

Drought-Induced Amplification and Epidemic Transmission of West Nile Virus in Southern Florida

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ABSTRACT We show that the spatial-temporal variability of human West Nile (WN) cases and the transmission of West Nile virus (WNV) to sentinel chickens are associated with the spatial-temporal variability of drought and wetting in southern Florida. Land surface wetness conditions at 52 sites in 31 counties in southern Florida for 2001–2003 were simulated and compared with the occurrence of human WN cases and the transmission of WNV to sentinel chickens within these counties. Both WNV transmission to sentinel chickens and the occurrence of human WN cases were associated with drought 2–6 mo prior and land surface wetting 0.5–1.5 mo prior. These dynamics are similar to the amplification and transmission patterns found in southern Florida for the closely related St. Louis encephalitis virus. Drought brings avian hosts and vector mosquitoes into close contact and facilitates the epizootic cycling and amplification of the arboviruses within these populations. Southern Florida has not recorded a severe, widespread drought since the introduction of WNV into the state in 2001. Our results indicate that widespread drought in the spring followed by wetting during summer greatly increase the probability of a WNV epidemic in southern Florida.

KEY WORDS West Nile virus, amplification, transmission, *Culex nigripalpus*, drought

SINCE IT FIRST APPEARED in New York City during summer 1999 (Marfin and Gubler 2001), West Nile virus (WNV) has spread throughout most of North America and has become a considerable public health concern. The processes driving rates of WNV transmission are still not well understood; however, the epidemiology of WNV in Florida is similar to that of St. Louis encephalitis virus (SLEV) (Rutledge et al. 2003). Four years of sentinel chicken surveillance in Florida (2001–present) support this observation and show that WNV transmission patterns are remarkably similar to those observed for SLEV transmission (Day and Stark 1996), although transmission rates of WNV are higher than those observed for SLEV. Both WNV and SLEV are maintained in an enzootic cycle involving avian amplifying hosts and vector mosquitoes (Day and Stark 1999; Sardelis et al. 2001; Komar et al. 2003). In southern Florida, *Culex nigripalpus* Theobald is the demonstrated enzootic and epidemic vector of SLEV (Chamberlain et al. 1964; Dow et al. 1964; Shroyer 1991). This mosquito has been shown to be a competent vector of WNV (Sardelis et al. 2001), and transmission of WNV by *Cx. nigripalpus* in the field has been documented (Rutledge et al. 2003).

During the 3 yr that complete annual WNV transmission cycles have been observed in Florida (2001–2003), sporadic and focal transmission have been reported (Blackmore et al. 2003). Florida has yet to record a major WNV epidemic. The WNV transmission patterns reported thus far in Florida (sporadic, focal, and rare epidemics) are very similar to transmission patterns reported for SLEV in the same region (Day and Stark 2000). A notable difference in this comparison is that there seem to be many more human cases reported during focal and sporadic outbreaks. This suggests that the number of infected mosquitoes is elevated during the amplification and early epidemic phases of the Florida arboviral transmission cycle (Day and Curtis 1999). A possible explanation for this is that wild birds and vector mosquitoes are more susceptible to infection with WNV and that wild birds may experience prolonged, elevated viremias (Komar et al. 2003).

Recently, we found an association between antecedent drought, coincident wetting, and transmission of SLEV in Indian River County, Florida (Shaman et al. 2002a, 2004a). We used a dynamic hydrology model (Stieglitz et al. 1997; Shaman et al. 2002b) to hindcast mean area water table depth (WTD), a measure of local land surface wetness, in Indian River County, and compared this simulated WTD to sentinel chicken seroconversion data. In Florida, seroconversions of sentinel chickens have been strongly correlated with the clinical disease in humans (Day and Stark 2000).

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Using logistic regression, we found the probability of sentinel chicken seroconversion, i.e., transmission of SLEV, to be strongly associated with low WTDs (drought) 11–17 wk prior and higher WTDs (wetting) 0–2 wk prior (Shaman et al. 2002a).

