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Dryland Salinity and the Ecology of Ross River Virus: The Ecological Underpinnings of the Potential for Transmission

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Abstract

Alterations in transmission of vector-borne zoonoses are often linked to environmental change. However, ecological processes that determine variability in potential for transmission are generally not well understood. Ross River virus (RRV, Togoviridae: *Alphavirus*) is a mosquito-borne zoonosis in Australia with a significant human disease burden. The inland southwest (Wheatbelt) of Western Australia (WA) is substantially affected by an anthropogenic salinization of agricultural land (dryland salinity). *Aedes camptorhynchus* Thomson (Diptera: Culicidae) is the dominant vector of RRV in southwest WA and is halophilic. As such, dryland salinity may influence potential for RRV transmission by influencing interactions between *Ae. camptorhynchus* and mammalian hosts. We surveyed areas of the Wheatbelt with varying salinity impacts and found *Ae. camptorhynchus* was more abundant in saline areas, whereas sheep *Ovis aries* (Linnaeus 1758, Bovidae) declined with increasing salinity. We used a deterministic model to examine interactions between *Ae. camptorhynchus* and mammals, and we assessed potential for RRV transmission. We found variation in potential for RRV transmission was positively related to increasing salinity and abundance of *Ae. camptorhynchus* and negatively associated with increasing abundance of *Macropus fuliginosus* (Desmarest 1817, Macropodidae). Abundance of *Ae. camptorhynchus* determined more variation in potential for RRV transmission than other variables. Accordingly, dryland salinity increases the zoonotic potential for RRV transmission primarily by facilitating abundance of *Ae. camptorhynchus*. Human RRV notifications do not currently reflect the salinity-RRV transmission potential in the Wheatbelt but appear to be associated with RRV activity in the enzootic coastal zone. We speculate dryland salinity is a determinant of potential for RRV transmission but not activity. Dryland salinity is predicted to expand two- to four-fold by 2050. Preservation and restoration of freshwater ecosystems may ameliorate the potential for transmission of RRV and possibly incidence of human disease.

Key Words: Disturbance—Secondary salinization—Community—Disease ecology—SIR model.

Introduction

Identifying ecological processes that govern pathogen transmission is essential to understand how environmental change will affect variability in dynamics of human and wildlife diseases (Ezenwa et al. 2007). Although change in land cover is often tied to spatial variability in disease risk and occurrence (Daszak et al. 2001, Derraik and Slaney 2007, Klinkenberg et al. 2004, Molyneux 2003, Patz et al. 2000, Ryan et al. 2001, Walsh et al. 1993), ecologic underpinnings of these correlations are often unknown (Ezenwa et al. 2007). In Australia, Ross River virus (RRV, Togoviridae: *Alphavirus*) is a mosquito-borne zoonosis, spilling over into the human population and causing a significant disease burden (Harley et al. 2001, Russell 2002). Numerous anthropogenic influences on the environment are linked to human incidence and risk of RRV infection (Foley et al. 2004, Harley et al. 2005, Jardine et al. 2004, 2007, Kelly-Hope et al. 2002, Lindsay et al. 2007, Russell 1998, 1999, Ryan et al. 2001, 2006), and disease burden appears to be governed by zoonotic transmission (Harley et al. 2001, Lindsay et al. 1996, Russell 2002). Yet investigations that specifically consider zoonotic transmission

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between vectors and hosts are rare (Carver et al. 2008b, Glass 2005, Kay et al. 1987b). Here, we use a mechanistic model to investigate links between anthropogenic salinization of the environment and the host-vector ecology of RRV transmission.

Environmental factors influence hosts and vectors and ultimately transmission of vector-borne zoonoses. Empirical and modeling studies have implicated a number of ecological processes that determine variability in transmission risk. Vector abundance is traditionally considered a determinant of transmission risk (Jardine et al. 2004, Kilpatrick et al. 2006b, Overgaard et al. 2003, Russell 1986), but this is not supported by all studies (Kanojia et al. 2003, Lindsay et al. 2005, Ryan et al. 1999). Vectors are not obligate generalists, consequently heterogeneities in vector feeding behavior may influence transmission (Tirados et al. 2006, van den Hurk et al. 2003), such as for West Nile virus (WNV, Flaviviridae: *Flavivirus*; Kilpatrick et al. 2006a, 2006b). More recently, diversity of hosts has also been identified as a determinant of transmission risk (Dobson 2004), such as for WNV, Lyme disease bacterium (*Borrelia burgdorferi*) and louping-ill virus (Flaviviridae: *Flavivirus*; Ezenwa et al. 2006, 2007, Hudson et al. 1995, LoGiudice et al. 2003, Ostfeld and Keesing 2000a, 2000b). Studies that examine links between environmental variables and vector-borne disease risk may benefit from considering ecological interactions between hosts and vectors (Carver et al. 2008a).

In southwest Western Australia (WA), RRV is principally transmitted by the halophilic mosquito *Aedes camptorhynchus* Thomson (Diptera: Culicidae), which feeds on a variety of, mostly mammalian, vertebrate species (Jardine 2007, Lindsay et al. 1993a, 1996, 1998, 2005, 2007). The putative reservoir host of RRV is thought to be the western grey kangaroo, *Macropus fuliginosus* (Desmarest 1817, Macropodidae), but other mammals are likely to influence transmission, due to the feeding behavior of *Ae. camptorhynchus* (Carver et al. 2008a). Anthropogenic salinization of land (dryland salinity) in inland southwest WA (the Wheatbelt) is postulated to influence potential for RRV transmission, by providing large areas of suitable habitat for *Ae. camptorhynchus* breeding (Biggs and Mottram 2008, Jardine et al. 2007, Lindsay et al. 2007). This is supported empirically by studies of mosquito larvae (Carver et al. submitted), but not supported by human clinical notifications (Jardine et al. 2008). The host-vector ecology of RRV transmission, in relation to salinity, has not been assessed. Currently more than one million hectares are saline in the Wheatbelt, and dryland salinity is expected to expand to between three and four and a half million hectares by 2050 (George et al. 2006, Jardine et al. 2007).

