (8 °C).

Mark-recapture grids

Sampling protocols were approved by the TTU Animal Care and Use Committee (permit #01134BX). Collection permits were granted by the Texas Parks and Wildlife Department (permit #APR-0498-944 and #SPR-0504-381). Rodents were live-trapped on four mark-recapture rectangular grids 7100-7700 m^2 in size (traps placed at 10 m intervals and numbers of traps ranged from 93-113, contingent upon coastline topography and flooding) in two macrohabitat types (upland and coastal marshland, each with one replicate grid) for 4-6 consecutive nights for each of four seasons (mid-March, late May, late August, mid-December) during the 30-month study period (McIntyre et al., 2005) (Fig. 1). Captured rodents were marked with an unique identifier, i.e. by toe-clipping or by subdermal insertion of a Passive Integrated Transponder (PIT) tag (Biomark, Inc., Boise, USA). Data recorded for each individual rodent included capture status (new or recapture), its unique identifier, species, trap station, age
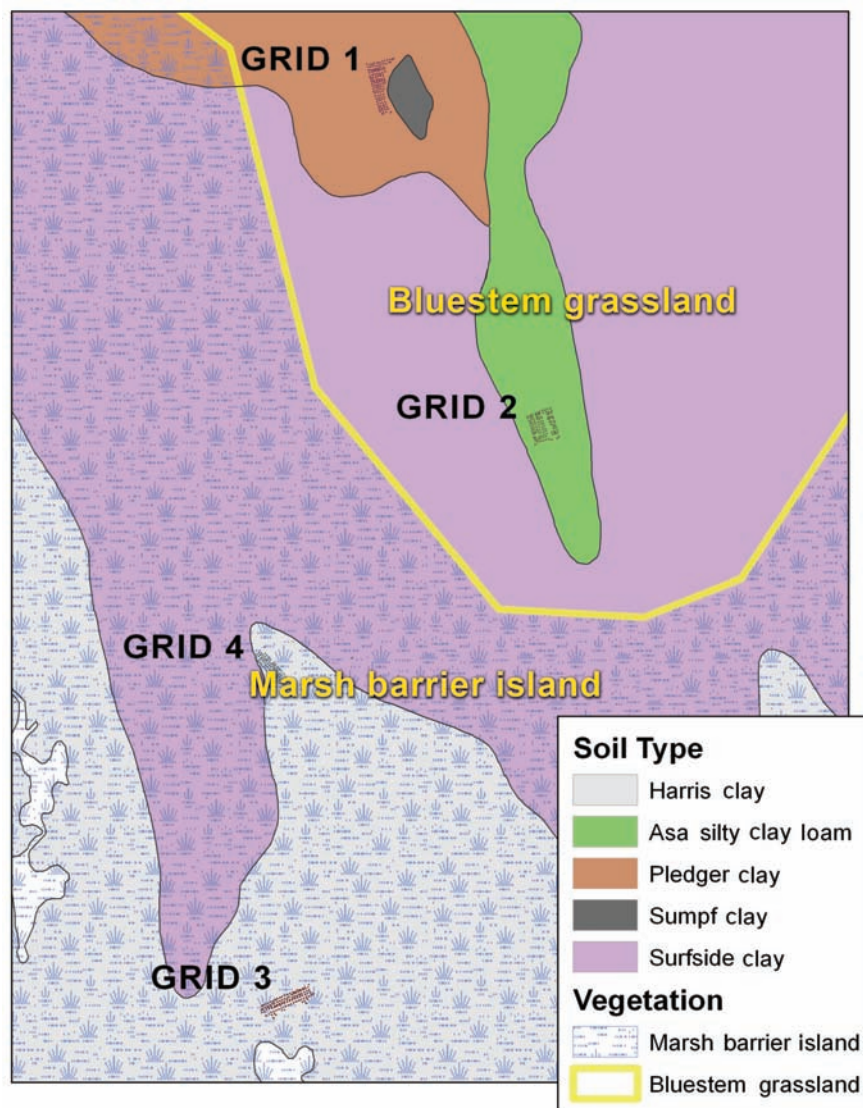

Fig. 1. Map of predominant soils and vegetation at Justin Hurst WMA, Texas, USA. Yellow line demarcates upland grids (1, 2). Stippling symbolizes coastal marshland grids (3, 4).

class (juvenile, subadult, adult), sex, weight (using a Pesola spring scale) and reproductive status (testes position: abdominal, inguinal or descended; vaginal patency: perforate or closed; pregnancy status: pregnant, recent parturition or lactating). Capture coordinates were recorded using a hand-held global positioning system (GPS). Using a sterile Pasteur pipet, a blood sample of several drops (0.1-0.5 ml) was extracted aseptically from the retro-orbital sinus and delivered to a sterile cryovial, after which the animal was released at the site of capture.