A mechanism for this empirical relationship was suggested by mosquito collection data, taken in Indian River County in densely vegetated “hammock” habitats used by *Cx. nigripalpus* females for daytime resting (Day and Curtis 1993). During the driest conditions (low modeled WTD) preceding heavy SLEV transmission, *Cx. nigripalpus* collections increased dramatically (Shaman et al. 2002a). Rather than indicate an increase of mosquito abundance, these data suggest that drought restricts *Cx. nigripalpus* activity to the more humid hammock habitats. Extreme drought periods in southern Florida tend to occur during the spring, a time when nesting wild birds also make use of the hammocks. Thus, drought drives the mosquitoes and birds into contact with one another. This forced interaction of vector mosquitoes and susceptible avian amplification hosts provides an ideal environment for the rapid epizootic amplification of SLEV. In addition, confinement of gravid *Cx. nigripalpus* females to the hammock habitats for extended periods allows infected females to complete the extrinsic incubation of acquired arboviruses during a single gonotrophic cycle (Day and Curtis 1993, 1999). Subsequently, when the drought ends and water resources increase, infected mosquitoes and birds disperse and carry the virus from the hammocks. Gravid female mosquitoes oviposit, refeed, and if infective, may transmit SLEV.

Similar drought and wetting patterns have been associated with the prevalence of SLEV in wild birds (Shaman et al. 2003a) and the occurrence of human cases of St. Louis encephalitis (SLE) throughout southern Florida (Shaman et al. 2004b). Together, these findings indicate that three factors conspire to create high epidemic risk in southern Florida: 1) a large population of susceptible wild birds; 2) severe springtime drought, which facilitates amplification of the SLEV among the *Cx. nigripalpus* vectors and a portion of the wild bird population; and 3) continued rainfall and wetting of the land surface in the summer and early fall, which sustains a large, active *Cx. nigripalpus* population. The continued biting and reproductive activity of infected *Cx. nigripalpus* maintains epizootic virus transmission between mosquitoes and susceptible wild birds throughout the summer and early fall. These conditions promote high levels of SLEV amplification and facilitate spillover transmission to humans resulting in sporadic or epidemic transmission of the virus (Day and Stark 2000).

In this study, we shift our analysis to WNV transmission and the occurrence of human WN cases throughout southern Florida, where *Cx. nigripalpus* is the dominant vector of SLEV. We simulated hydrological conditions by using a dynamic hydrology model at 52 sites in 31 southern Florida counties and compared simulated mean area WTD at each of these sites with sentinel chicken transmission data and the

occurrence of human WN infections within each county.

Materials and Methods

Topographically Based Hydrology (TBH) Model. We use a dynamic hydrology model (Stieglitz et al. 1997, Shaman et al. 2002b), here referred to as the TBH model, to simulate variations in WTD at 52 station sites. Mean area WTD provides an integrated measure of near surface soil wetness. Modeled WTD is measured in meters relative to the surface. During drought modeled WTD is further below the surface (more negative). It is the rise and fall of the water table that determines where and when pools of water form at the land surface, thus creating potential larval mosquito habitats.

Forcing meteorological data for the TBH model were assembled from National Climate Data Center archives for all stations with near complete daily records of precipitation and temperature spanning 1988–2003 (>80% complete) for 31 southern Florida counties. Data before 2001, the year WNV occurred in Florida, were used for model spin up. Gaps in the daily records were filled with data from adjacent stations. A total of 52 records of 1988–2003 daily data were assembled. Hourly meteorological forcing data sets were generated from daily records of precipitation and temperature data by using a resampling procedure (Shaman et al. 2003b, 2004b).

The TBH model was calibrated and validated at the Vero Beach 4W site as described previously (Shaman et al. 2002a, 2003b, 2004a, b). Model simulations at all 52 station sites were performed using the calibrations established at the Vero Beach 4W site.

Sentinel Chicken Data. We used data from 196 different sentinel flocks maintained in 23 southern Florida counties (Appendix 1). Eight of the counties within the study area have not maintained sentinel flocks since the introduction of WNV into Florida. Generally, a 1.0-ml blood sample was drawn weekly from each bird during peak transmission periods (July–November) and twice a month during the rest of the year. Serum samples were assayed for Flavivirus and Alphavirus hemagglutination inhibition (HI) antibodies. Group-positive HI serum samples were identified to species by IgM enzyme immunoassays and plaque reduction neutralization tests at the Florida Department of Health and Rehabilitative Services, Tampa Branch Laboratory. All arboviral-positive sentinel chickens were replaced immediately with baseline-negative birds. Most flocks were replaced with baseline-negative birds each May.