In this study, we examine the relationship between dryland salinity and ecology of potential RRV transmission in the WA Wheatbelt. Initially, we examine empirical associations between salinity, abundance of *Ae. camptorhynchus*, and assemblages of mammals. Using a simple susceptible-exposed-infectious-recovered (SEIR) model of vector-host interactions, we simulate zoonotic interactions that influence temporal and spatial variability in potential for RRV transmission. We then retrospectively examine which factors (salinity, mosquito, or mammal) explained the greatest amount of variation in potential for RRV transmission. We hypothesize that salinity will promote the spatial potential for RRV transmission. Humans are not specifically considered in our analysis, but by extension our results are relevant to humans. In general, the model used here is widely applicable to the ecology of RRV across Australia and other mosquito-borne zoonoses with multiple host species.

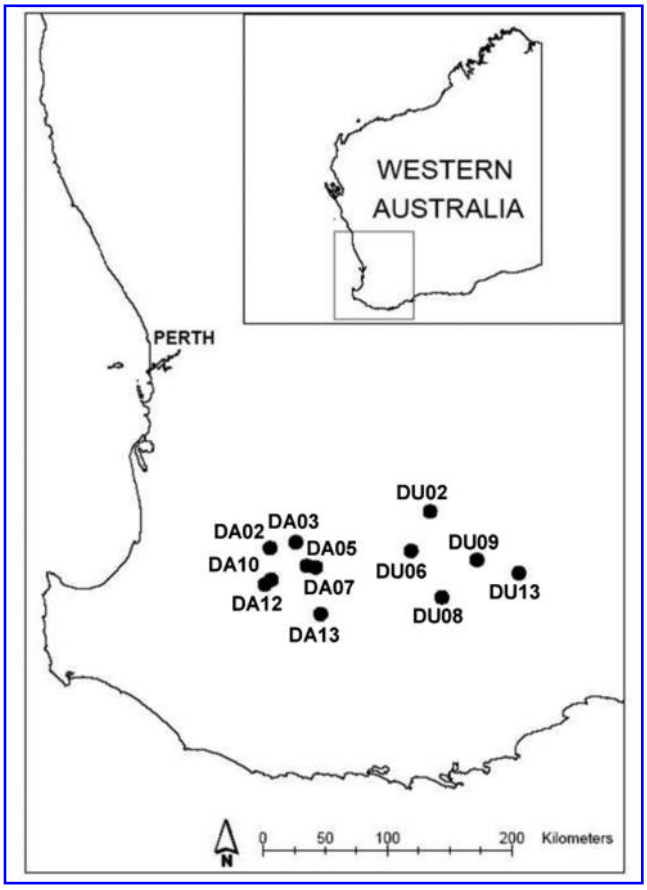

FIG. 1. Sites surveyed for *Ae. camptorhynchus* and mammal fauna in the Wheatbelt of southwest Western Australia.

Methods

Study area

This study was undertaken in the Great Southern meteorologic district of the WA Wheatbelt (Fig. 1). The study area has a Mediterranean climate with hot dry summers and mild wet winters. Annual rainfall declines from approximately 600 mm at the western boundary of our study area to 350 mm in the east (Australian Bureau of Meteorology). Approximately 80–90% of the region has been cleared for agriculture (Halse et al. 2004). Sites were separated by 5 km or more, located in remnant native vegetation, and chosen to correspond with locations previously used by the WA Department of Environment and Conservation to assess impacts of secondary salinization (Keighery et al. 2004).

Modeling

To investigate links between salinity and zoonotic RRV transmission in the Wheatbelt, we simulated the ecology of RRV transmission between *Ae. camptorhynchus* and multiple mammalian host species, using a simple deterministic SEIR model (Eq. 1, Table 1).

Table 1. Definitions of Parameter Used in the Model

b	bite rate of mosquitoes
r	rate at which hosts are bitten by mosquitoes
f_{H_i}	fraction of vectors that feed on host species i
T_{MH_i}	transmission probability (following a bite) from mosquito to host species i
T_{H_iM}	transmission probability from host species i to mosquito
σ_i	rate at which individuals of species i move from exposed to infectious classes
γ_{H_i}	recovery rate for host species i
μ	per capita death rate for mosquitoes
S_i	number of individuals of species i that are susceptible
E_i	number of individuals of species i that are exposed
I_i	number of individuals of species i that are infectious
R_i	number of individuals of species i that are immune
N_i	population size of species i

$$\frac{dS_M}{dt} = -r\sum_H T_{H,M}I_{H_i})S_M - \mu S_M$$

$$\frac{dE_M}{dt} = r(\sum_H T_{H,M}I_{H_i})S_M - \sigma_M E_M - \mu E_M$$

$$\frac{dI_M}{dt} = \sigma_M E_M - \mu I_M$$

$$\frac{dS_{H_i}}{dt} = -rf_i T_{MH_i} I_M S_{H_i}$$

$$\frac{dE_{H_i}}{dt} = rf_i T_{MH_i} I_M S_{h_i} - \sigma_{H_i} E_{H_i}$$

$$\frac{dI_{H_i}}{dt} = \sigma_{H_i} E_{H_i} - \gamma_{H_i} I_{H_i}$$

$$\frac{dR_{H_i}}{dt} = \gamma_{H_i} I_{H_i}$$

Where: $r = \dfrac{b}{N_H}$

$$R_0 = \sum_H \frac{(bf_{H_i})^2 T_{H_iM} T_{MH_i} N_M}{\mu \gamma_{H_i} N_{H_i}} \qquad \text{(Eq. 1)}$$

Equation 1 is the model of RRV transmission between *Ae. camptorhynchus* and multiple host species, and calculation of R_0. Mosquitoes (M) are divided into susceptible, exposed and infectious (S, E, and I, respectively) classes. Hosts (H) are divided into susceptible, exposed, infectious, and recovered (R) classes. For definition of parameters see Table 1.

Our model of epizootics assumes RRV is introduced into sites, where local transmission occurs, briefly, and is followed by local extinction of the virus. This assumption is consistent with observations of human cases by Jardine et al. (2008). Arboviruses can be transported by infected vectors (Kay and Farrow 2000) and hosts (Aaskov et al. 1981, Kelly-Hope et al. 2002, Lindsay et al. 1993c, McBride 2008, Ryan et al. 1997). We assumed RRV would most likely be introduced to a site by either a single infectious *Ae. camptorhynchus* or host. Initial trials of our model found RRV became extinct for all sites and dates, unless an artificially large vector population (2–10 million) was simulated. Consequently, further simulations were based on the introduction of a single infectious host, the hypothesized RRV reservoir in southwest WA, *M. fuliginosus* (Lindsay et al. 1996). Due to the brief temporal nature of RRV in the Wheatbelt, births and deaths of hosts were considered to be negligible during epizootics (Eq. 1). We made conservative assessments of *Ae. camptorhynchus* production for each simulation, assuming mosquitoes were introduced in a single pulse, death rate was constant, and infection with RRV chronic (Eq. 1, Ballard and Marshall 1986). The salinity of water bodies was assumed to have no significant effect on survival and developmental rate of larval *Ae. camptorhynchus* (Barton and Aberton 2005).