Anti-BAYV IgG determination by immunofluorescence microscopy (IFA)

Antibody detection assays using rodent blood tissues were conducted at the Southern Research Institute in Birmingham, USA, and adhered to CDC and BSL3 guidelines. Protocols were developed and validated previously (Chu et al., 1995, 2003). Stepwise details are in McIntyre et al. (2005).

Microhabitat composition

Based on capture, recruitment and seropositivity rates being higher during one particular period on one trapping grid than on the other three grids in any other season, microhabitat selection analyses are from this season and grid (August 2003, Grid 3), located within coastal marshland macrohabitat. However, the patterns discussed also hold true in other locations and time periods, but with smaller representative sample sizes of adult males and females (Table 1). Microhabitat composition (percent ground cover of 10 mutually exclusive categories: grass, herbaceous,

bare ground, tree, shrub, litter (duff), vine, coarse woody debris, water, other) was quantified in a 3 m radius circle centered on each trap station (N = 111 trap stations for Grid 3, ~7700 m²) following Bullock's methodology (1996). The identity of plant species within each of these categories was also determined. These categorizations were utilised further to determine and compare microhabitat selection of adult breeding and non-breeding *O. palustris* females.

Spatial relationships, GIS

Location coordinates for the habitat and capture data had been recorded previously in a Microsoft Excel spreadsheet. To bring the coordinates into the GIS, the x-y values were converted to decimal degrees, with latitude values being positive and longitude values being negative. The spreadsheet was imported into ArcMap 9.3 (ESRI, Redlands, USA) as an event layer and inspected for missing data. After the quality control check, the event layer was exported to a file geodatabase (Natural Resources Conservation Service (NRCS), Geospatial Data Gateway, 2008; Soil Data Mart, 2009; U.S. Census Bureau, Census TIGER 2000 Data; USGS Seamless Server, Brazoria County, Texas and National Elevation Dataset), and saved as a feature class. The main feature class was sorted into separate categories and analysed according to trapping session, habitat, sex, age class, reproductive condition and serostatus. Spatial relationships between adult *O. palustris* males and females were evaluated using the "Select by Location" tool in ArcMap, which includes a buffer option that allows records to be selected at varying distances. Each male *O. palustris* was categorised according to the following location criteria (i.e. spatial

Table 1. Demographics of four populations of *O. palustris* at Justin Hurst WMA from May 2002 to May 2004 (in March 2002, pilot study did not include grid trapping, but see bottom of table for harvest trapping results).

Grid	1			2			3			4		
Demography	J/S	A	+	J/S	A	+	J/S	A	+	J/S	A	+
May 2002	0	5	1	0	3	0	8	25	8	1	4	1
August 2002	0	4	0	0	3	0	4	12	0	5	15	0
December 2002	8	14	0	2	25	1	0	14	4	0	19	5
March 2003	1	4	0	4	5	1	5	8	6	2	6	0
May 2003	1	5	2	0	1	1	13	20	8	5	4	1
August 2003	0	2	2	1	2	0	14	40	11	3	8	0
May 2004	1	0	0	0	2	1		*N/A		6	16	2

Grid: 1, 2 - Bluestem Grassland (upland); 3, 4 - Coastal Marshland.
Demography: J/S = juvenile/subadult; A = adult; + = anti-BAYV IgG antibody positive.
March 2002: Harvest trapping conducted only (4 J/S, 37 A, 8 +).
*In May 2004, Grid 3 closed due to extreme coastal flooding.

scales) in relation to a breeding female: detection within the same grid; within 30 m, and in the same trap.

Statistical analyses

Spatial data were analysed using the built-in statistical software in ArcToolbox to determine the spatial distribution of the sexes by reproductive status (for females) or serological status (for males). Chi-square (χ^2) goodness-of-fit tests were used to determine differences: (i) in microhabitat use versus availability for adult females by reproductive condition; and (ii) between serological status of adult males and proximity to receptive females. The χ^2 tests were run using the function "prop.test" (with the default continuity correction) in R version 2.2.1 (R Development Core Team, 2005).