Human WN Data. Summaries of mosquito-borne arboviral human case data are compiled, analyzed, and reported weekly, monthly, and annually by the Florida Department of Health, Tallahassee, FL. For this study, we used monthly human West Nile cases, both neuroinvasive encephalitis and milder WN fever, as reported by southern Florida counties for 2001–2003 (Table 1).

Table 1. Reported human WN cases by month of onset in southern Florida for 31 counties in southern Florida, 2001–2003

Year	County of residence	No. human SLE cases	Mo of onset
2001	Sarasota	1	July
2001	Monroe	1	Aug.
2001	Monroe	1	Sept.
2001	Palm Beach	1	Sept.
2002	Dade	1	July
2002	Dade	1	Aug.
2002	Hillsborough	1	Aug.
2002	Orange	1	Aug.
2002	Polk	1	Aug.
2002	Sarasota	1	Aug.
2002	Citrus	1	Sept.
2002	Lake	1	Sept.
2002	Lee	1	Sept.
2002	Brevard	1	Oct.
2002	Collier	1	Oct.
2002	Highlands	1	Oct.
2002	Palm Beach	2	Oct.
2002	Manatee	1	Nov.
2002	Pasco	1	Nov.
2002	Sarasota	1	Nov.
2003	Brevard	1	July
2003	Broward	4	July
2003	Dade	2	July
2003	Lee	1	July
2003	Collier	1	Aug.
2003	Dade	4	Aug.
2003	Lee	2	Aug.
2003	Sarasota	1	Aug.
2003	Seminole	1	Aug.
2003	Volusia	1	Aug.
2003	Citrus	2	Sept.
2003	Desoto	1	Sept.
2003	Monroe	1	Sept.
2003	Seminole	1	Sept.

Logistic Regression. Bivariate logistic regression analysis was used to associate the probability of countywide dichotomous categories of WNV transmission to sentinel chickens and human WN cases with lag combinations of half-monthly modeled WTD at each station site within the county. WTD was aggregated in half-monthly averages. Lag comparisons were made in which the half-monthly average WTD for 16–31 May was considered lagged one-half month with June WNV transmission to sentinel chickens. All counties were analyzed in aggregate. Whole model goodness-of-fit was measured by log-likelihood ratio and the pseudo r-squared (uncertainty) coefficient. Individual parameter estimates were made using a maximum

likelihood procedure; Wald χ^2 tests were used to determine whether these estimates were significantly different from zero.

Nonparametric Analysis. Nonparametric analyses were performed to determine whether drought and wetting were associated with human WN cases. During 2001–2003, for the counties represented in this study, there were 34 instances in which a county reported one or more monthly human WN cases. We therefore calculated the number of these 34 occurrences for which antecedent drought fell below a given mean half-monthly WTD and near lag wetting was above a second mean half-monthly WTD (e.g., a WTD below -1.4 m 4 mo prior and above -1.2 m 0.5 mo prior) somewhere within the county. A range of such thresholds was used. Time lags used for this analysis were chosen from the best-fit models of the logistic regression analysis. Many counties have more than one station record, and for this analysis we only required that at least one station meet the drought and wetting criterion.

Bootstrap confidence intervals then were estimated using a Monte Carlo procedure. Ten thousand combinations of the 34 county-months were sampled randomly among the years 2001–2003, and a distribution of the totals meeting each defined criterion of drought and wetness was constructed. The significance of the actual number of antecedent drought and near lag wetting occurring with human WN case occurrence then was assessed based on this distribution of 10,000. The null hypothesis was that the number of counties meeting the drought and wetting criterion was no greater than that due to chance.

Results

We first defined dichotomous categories of monthly transmission of WNV to sentinel chickens within a county: 1, if greater than a cut-off percentage of the chickens tested positive for WNV antibodies; and 0, if less than (or equal to) the cut-off percentage of the chickens tested positive for WNV antibodies. The cut-offs tested were 0 (i.e., whether any chickens tested positive), 10, 20, and 30%. Increasing cut-off percentages reflected greater transmission activity.