Our model assumes RRV transmission follows mass action (de Jong et al. 1995). Inclusion of the parameter r (Eq. 1, Table 1) means mosquito-to-host transmission is frequency-dependent, whereas host-to-mosquito transmission is density-dependent (Keeling and Rohani 2008). Simulations were conducted using MATLAB® R2007a (The MathWorks Inc., Natick, MA). Two assessments of potential for RRV transmission were calculated: epidemic size (ES, the number of infectious mosquitoes produced over the duration of the simulation) and reproductive ratio (R_0, the number of secondary infections in mosquitoes generated, assuming all hosts are susceptible, Eq. 1; Keeling and Rohani 2008).

Ae. camptorhynchus and mammal abundance parameters

The model was parameterized by our empirically derived estimates of mosquito and mammal abundance (Table 2). Surveys of larval *Ae. camptorhynchus* were conducted from September to December 2005 (spring) and February to May 2006 (late summer and autumn), and mammals from September to December 2006 and February to May 2007. These seasons were chosen to reflect the times of year when rainfall occurs, *Ae. camptorhynchus* were most abundant, and temperatures permissive for viral replication.

Surveys of *Ae. camptorhynchus* larvae were undertaken in (0.2×10^{-5}–0.97 ha) rain-fed ephemeral water bodies fortnightly across 12 sites (Fig. 1, described in detail by Carver et al., submitted). At each site, a 1-hectare quadrat was established in a low-lying area, and on each fortnightly sampling occasion, the surface area of the quadrat occupied by ephemeral water bodies calculated. In total, *Ae. camptorhynchus* larvae were sampled from 180 water bodies during the course of the surveys. Surveys of *Ae. camptorhynchus* were undertaken using a standard D-frame 500-mm diameter FBA pond net (250-μm mesh size: Australian Entomological Supplies Pty. Ltd., Bangalow, New South Wales),

Table 2. Salinity Category for Each Site and the Associated: Abundance of *Ae. Camptorhynchus* (Larval Abundance Adjusted to Number Surviving to Emergence) in a 1-Hectare Area (Empty Cells Indicate Dates When Sites Were Dry), for Each Sampling Period, and Average Abundance and Diversity of Mammals Occurring in a 1-km Radius Around the Mosquito Sampling Site

Site	*DA10*	*DA13*	*DU02*	*DU09*	*DA03*	*DA12*	*DA05*	*DA02*	*DA07*	*DU06*	*DU08*	*DU13*
Salinity	1	1	1	1	2	2	3	4	4	4	4	4
Ae. camptorhynchus												
12-14 Sep	0	0	5	0	1531	0	0	898	611	26490	0	580
24-26 Sep	0	0	0	0	227	0	0	3468		6101	4	3619
8-10 Oct	0	0	66	0	0	0	0	23882		3523	29	0
25-26 Oct	825		0		0	0		7750		7751	0	0
7-8 Nov	0		0		0	0		117		8342		0
27 Feb			0									
12 Mar			0									
27 Mar			0									
11 Apr			0									
24 Apr			0					0		9		
8 May								30		27		
Mammals												
Abundance	1502	5993	2061	3299	3550	1955	1272	1722	4605	5029	3753	3367
Diversity	5	6	4	5	5	5	4	5	6	4	5	6
O. aries[a]	742	669	515	432	668	454	391	301	299	53	192	197
M. fuliginosus	47	39	143	54	81	95	171	12	75	74	51	13
M. domesticus[a]	701	5257		2804	2103	1402	701	1402	1402	4205	3504	
O. cuniculus[a]	2	2	2	7		3	10	3	10		5	2
V. vulpes[a]		2		3	3	1					1	1
T. vulpecula[a]					696				2799	696		
P. calura[a]			1402									701
N. mitchelli[a]												2453
M. irma[a]								5				
C. hircus[a]										20		
E. caballus[a]		24										
S. scrofa[a]	10											

[a]Common name, genus and species, and authority: sheep *Ovis aries* (Linnaeus 1758, Bovidae), house mouse *Mus domesticus* (Schwarz & Schwarz 1943, Muridae: syn. *Mus musculus* Linneaus 1758), European rabbit *Oryctolagos cuniculus* (Linnaeus 1758, Leporidae), fox *Vulpes vulpes* (Linnaeus 1758, Canidae), brush-tailed possum *Trichosurus vulpecula* (Kerr 1792, Phalangeridae), red-tailed phascogale *Phascogale calura* (Gould 1844, Dasyuridae), Mitchell's hopping mouse *Notomys mitchelli* (Ogilby 1838, Muridae), brush wallaby *Macropus irma* (Jourdan 1837, Macropodidae), goat *Capra hircus* (Linnaeus 1758, Bovidae), horse *Equus cabalus* (Linnaeus 1758, Equidae), and pig *Sus scrofa* (Linnaeus 1758, Suidae).

which was swept through all water bodies and microhabitats within each water body at each site, and the area sampled for *Ae. camptorhynchus* was recorded. Samples were preserved in 70% ethanol and returned to the laboratory, where 6266 *Ae. camptorhynchus* were identified under a microscope (Liehne 1991). *Ae. camptorhynchus* abundance at each site for each sampling interval was calculated by multiplying the area sampled by the area occupied by standing water within each 1-hectare quadrat.