Results

Macrohabitat description

From the vegetation and soil layers (Fig. 1), the upland grids (Grids 1, 2) are both in bluestem grassland upland habitat, with Grid 1 composed of pledger clay and Grid 2 composed of asa silty clay loam. Grids 3 and 4 are in coastal marshland ("Marsh Barrier Island"), both comprised by Harris clay. Most recruitment of *O. palustris* young and immigrant adults occurred in the coastal marshland grids, with adult females detected more frequently in the Harris clay-saltmarsh habitats, with the exception of December 2002 (Table 1).

Microhabitat description

Because each trap station had both GPS coordinates and habitat data, these could be linked and brought into the GIS for spatial analysis (Fig. 2). Thus, 90:111 trap stations were characterised by >75% grass cover (several species), with the remaining cover made up of sedge (*Carex* sp.). Going in descending order: 12 trap stations were characterised by 50-75% grass/remainder sedge; three trap stations described by 50-75% grass/remainder water; three trap stations described by 25-50% grass/remainder sedge; one trap station described by 25-50% grass/remainder water; one trap station with 50-75% grass/remainder saltwort (*Batis maritima*), and one trap station with >75% grass cover/remaining cover was reed (*Juncus effusus*). The most common plant species on Grid 3 (in descending order) were saltmarsh grass (*Distichlis spicata*), saltwort (*Batis maritima*), wiregrass (*Spartina patens*) and bulrush (*Scirpus robustus*).
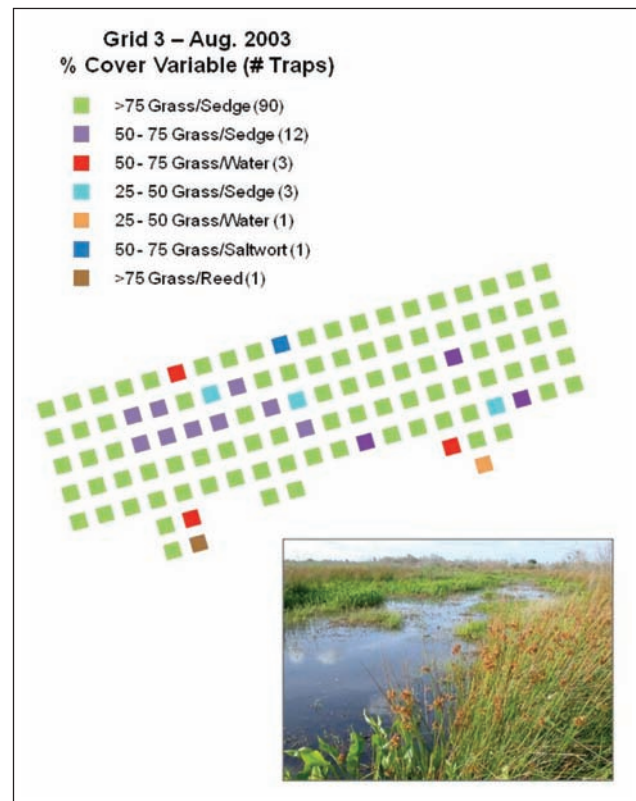

Fig. 2. Percent habitat cover variables within 3 m of each trap; remaining cover follows slash. In parentheses are numbers of traps characterised by percentages of respective cover classes. Layout of Grid 3 (center). Total trap (n) = 111. Photo of typical marshland habitat, lower right (courtesy of NEM).