Table 2 shows the best-fit results of logistic regression analysis with this categorical sentinel chicken data. Table 2 presents only the best-fit results, but in

Table 2. Best-fit empirical relationships based on bivariate logistic regression analyses of dichotomous categories of monthly countywide WNV transmission to sentinel chickens (2001–2003) on half-month lags of modeled WTD as simulated by the TBH model at each station site within the county

Dichotomous predictand	Lag 1 (mo)	Lag 2 (mo)	Intercept	Lag 1 slope	Lag 2 slope	Whole model fit
>0% Chickens positive	4	1	-0.73 ($P < 0.005$) (0.26)	0.73 ($P < 0.0005$) (0.21)	-1.85 ($P < 0.0001$) (0.20)	$P < 0.0001$
>10% Chickens positive	4	1.5	1.82 ($P < 0.0001$) (0.34)	2.11 ($P < 0.0001$) (0.29)	-2.03 ($P < 0.0001$) (0.23)	$P < 0.0001$
>20% Chickens positive	3.5	1.5	2.98 ($P < 0.0001$) (0.44)	2.59 ($P < 0.0001$) (0.40)	-2.27 ($P < 0.0001$) (0.44)	$P < 0.001$
>30% Chickens positive	3.5	1.5	4.72 ($P < 0.0001$) (0.81)	2.79 ($P < 0.0001$) (0.69)	-1.99 ($P < 0.0001$) (0.51)	$P < 0.0001$

All 23 counties with posted sentinel chickens are analyzed in aggregate. Parameter significance and the estimate of standard error are given in parentheses.