Surveys of mammals were undertaken using a combination of transect counts and trapping across 12 sites (Fig. 1, described in detail by Carver 2008c). Transect surveys were undertaken during the hour immediately after dawn and the half hour before dusk. Surveys consisted of walking an established line transect through remnant vegetation or slowly driving a transect along a farm track/dirt road through or adjacent to the remnant. Each site was surveyed repeatedly (6–8 times), and surveys were averaged to account for temporal and spatial variability in observations ($n = 87$ surveys). Densities of mammals at each site were calculated as the number observed per hectare, adjusted for observational area within each habitat type. Trapping grids were laid in areas of remnant vegetation at each site using box traps ($90 \times 90 \times 350$ mm, Elliott Scientific Equipment, Upwey, Victoria) and wire cage traps ($220 \times 220 \times 550$ mm, Sheffield Wire Products, Welshpool WA), baited with peanut butter (Sanitarium®, New South Wales) and rolled oats (Asia/Pacific Wholesalers Pty. Ltd., Parramatta, New South Wales). Traps were set just before dusk, then cleared and closed shortly after dawn. Each site was trapped twice (once in spring and once in autumn) for 3 consecutive nights, giving a total of 6480 trap nights. Trapping was used to estimate the minimum number alive of any mammal within the trapping grid and approximate densities per hectare for each site.

Abundance of adult *Ae. camptorhynchus* was calculated by adjusting larval abundance by survival rate (0.844 at 20°C, Barton and Aberton 2005; Table 2). Dispersal studies have found the majority (~90%) of adult *Ae. camptorhynchus* dispersal occurs within a 1-km radius of release site (Jardine 2007, Robertson 2006). As such, our measurement of mammal density (number per hectare) was scaled to abundance occurring in a 1-km radius around the mosquito sampling site (3.14 km^2, Table 2). This radius is also within the tran-

Table 3. Host Parameters and Assumptions for the Model

Species	f	T_{MH}	T_{HM}	σ	γ	*Reference*
O. aries	0.478	0.7[a]	0.5[b]	0.5–1[c]	0.25–1[c]	Jardine 2007, Spradbrow 1973
M. fuliginosus	0.290	1[a]	0.5[b]	1[b]	0.167	Jardine 2007, Kay and Aaskov 1989
M. domesticus	0.014	0.25–1[c]	0.75	1	0.125–1[c]	Ballard and Marshall 1986, Lindsay et al. 1998, Seay et al. 1981
O. cuniculus	0.027	0.5–0.778[a,c]	0.5[b]	1	0.333–1[c]	Jardine 2007, Kay and Aaskov 1989, Whitehead 1969
V. vulpes	0	0.1	0	0	0	Boyd and Kay 2002, Jardine 2007
T. vulpecula	*M. fuliginosus*[d]	0.3	0.53	1	1	Boyd et al. 2001, Jardine 2007
P. calurae	*M. domesticus*[f]	1[a]	0.5[b]	1	0.167–1[c]	Lindsay et al. 1998, Whitehead 1969
N. mitchelli	*M. domesticus*[f]	1[a]	0.5[b]	1	0.167–1[c]	Lindsay et al. 1998, Marshall and Miles 1984, Whitehead 1969
M. irma	*M. fuliginosus*[d]	1[a]	0.5[b]	1[b]	0.333–0.5[c]	Jardine 2007, Marshall and Miles 1984
C. hircus *E. caballus*	*O. aries*[d]	0.7[a]	0.5[b]	0.5	0.25[c]	Jardine 2007, Kay et al. 1987a
S. scrofa	0	0.909–1[a,c]	0.5[b]	1	0.2–1[c]	Jardine 2007, Kay and Aaskov 1989, Spradbrow 1973

See Table 1 for definitions of parameters f, T_{MH}, T_{HM}, σ, and γ.
[a]Transmission to host by subcutaneous inoculation.
[b]In the absence of empirical data, T_{HM} and σ assumed to equal 0.5 and unity, respectively.
[c]Where a range of values were available, a middle value was used.
[d]When blood meal data could cross-react with another host species at a site, f was partitioned between the cross-reacting species, based on the density of both hosts.
[e]Parameter values based on Bandicoot (*Isoodon macrourus*) from Whitehead (1969), Marsupial mouse (*Antechinus* sp.) from Whitehead (1969), Tammar wallaby (*Macropus eugenii*) from Marshall and Miles (1984), and *O. aries* from Spradbrow (1973).
[f]The contact rate (f) of *P. calura* and *N. mitchelli* with *Ae. camptorhynchus* was assumed to be consistent with the similar-sized mammal, *M. domesticus*.

sect survey boundaries from mammal surveys and similar to the size of vegetation remnants in which mammal trapping and surveys were conducted.

Salinity parameters

Salinity of sites was designated into four categories by the WA Department of Environment and Conservation (Keighery et al. 2004, McKenzie et al. 2003, van Gool and Moore 1999), and these categories were modified and supplemented by our own observations of dead trees (stags) and samphire in saline areas, which are known indicators of soil salinity and shallow water tables (Table 2): (1) nonsaline, due to absence of stags and samphire, high position in the landscape, low water table, high soil permeability, and/or the low salt store in the regolith; (2) low salinity impact or risk, due to stags and samphire being uncommon, small variation in local relief and geology where rising water tables may not affect all the land area, or where rising water tables are not currently saline, and the salt store in the regolith is low; (3) intermediate salinity impacted, due to common occurrence of stags and samphire, salinity occurring in limited areas, or from shallow saline groundwater with a rising trend; and (4) saline land, due to widespread occurrence of stags and samphire and obvious salt effects (such as large patches of bare earth) in the area. These salinity categories provided a good indication of the continuum of salinity changes in the field and are equivalent to those used by Carver (2008c), Keighery et al. (2004), and McKenzie et al. (2003).

RRV transmission parameters

Ae. camptorhynchus were predicted to seek a blood meal at a rate (b) of once per gonadotrophic cycle (7 days, Barton and Aberton 2005). Infected *Ae. camptorhynchus* become infectious at a rate (σ_M) of 1/3 days (Ballard and Marshall 1986). A specific mortality rate for adult *Ae. camptorhynchus* is unknown, so a general figure ($\mu = 0.1$) for *Aedes* sp. was used (Canyon et al. 1999, Carron et al. 2008, Harrington et al. 2001, Leisnham et al. 2008, Muir and Kay 1998, Niebylski and Craig 1994, Watson et al. 2000). Blood meal analysis of *Ae. camptorhynchus* in the Wheatbelt were conducted by Jardine (2007), and this information was used to determine f for each mammal species (Tables 1 and 3). For cases where mammal species blood was not examined by Jardine (2007), such as *M. domesticus*, f was approximated from Lindsay et al. (1998). The remaining parameters for hosts were derived from reports of RRV infections of mammals and approximated, where data were unavailable (Table 3).