Female microhabitat selection by reproductive condition

In a GIS, one can run a "Location Query", use a "Select by Location" tool, buffer the feature class of interest and visualise the data (the steps followed in this section and the next, Figs. 3 and 4, respectively). In Fig. 3, non-receptive females (denoted by pink circles) primarily occupy habitat dominated by >75% grasses and ≤24% sedge. Buffering the layer containing the receptive females (purple circles) revealed that they utilise slightly more diverse areas: the >75% grass/≤24% sedge, but also the 50-75% grass/25-50% water, and >75% grass/≤24% reed traps. Nevertheless, χ^2 results indicated no significant association in female microhabitat selection by reproductive condition when compared to an equal number of randomly selected traps ($\chi^2 = 0.05$, P = 0.819). When the spatial-habitat data for both groups are compared (Fig. 3, center), some overlap is noted between the two and also something interesting: apparent non-use of the grid interior and thus possible avoidance of the 50-75% grass/25-50% sedge cover (purple squares). Currently, the significance of this finding is
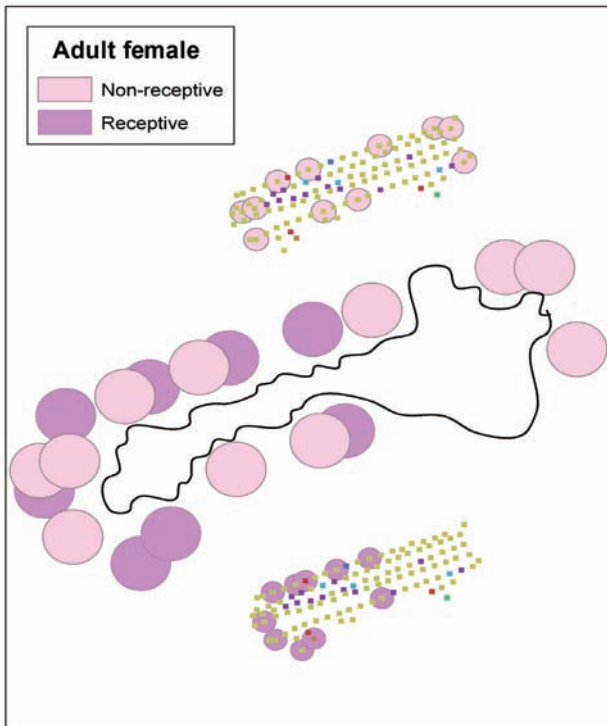
Fig. 3. Grid 3, August 2003. Habitat occupancies and spatial relationships of non-receptive (i.e. non-breeding; pink circles) and receptive (i.e., breeding; purple circles) adult females separately (non-receptive, top; receptive, bottom) and combined (center). Black line encloses area unused by both groups (grid removed for ease of viewing).
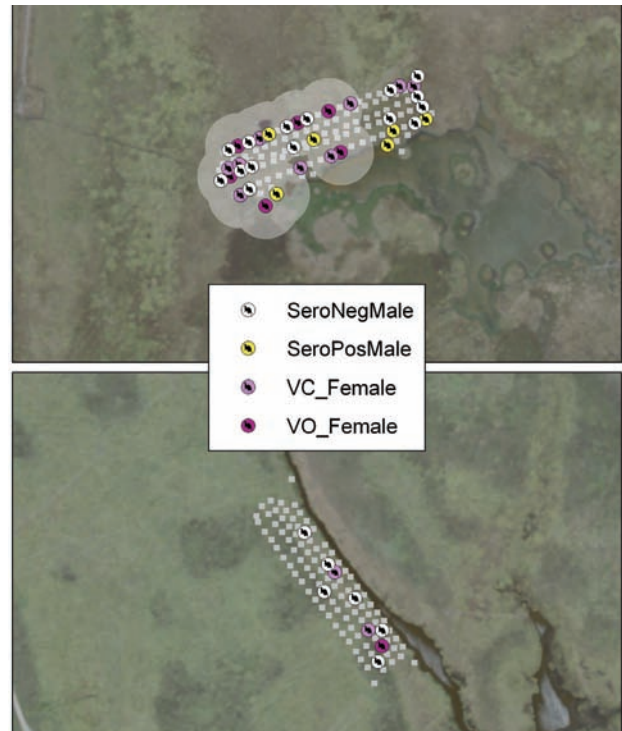

Fig. 4. Grid 3 (top) and 4 (bottom), August 2003. Map of adult female-male spatial relationships using buffer tool. Adult males have been added by serostatus. Each buffer (opaque circle) represents a receptive female (VO = vagina open) found ≤30 m from a seropositive male. VC = vagina closed, or non-receptive female.

unknown, but could be related to predator avoidance behaviour.

Spatial relationships of females (based on breeding status) to males (based on serostatus)

For this analysis, breeding (vagina open; VO) females were buffered to include at least one seropositive male (Fig. 4). Other results (not shown) are that no seropositive males were located within 30 m of a non-breeding (vagina closed; VC) female, and no seronegative males were found within 30 m of a breeding female. The lack of opaque circles on Grid 4 is due to the absence (or our inability to detect the presence) of seropositive males

there during the August 2003 trapping period. The fact that no seropositive males were captured on Grid 4 in August 2003 could be explained by low *O. palustris,* population abundance in general and by the presence of only one breeding female specifically.