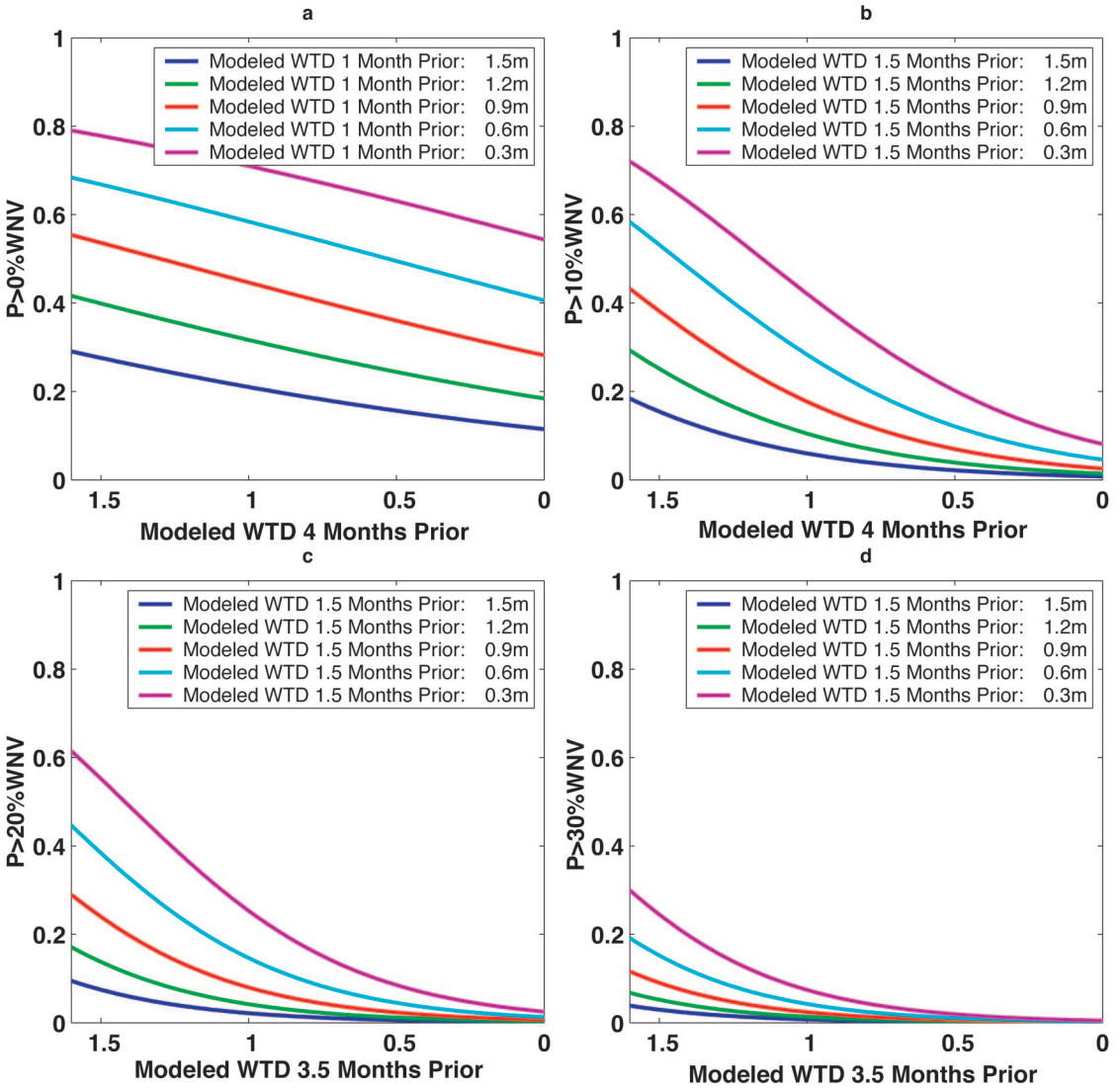


Fig. 1. Best-fit logistic regression model predicted probabilities showing the likelihood for a given county and month that greater than a cut-off percentage of the posted sentinel chickens will be infected with WNV. The logistic regression model equation is of the form $P(>X\%WNV) = (1 + \exp(a + b*WTD_1 - c*WTD_2))^{-1}$, where $P(>X\%WNV)$ is the predicted probability, X is the cut-off percentage, WTD_1 is WTD at lag 1 prior the prediction, WTD_2 is WTD at lag 2 prior the prediction, a is the intercept estimate, b the lag 1 slope estimate, and c the lag 2 slope estimate. Plotted for a continuous range of modeled WTDs lag one before the predicted outcome and fixed values of modeled WTD lag 2 before the predicted outcome. The x-axis indicates the level of antecedent drought (modeled WTD in meters relative to the surface); drier conditions are to the left. Cut-off percentages are 0% (a), 10% (b), 20% (c), and 30% (d).

fact a range of time lags was found similarly to be significantly associated with WNV transmission to sentinel chickens (data not shown). This range of time lags reflects the slow variability of land surface wetness conditions (Shaman et al. 2003b). Within counties, wetter local conditions in the 0.5–1.5 preceding months are significantly associated with an increased probability of WNV transmission to sentinel chickens. Antecedent drought conditions in the two to six preceding months also are associated significantly with an

increased probability of WNV transmission to the sentinel chickens in southern Florida.

The sensitivity of the association with drought increases (shown in Table 2 by the increasing magnitude of the parameter estimates) when higher categorical levels of WNV transmission are used for regression (i.e., >10% of posted chicken positive, >20% posted chickens positive). This sensitivity also is seen in Fig. 1, which presents the best-fit logistic regression model predictions of the probability that more than a cut-off

Table 3. Best-fit empirical relationships based on bivariate logistic regression analyses of dichotomous categories of monthly countywide human WN cases (2001–2003) on half-month lags of modeled WTD as simulated by the TBH model at each station site within the county

Dichotomous predictand	Lag 1 (mo)	Lag 2 (mo)	Intercept	Lag 1 slope	Lag 2 slope	Whole model fit
1 or more human WN cases	4.5	1.5	3.68 ($P < 0.0001$) (0.19)	0.57 ($P < 0.005$) (0.18)	−0.89 ($P < 0.0001$) (0.15)	$P < 0.0001$
2 or more human WN cases	4	1.5	5.48 ($P < 0.0001$) (0.45)	0.84 ($P < 0.02$) (0.35)	−1.21 ($P < 0.0001$) (0.29)	$P < 0.0001$

All 31 counties are analyzed in aggregate. Parameter significance and the estimate of standard error are given in parentheses.

percentage of the posted chickens within a county during a given month become WNV positive. Low levels of WNV transmission (Fig. 1a) occur for all local modeled hydrological conditions; however, for higher cut-off percentages (higher rates of WNV transmission) the regression model predicted probabilities decrease (higher rates of transmission are rarer) but the sensitivity to hydrological conditions increases.