Analyses

Linear regression analysis was used to examine the relationship between salinity category and the abundance of *Ae. camptorhynchus*, abundance and diversity of mammals, and abundance of mammal species (occurring at three or more sites). Linear regression was preferred over analysis of variance (in this and subsequent analyses) because salinity categories were indicative of a linear continuum of environmental change in the field, and there were few sites occurring at low and intermediate salinity categories (Cottingham et al. 2005). *Aedes camptorhynchus* exhibit temporal fluctuations (Table 2) associated with rain and temperature (Barton et al. 2004), and this is not easily controlled for in our analysis. Rather than using an average abundance of *Ae. camptorhynchus* per site, which would mask the observed natural variation, all samples were used in analyses, which contrib-

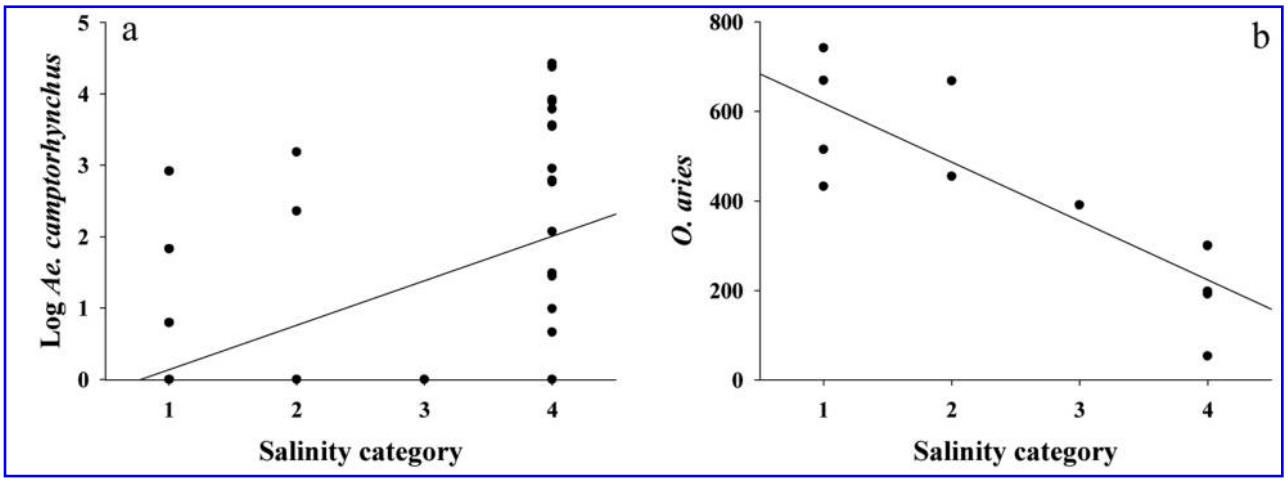

FIG. 2. Relationship between salinity category (1 = nonsaline, 2 = low saline, 3 = intermediate saline, and 4 = saline; Table 1) and **(a)** the abundance of *Aedes camptorhynchus* in 1-hectare area, at each sampling session, and **(b)** average abundance of *Ovis aries* in 1-km radius surrounding mosquito sampling site (linear regressions plus predictor and constant coefficients (± standard error): $r^2 = 0.305$, $F_{1,6} = 24.597$, $p < 0.001$, 0.624 (0.126), and −0.491 (0.359); and $r^2 = 0.720$, $F_{1,10} = 25.665$, $p < 0.001$, −131.34 (25.93), and 748.77 (75.21) respectively; critical α-value 0.007, Table 2). Figure 2b modified and reproduced with permission from Carver, 2008c.

uted variation but provided a more holistic view of the relationship between abundance of *Ae. camptorhynchus* and salinity category. Abundance data of mosquitoes were log transformed to achieve normality. For all statistical tests, the significance level was set at 0.05. But to reduce the probability of committing type I statistical errors, α was adjusted for multiple comparisons using the sequential Bonferroni method (Rice 1989), where k is the number of analyses testing the same hypothesis. Analyses were undertaken using SPSS 15.0 (SPSS Inc., Chicago, IL).

After calculating R_0 and ES from our simulations, we retrospectively examined which factors (salinity, mosquito, or mammal) explained the greatest amount of variation in the potential for RRV transmission. We used linear regressions to examine the relationship of R_0 and ES to salinity category, abundance of *Ae. camptorhynchus*, abundance and diversity of mammals, and abundance of mammal species (occurring at three or more sites). In cases where *Ae. camptorhynchus* or mammals were significantly related to salinity, we examined residual variation to control for salinity interrelationships in regressions. R_0, ES, and abundance data of mosquitoes and mammals were log-transformed to achieve normality, and á was adjusted for multiple comparisons using the sequential Bonferroni method (Rice 1989). Analyses were undertaken using SPSS 15.0 (SPSS Inc.).

Results

Vectors, mammals, and salinity

Aedes camptorhynchus were predominantly detected in the highest salinity category (Table 2 and Fig. 2a). However, this mosquito was also occasionally detected at low saline and nonsaline sites (DA10, DU02, and DA03, Table 2 and Fig. 2a). There was temporal variability in the existence of standing water between sites and the number of *Ae. camptorhynchus* within and between sites (Table 2). The overall abundance of *Ae. camptorhynchus* increased positively with salinity category (Fig. 2a). For mammals, *O. aries* decreased in association to increasing salinity category (Fig. 2b). The remaining measures of host species were not significantly related to salinity (Table 2, linear regressions $p > 0.05$ in all instances, Carver, 2008c).

Modeling results

R_0, as a measure of potential for RRV transmission, did not exceed unity at any site or sampling time in the first three salinity categories (Table 4). *Ae. camptorhynchus* were encountered on 5/34 sampling occasions in the first three salinity categories (Table 1), meaning that both R_0 and ES values for our model were 0 for 25/34 sampling occasions (Table 4). Comparatively, *Ae. camptorhynchus* was detected on 18/24 sampling occasions in the fourth salinity category (Table 4). R_0 and ES values varied between sites and over time within sites (Table 4). Both R_0 and ES values were higher during spring and at DA02, DU06, and DU13 than in autumn and at other sites (Table 4). Epidemic size values from introducing a single infectious host (*M. fuliginosus*) were small, only exceeding unity for 2/58 simulations (Table 4).