Proportion of breeding to non-breeding females, degree of spatial clumping

We noted breeding throughout the year (Goldman, 1918; McIntyre et al., 2005). An almost 1:1 ratio in terms of breeding and non-breeding females was revealed from all four grids (data not shown). From the nearest-neighbor ratio (Table 2), there was a ran-

Table 2. Results of *K*-parameterization, a measure of spatial aggregation, for non-breeding (vagina closed) and breeding (vagina open) females on Grid 3, August 2003. Equal sample sizes (total N = 26). Asterisks indicate level of statistical significance (P <0.001).

Vagina closed (non-receptive)		Vagina open (receptive)	
Observed mean distance	0.0014	Observed mean distance	0.0024
Expected mean distance	0.0015	Expected mean distance	0.0016
Nearest neighbour ratio	0.9536	Nearest neighbour ratio	1.4945
Z score	-0.3761	Z score	3.6637
P-value	0.707 (randomly distributed)	P-value	<0.001 **** (overly dispersed)

Table 3. χ² goodness-of-fit results for coastal marshland grids (3, 4) for study period (2002-2004).

	Location: same grid	Location: ≤30 m	Location: same trap
Sample size (n) by serostatus	(n)Neg = 73 (n)Pos = 31	(n)Neg = 39 (n)Pos = 22	(n)Neg = 2 (n)Pos = 5
χ² test statistic	6.25	9.84	11.57
P-value	0.012 *	0.002 **	0.001 ***
95% confidence interval	0.216, 0.390	0.249, 0.484	0.379, 0.935

All d.f. = 1.
Significant at level: * P ≤0.05; ** P ≤0.005; *** P ≤0.001.

dom distribution for non-breeding females (P = 0.707), and significant overdispersion of breeding females (P <0.001).

Association between male serostatus and proximity to a receptive female

At weaning, the sex ratio of *O. palustris* is roughly 1:1 (Park and Nowosielski-Slepowron, 1972). We had a somewhat male-biased sex ratio in adults (1.8:1); in nearby Galveston, Texas, Kruchek (2004) noted strongly male-skewed adult populations (2.3:1). Although adult males were 2.5 times more likely to be seronegative than seropositive, χ² analysis results indicated a significant association between male seropositivity and spatial proximity to a breeding female (Table 3; data pooled for analysis to reduce the probability of an inflated type 1 error). Compared to seronegatives, seropositive males were more frequently associated with receptive females by grid ($χ^2$ = 6.25, P = 0.012), within a 30 m radius ($χ^2$ = 9.84, P = 0.002), and occupying the same trap ($χ^2$ = 11.57, P = 0.001).

Discussion

Although our study focused on a grass-dominated, coastal marshland macrohabitat, where only four out of 111 trap stations were surrounded by <50% grass cover, microhabitat selection in females was noted that could explain the distribution of males as well as the distribution of BAYV as assayed by serological status. Seropositive *O. palustris* males have been reported from JHWMA to avoid grasses on a microhabitat scale, which was attributed to the increased ranging seen in seropositive males (McIntyre et al., 2009). However, the pattern of habitat selection in males could instead be due to the fact that receptive (i.e. breeding) females tend to occur in areas with greater microhabitat diversity (e.g. in the >75% grass /≤24%

sedge, the 50-75% grass/25-50% water, and in the >75% grass/≤24% reed traps) rather than in the areas with the greatest grass cover (as was the case for the non-receptive females). Seropositive males averaged significantly larger home ranges than seronegative males at our study site (McIntyre et al., 2009). A male that maintains a large home range increases the probability his range will include a receptive female; if he monitors his range vigilantly, then he has a better chance of crossing paths and copulating with her (Tew and Macdonald, 1994). In light of our study, male home range sizes by serostatus make sense: diffuse, breeding females (overdispersed spatial distribution) induce larger home ranges for seropositive males, who tend to be socially dominant, larger and/or older (McIntyre et al., 2009). Socially dominant, seropositive males also were more frequently associated with breeding females by grid, within a 30 m radius, and by trap station. This socio-ecological explanation of host distributional patterns, based on female receptivity and habitat preferences *rather than just* male aggression, is an original approach to distill the links between hantaviral maintenance and circulation in natural host populations.