For the human data, we defined dichotomous categories of human WN case occurrence: 1, if greater than or equal a cut-off number of human WN cases were recorded within a given county for a given month; and 0, if the number of human WN cases were less than that cut-off. The cut-off numbers tested were one and two cases per county per month. Table 3 shows the best-fit results of logistic regression with these categorical data. Again, a range of time lags was found to be associated with the occurrence of human WN cases (data not shown). Drought 3.5–6 mo prior and land surface wetting 0.5–1.5 mo prior are associated with an increased probability of human WN cases within counties. As for the sentinel chicken data, the sensitivity of the association with drought increases for the higher cut-off of two or more human WN cases per county per month, indicating that drought favors greater numbers of human WN cases.

We also performed nonparametric analysis to affirm whether antecedent drought followed by wetting were associated with subsequent human WN cases. Drought and wetting lags were chosen based on the best-fit regression models. The results of this analysis also showed that within a county drought followed by wetting of the land surface is significantly associated with the subsequent appearance of one or more human WN cases (bootstrapped confidence intervals; $P < 0.05$). Two or more human cases of WN were more significantly associated with these hydrological conditions (bootstrapped confidence intervals; $P < 0.001$) than were one or more human cases.

Discussion

Our results indicate that the spatial-temporal variability of both human WN cases and the transmission of WNV to sentinel chickens are associated with the spatial-temporal variability of land surface wetness conditions in southern Florida. Given the sparse coverage of meteorological station sites (Fig. 2) and the

uncontrolled movement of mosquitoes, wild birds, and humans, the within county association of drought followed by wetting leading to subsequent WNV transmission is remarkable. These results indicate that, as for SLEV, drought brings *Cx. nigripalpus* and wild birds into close contact, facilitating epizootic WNV amplification and generating the mosquito infection rates necessary to support high levels of WNV transmission.

The associations of WNV transmission and human WN occurrence with a modeled physical quantity, i.e., WTD, should permit probabilistic seasonal forecast of these epidemiological variables through a coupling of the logistic regression models with skillful seasonal forecasts of WTD (Shaman et al. 2003b). Similar forecasts have been successfully developed for SLEV transmission in southern Florida (Shaman et al. 2004a).

Outside of southern Florida, mosquitoes other than *Cx. nigripalpus* serve as vectors of WNV. The WNV amplification and transmission dynamics in these regions need to be investigated for a similar responsiveness to land surface wetness variability. The analysis presented here also needs to be extended to northern Florida, where both *Cx. nigripalpus* and *Cx. pipiens quinquefasciatus* Say are likely vectors of WNV (Rutledge et al. 2003).

Wild birds infected with WNV maintain a longer and higher viremia than those infected with SLEV (Reisen et al. 2003; Komar et al. 2003). Because of the long viremic period of WNV in wild birds, it is likely that higher mosquito infection rates and a higher annual baseline level of WNV transmission (compared with SLEV) are maintained throughout southern Florida. This inference of higher WNV transmission rates is supported by the sentinel chicken record, which shows higher rates of seroconversion for WNV than SLEV (Blackmore et al. 2003). A significant, widespread spring drought has not been reported in south Florida during the 3 yr since the arrival of WNV (Fig. 2). Our results indicate that epidemic levels of WNV transmission depend on hydrological conditions. Consequently, a widespread, intense spring drought followed by wetting, such as was reported during the 1990 SLE epidemic in southern Florida, could produce unprecedented numbers of infected *Cx. nigripalpus*, high levels of WNV transmission, and many human WN cases.