Analysis of R_0 and ES found these measures of potential for RRV transmission were significant and positively related to salinity category and abundance of *Ae. camptorhynchus* (Table 5, Fig. 3a and 3b). Additionally, there was a significant negative relationship between R_0 and the abundance of *M. fuliginosus* (Fig. 3c). Regressions between R_0 and the abundance of *V. vulpes* and ES and the abundance of *M. fuliginosus* and *V. vulpes* were all negative, but not significant (Table 5), implying that sampling of a greater number of sites may have picked up an effect. Abundance of *Ae. camptorhynchus* explained more variation in R_0 and ES potential for RRV transmission than any other variable (Table 5, Fig. 3b).

Discussion

RRV transmission is governed by ecological interactions between zoonotic hosts and vectors (Harley et al. 2001,

TABLE 4. R_0 AND EPIDEMIC SIZE VALUES (R_0/ES) FOR SITES AND DATES IN WHICH EPHEMERAL WATER BODIES WERE SAMPLED FOR *AE. CAMPTORHYNCHUS* (SALINITY CATEGORY FOR EACH SITE ALSO LISTED)

Site	*Salinity*	*12–14 Sept*	*24–26 Sept*	*8–10 Oct*	*25–26 Oct*	*7–8 Nov*	*24 Apr*	*8 May*
DA10	1	0/0	0/0	0/0	0.96/0.12	0/0		
DA13	1	0/0	0/0	0/0				
DU02[a]	1	0.002/0.001	0/0	0.03/0.01	0/0	0/0	0/0	
DU09	1	0/0	0/0	0/0				
DA03	2	0.08/0.09	0.01/0.01	0/0	0/0	0/0		
DA12	2	0/0	0/0	0/0	0/0	0/0		
DA05	3	0/0	0/0	0/0				
DA02	4	2.39/0.11	9.22/0.43	63.5/2.98	20.61/0.95	0.31/0.01	0/0	0.08/0.04
DA07	4	0.06/0.03						
DU06	4	13.22/1.11	3.05/0.26	1.76/0.15	3.87/0.32	4.16/0.35	0.004/0.004	0.01/0.001
DU08	4	0/0	0.004/0.0002	0.03/0.002	0/0			
DU13	4	2.43/0.04	15.14/0.23	0/0	0/0	0/0		

[a]Ephemeral water bodies also occurred and were sampled on February 27, March 12, March 27, and April 11, 2006, but no *Ae. camptorhynchus* were detected on these dates (Table 1) giving an R_0/ES value of 0/0 for each.

Russell 2002). Accordingly, anthropogenic impacts on the environment that affect the dynamics of these interactions may influence potential for transmission. This study supports the hypothesis that salinity promotes the spatial potential for RRV transmission. We also observed temporal variability in transmission potential within our study sites. Our modeling results are best explained by salinity and variation in abundance of *Ae. camptorhynchus* and *M. fuliginosus*.

This study found abundance of *Ae. camptorhynchus* explained more variation in potential for RRV transmission than any other variable. Abundance of *Ae. camptorhynchus* also determined temporal variability in potential for RRV transmission, because there were fewer standing water bodies during late summer and autumn, reflecting low regional rainfall. *Ae. camptorhynchus* larvae have a broad salinity tolerance, and their abundance is positively associated with in-

TABLE 5. REGRESSION ANALYSES OF R_0 AND ES AGAINST SALINITY, *AE. CAMPTORHYNCHUS,* MAMMAL ABUNDANCE, DIVERSITY, AND THE ABUNDANCE OF THE MOST COMMON MAMMALS

	R_0			*Regression coefficients (± SE)*		ES			*Regression coefficients (± SE)*	
	r	$F_{1,56}$	p[a]	*Predictor*	*Constant*	r^2	$F_{1,56}$	p[a]	*Predictor*	*Constant*
Salinity	0.225	16.292	**<0.001**	0.140 (0.035)	−0.171 (0.099)	0.133	8.600	**0.005**	0.027 (0.009)	−0.032 (0.026)
Ae. camptorhynchus	0.438	43.614	**<0.001**	0.208 (0.031)	0.182 (0.040)	0.336	28.354	**<0.001**	0.045 (0.008)	0.035 (0.011)
Abundance	0.002	0.120	0.731	0.092 (0.267)	−0.314 (0.916)	0.001	0.001	0.974	0.002 (0.066)	0.028 (0.227)
Diversity	0.001	0.005	0.944	0.005 (0.078)	0.116 (0.379)	0.004	0.206	0.652	−0.009 (0.019)	0.077 (0.093)
O. aries	0.001	0.024	0.878	−0.000 (0.001)	0.182 (0.053)	0.001	0.009	0.925	−0.000 (0.001)	0.035 (0.013)
M. fuliginosus	0.196	13.686	**<0.001**	−0.482 (0.130)	1.026 (0.233)	0.104	6.495	0.014	−0.087 (0.034)	0.187 (0.061)
M. domesticus	0.012	0.656	0.421	0.029 (0.036)	0.111 (0.103)	0.031	1.773	0.188	0.012 (0.009)	0.007 (0.025)
O. cuniculus	0.031	1.775	0.188	−0.237 (0.178)	0.293 (0.098)	0.020	1.156	0.287	−0.048 (0.044)	0.058 (0.024)
V. vulpes	0.062	3.674	0.060	−0.461 (0.240)	0.258 (0.065)	0.053	3.165	0.081	−0.106 (0.060)	0.053 (0.016)
T. vulpecula	0.017	0.954	0.333	0.043 (0.044)	0.155 (0.060)	0.018	1.047	0.311	0.011 (0.011)	0.028 (0.015)

R_0, ES, and *Ae. camptorhynchus* were log-transformed for the analyses. Regressions were against residuals for *Ae. camptorhynchus* and *O. aries* to control for salinity interrelationships. Significant results adjusted for multiple comparisons using the sequential Bonferroni method and shown in bold. SE, standard error.

[a]Critical α-values for $R_0 = 0.007$ and ES = 0.006.