From his coastal Mississippi study dated 1981-1984, Wolfe (1990) states, "Documenting details of the (...) environmental influences on the distribution of [marsh rice rat] individuals is needed to understand the factors facilitating survival and resource use in this habitat." These words might resonate more truthfully today. *O. palustris* has been called an "ecosystem engineer" in coastal marsh systems (Wolfe, 1982), because it is often the only small mammal to occupy almost exclusively this vital yet vanishing habitat. Its major roles and low functional redundancy in this trophic web (Chabreck, 1988) are highlighted by efficient extraction and recycling of marsh resources (Wolfe, 1982). Reservoir competence in *O. palustris* also has been demonstrated for multiple parasites of commu-

nity assemblage importance (Morlan, 1951; Barnard et al., 1971; Levin et al., 1995). Lastly but not exhaustively, its long-distance, frequent dispersal behaviours (Esher et al., 1978) provide a flexible adaptation to survive periodic storm surges (Abuzeineh et al., 2007), minimise competition and inbreeding depression (Loxterman et al., 1998), and produce founder and rescue populations in nearby island systems (Forys and Dueser, 1993).

Evidence of *Peromyscus maniculatus* (deer mouse; principal host for Sin Nombre virus and Monongahela virus) in or near human dwellings has been shown to be an unambiguous, HPS risk factor in southwestern Colorado (Calisher et al., 2011) and elsewhere. Unlike *P. maniculatus*, *O. palustris* normally does not invade human dwellings or co-habit with humans; rather, its behavioural ecology is one of a semi-aquatic, solitary species. Its riparian marsh-grassland as opposed to suburbia occupancy is likely one reason why BAYV occurrence in humans has remained low; however, it is possible that at least some HPS cases caused by BAYV are misdiagnosed and therefore underreported, as the complex symptoms of BAYV-HPS can involve multiple body systems either sequentially or simultaneously (Hjelle et al., 1996). For the handful of BAYV-HPS cases identified clinically, there is insufficient evidence to determine whether or not infections were acquired through occupational or recreational exposure to *O. palustris* and/or their excreta. Nevertheless, among BAYV-HPS patients, two noticeable commonalities are outdoor activities (near permanent water and dense grasses) during which large amounts of airborne dirt were inhaled repeatedly over time, and also fishing in areas with household refuse and visible rodents (Hjelle et al., 1996; Torrez-Martinez et al., 1998). Minimally, Gulf Coast fishermen and landfill laborers could be at particular risk in areas where their activities fall within the habitat range and preferences of *O. palustris* (Wolfe, 1982, 1985; McIntyre et al., 2009).

The remaining riverine wetlands and tidal marshes of the northern Gulf of Mexico and southern Atlantic Coast approach unprecedented levels of contamination, degradation and discontinuity (Ketchum, 1972; Bartlett and Smith, 2005). The decay of this ecoregion is not expected to decelerate, further complicating hantaviral disease projections based on typical rodent life history traits and patterns, including preferential habitat uses, dispersal distances and Hamiltonian sex ratios. It is risky to attempt response predictions of the marsh rice rat to continual loss of its natural habitats and looming "coastal squeeze" (Schleupner, 2008). Nevertheless, if a change in population biology results

in marsh rice rats subjected to artificial co-existence with dense populations of humans, then more cases of BAYV infection should be anticipated, especially where rodent densities are abnormally high (e.g. in remnant, high quality patches), and when male rodents travel and fight for breeding rights to spatially segregated, receptive females.

Although hantaviruses are not of recent origin (there is evidence for their problematic presence from at least 1000 years ago; McKee et al., 1991), both drivers and outcomes of their "re-emergences" appear to be phenomenologically new. Deciphering the enigmatic conditions of how and why ancient hantaviruses only recently have become of epizootic importance has not proven easy. Regardless of the underlying mechanisms, rodent phenotypic and viral genetic plasticity coupled with anthropogenic landscape alterations can be expected to increase the liability and geographical scope of human hantavirus afflictions in the future. For example, shifts in host ecology are accompanied by compensatory shifts in virus ecology (owing to vicariance) and sometimes result in environmental release of more pernicious viral subtypes to humans following molecular reassortment events (Dragoo et al., 2006). To disentangle these complex, non-linear disease transmission dynamics, we must employ all the techniques available. If the techniques are inadequate, new ones should be invented. Equally important, it might be fruitful to apply established theories and practices in a fresh way. With this, application of the socio-ecological framework and GIS might provide powerful prediction tools for human hantavirus exposure and infection risk across coastal regions of North America and elsewhere.

Acknowledgements

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