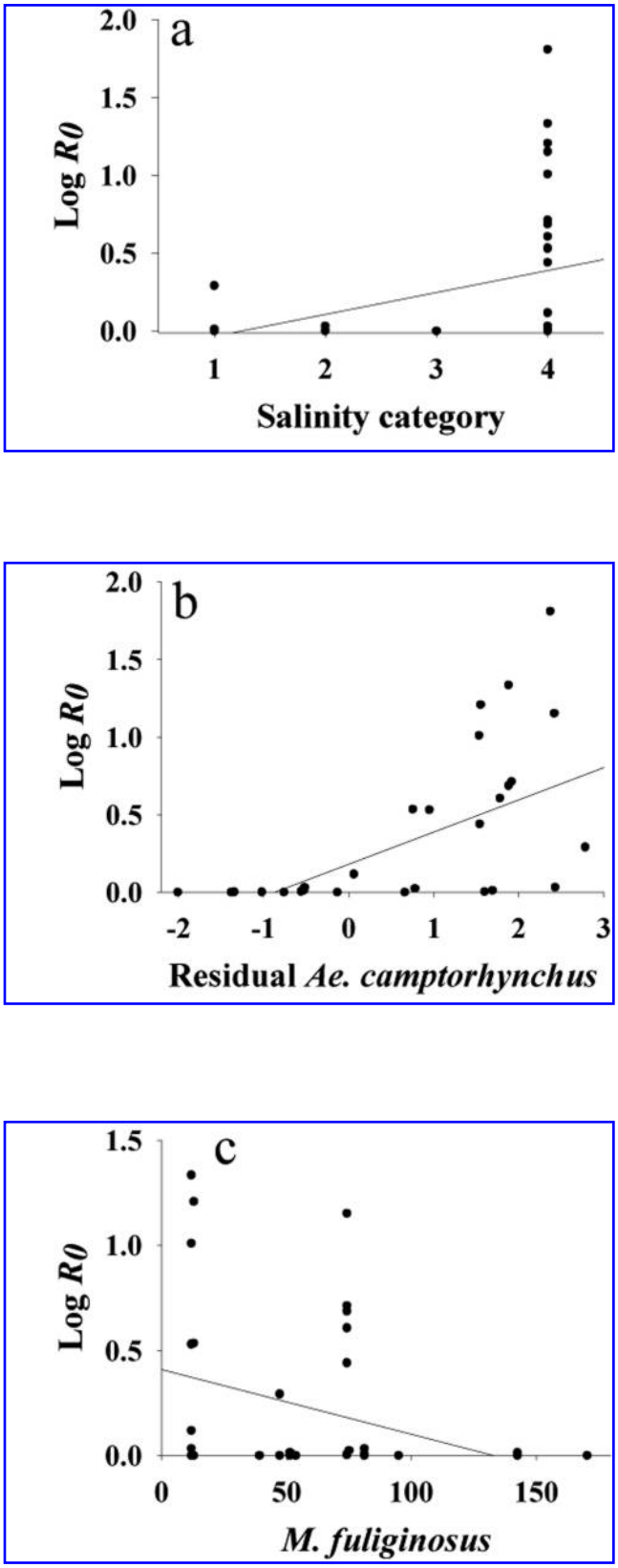

FIG. 3. Relationships of R_0 with **(a)** salinity category, **(b)** the abundance of *Aedes camptorhynchus* and **(c)** *Macropus fuliginosus* (linear regressions: $r^2 = 0.225$, $F_{1,56} = 16.292$, $p < 0.001$; $r^2 = 0.438$, $F_{1,56} = 43.614$, $p < 0.001$; and $r^2 = 0.196$, $F_{1,56} = 13.686$, $p < 0.001$, respectively, Table 5).

creasing salinity, irrespective of the temporal variability in their abundance, due to standing water and rainfall. It is possible the positive relationship between *Ae. camptorhynchus* reflects release from interspecific competition (Carver et al. submitted). It should, however, be noted that our estimates of mosquito abundance, and by extension potential for RRV transmission, are conservative. In each simulation, we assumed all mosquitoes in space were derived from our 1-hectare sampling site. We also assumed no additional mosquitoes were produced during the temporal period of each simulation. Both of these assumptions are likely to underestimate *Ae. camptorhynchus* abundance. As such, our estimates of potential for transmission are spatially and temporally conservative.

A possible caveat involving *Ae. camptorhynchus*, in this study, is when the percentage of blood meals obtained from each mammal species were added together, 16.9% of blood meals were not accounted for. We assumed these blood meals were derived from vertebrate species, which are incompetent RRV hosts. However, if some of these blood meals are derived from competent hosts, our estimates of potential for RRV transmission may increase. Our model also did not consider vertical transmission of RRV, though this is known to occur for *Ae. camptorhynchus* (Dhileepan et al. 1996). Vertical transmission may influence persistence of RRV (Glass 2005, Lindsay et al. 1993b), but we considered it unlikely to influence the difference between saline and nonsaline areas (the focus of this study). Finally, other mosquito species occur in the WA Wheatbelt (Lindsay et al. 2007), and it is possible these species may contribute to RRV transmission. *Aedes camptorhynchus* is the dominant vector in southwest WA (Lindsay et al. 1996, 2007). Other mosquito species identified in the Wheatbelt have not been shown to transmit RRV or are infrequent in occurrence, suggesting *Ae. camptorhynchus* is likely to be the only relevant vector mosquito (Lindsay et al. 2007).

The negative relationship of R_0 to abundance of *M. fuliginosus* is in contrast to the putative reservoir status of this host. However, there is a negative correlation between the abundance of *M. fuliginosus* and *Ae. camptorhynchus* (Spearman correlation, $\rho = -0.325$, $p = 0.013$). This correlation suggests the relationship between potential for RRV transmission and abundance of *M. fuliginosus* may be due to a correlation with *Ae. camptorhynchus*, rather than a causal relationship. It is possible *M. fuliginosus* may avoid areas where they are likely to receive many nuisance bites from *Ae. camptorhynchus* or this correlation could reflect the effect of a combination of salinity and vegetation variables on abundance of *M. fuliginosus* not captured in this study. Abundance of *Ae. camptorhynchus*, according to our model, appears to be a better predictor of potential for RRV transmission in the Wheatbelt than abundance of *M. fuliginosus*. In addition, *O. aries* comprise the majority (47.8%) of mosquito blood meals in the Wheatbelt (Jardine 2007). This mammal declined in association with increasing salinity, reflecting degradation of agricultural land and a reduction in pasture for grazing (Barrett-Lennard 2003, Dorrough et al. 2004, McFarlane and Williamson 2002, Spradbrow 1973). *Ovis aries* has a moderate capacity as a host for RRV but did not explain variation in the potential for RRV transmission when regressions were controlled for salinity.

Our estimates of abundance of some trapped mammals at some sites, such as *T. vulpecula*, *M. domesticus*, *P. calura*, and *N. mitchelli*, appear relatively high, reflecting high trap success. Consequently, our estimates of abundance over the 3.14 km^2 area, used in the modeling, were also high, and it is possible mammal abundance results may influence our estimates of potential for RRV transmission. The abundance of trapped mammals presented in this study are either within the range of other published accounts or have not previously been documented (Brockie et al. 1997, Brown et al. 1997, De Long 1967, Efford et al. 2005, Fox et al. 2003, How and Hillcox 2000, Isaac 2005, Jacob et al. 2007, Sinclair et al. 1990, Southgate and Masters 1996, Wayne et al. 2005). Notwithstanding a more detailed study of mammal abundance at each of our sties, the results here do reflect spatial differences in abundance of mammals between sites. In addition, none of these mammals were either common enough between our sites and/or had a significant effect on our measure of potential for RRV transmission.

Spatial and temporal variability in *Ae. camptorhynchus* blood meals may influence variability in potential for RRV transmission. In this study, our values for f were based on the total percentage of blood-engorged *Ae. camptorhynchus* collected in the Wheatbelt by Jardine (2007). However, Jardine (2007) did demonstrate some spatial and temporal variability within *Ae. camptorhynchus* blood meals. We did not incorporate this variability into our model due to difficulties in matching sites spatially and confidently attributing salinity categories. However, given dominance of *Ae. camptorhynchus* in explaining potential for RRV transmission, spatial and temporal variability in f may only have a minor influence on our results. It is also possible T_{MH} may be an overestimated parameter where subcutaneous inoculations were used, and R_0 and ES may be influenced by the use of a central value for T_{MH}, σ, and γ, rather than a range of values. But again, these possible caveats do not influence our spatial comparison between sites and salinity categories.

It is important acknowledge that population cycles differ for *Ae. camptorhynchus* and mammal species in the Wheatbelt. In addition to salinity, results from this study reflect temporal variability in abundance of *Ae. camptorhynchus*, due to standing water and rainfall. However, the abundance of individual mammal species may vary over longer temporal periods (i.e., seasonal or interannual), which could influence the outcome of our model, but is beyond the timescale of this study. Further research is needed to assess how long-term cycles in the abundance of host species and communities, such as those caused by long-term drought, influence the potential for transmission of vector-borne diseases.

In contrast to studies of WNV and Lyme disease (Ezenwa et al. 2006, 2007, LoGiudice et al. 2003), we did not find an association between potential for RRV transmission and host diversity. The variability in mammal species diversity, between sites, was low (4–6) in this study. Consequently, we cannot confidently assess whether host diversity influenced potential for RRV transmission. The contribution of host diversity to RRV transmission requires more detailed investigation (Carver et al. 2008a). Additionally, the relative density and community of mammals necessary for RRV transmission (zoonotic, epizootic, or epidemic) is not well understood. Greater focus on hosts of RRV and their role in transmission is warranted (Carver et al. 2008a).

This study suggests that potential for transmission of RRV is greater in saline areas of the Wheatbelt, particularly during the months of September to November, when rainfall and *Ae. camptorhynchus* are common and temperatures are permissive for viral replication. Heavy rain, which facilitates abundance of *Ae. camptorhynchus*, may also promote potential for RRV activity at other times of the year (i.e., summer). However, human notification data does not currently reflect the salinity-RRV potential (Jardine et al. 2008). It is possible the examination by Jardine et al. (2008) of a sparse human population over a large geographical area may be an inappropriate scale of spatial variability in RRV transmission. In support, other studies have found evidence of variability in vector-borne transmission and transmission risk over smaller spatial scales (Ezenwa et al. 2006, 2007, Hu et al. 2004, Ostfeld et al. 2002, 2006, Ryan et al. 2006). In fact, our site with greatest potential for RRV transmission, DA02, occurred within the lowest saline area of Jardine et al. (2008). It is also possible salinity may influence potential for RRV transmission, but not activity. RRV appears to be episodic and nonpersistent in the Wheatbelt (Jardine et al. 2008). For example, a limited outbreak of RRV occurred in Wickepin in early 2006 but not elsewhere in the region (Jardine 2007). Comparison of RRV clinical notifications between the Wheatbelt and the endemic coastal zone indicates RRV activity in the Wheatbelt is linked to coastal epidemics and movement of infected vectors or hosts inland (Spearman correlation of published RRV notifications from Wheatbelt with southwest coastal and metropolitan Perth 1988–89, 1991–92, 1995–96, and 2001–04, $\rho = 0.750$, $p = 0.05$; Jardine et al. 2008, Lindsay et al. 1997, 2005). The Peel region, 70–130 km south of Perth, appears to be significant source from which coastal RRV activity may originate (Lindsay et al. 1996, 1997, 2005). We speculate that although salinity influences potential for RRV transmission, coastal RRV activity is a more parsimonious determinant of RRV activity in the Wheatbelt.

This study suggests dryland salinity is the proximate cause of enhanced potential for RRV transmission, but not activity, in the WA Wheatbelt. Our results indicate the ecologic determinant of this potential is predominantly enhanced abundance of *Ae. camptorhynchus*, which is halophilic. Other studies have also found links between vector-borne disease activity and salinity. Biggs and Mottram (2008) linked dryland salinity, abundance of *Aedes vigilax* Skuse (Diptera: Culicidae), and RRV notifications in Queensland; Temel (2004) identified salinity to be positively associated with malaria (*Plasmodium falciparum*) incidence in Azerbaijan; and Klinkenberg et al. (2004) found malaria incidence in southern Punjab was negatively related to increasing salinity and changes in the composition of *Anopheles stephensi* Liston (Diptera: Culicidae) and *Anopheles culicifacies sensu lato* (Diptera: Culicidae). Currently, more than one million hectares are saline in the Wheatbelt, and dryland salinity is expected to expand to between three and four and a half million hectares by 2050 (George et al. 2006, Jardine et al. 2007). This expansion of dryland salinity is likely to enhance the potential for RRV transmission in inland southwest WA and may influence RRV activity. Preservation and restoration of the natural environment and, by extension, intact freshwa-

ter communities may represent a valuable ecosystem approach to ameliorating potential for transmission of RRV.

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