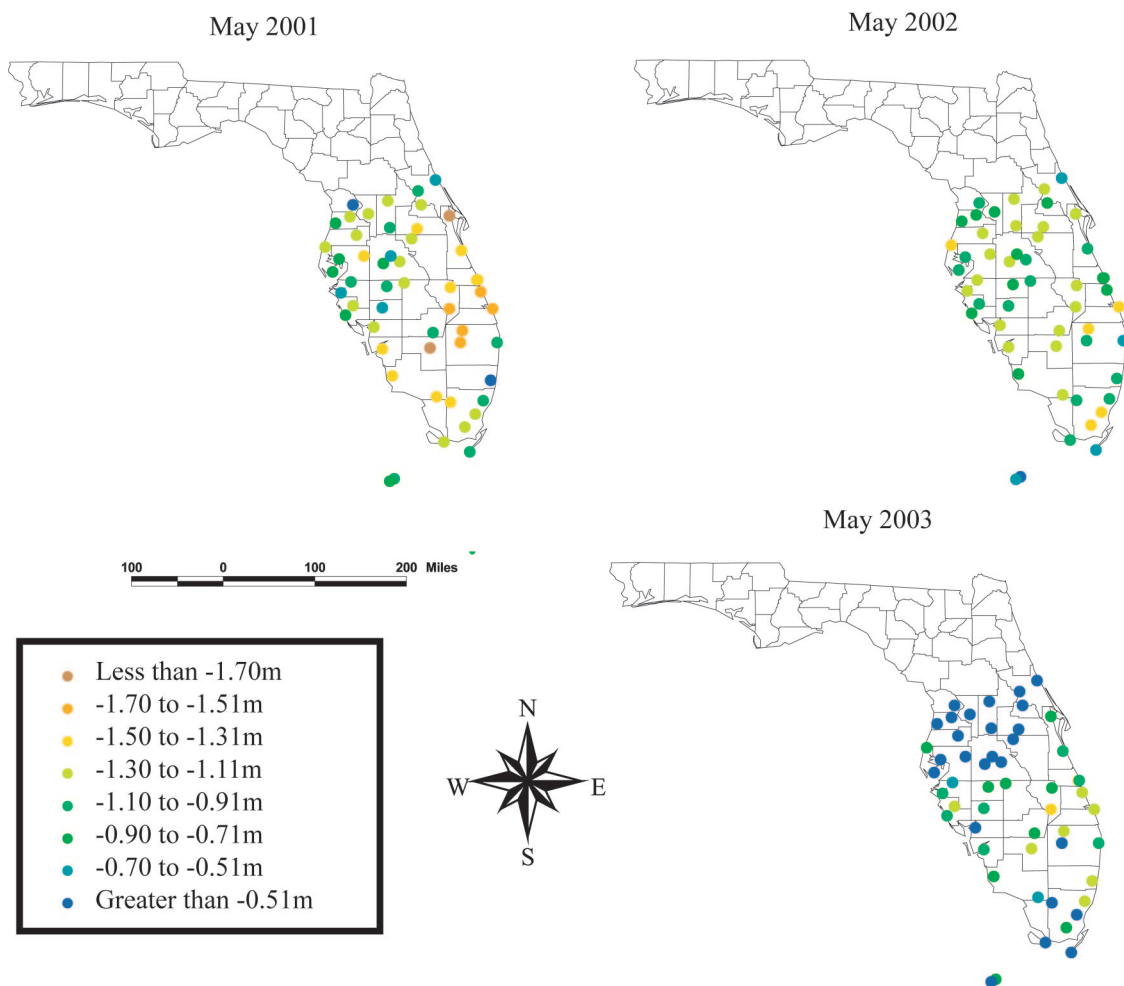


Fig. 2. Maps of mean local WTD as simulated by the TBH model at 52 sites in southern Florida for May 2001, 2002, and 2003. Springtime drought, loosely represented by the May average, is not widespread in the years since introduction of WNV into southern Florida. 2003 was a particularly wet year.

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References Cited

- Blackmore, C.G.M., L. M. Stark, W. C. Jeter, R. L. Oliveri, R. G. Brooks, L. A. Conti, and S. T. Wiersma. 2003. Surveillance results from the first West Nile virus transmission season in Florida, 2001. *Am. J. Trop. Med. Hyg.* 69: 141–150.
- Chamberlain, R. W., W. D. Sudia, P. H. Coleman, and L. D. Beadle. 1964. Vector studies in the St. Louis encephalitis epidemic. Tampa Bay area, Florida. *Am. J. Trop. Med. Hyg.* 13: 456–461.
- Day, J. F., and G. A. Curtis. 1993. Annual emergence patterns of *Culex nigripalpus* females before, during and after a widespread St. Louis encephalitis epidemic in south Florida. *J. Am. Mosq. Control Assoc.* 9: 249–53.
- Day, J. F., and G. A. Curtis. 1999. Blood feeding and oviposition by *Culex nigripalpus* (Diptera: Culicidae) before, during, and after a widespread St. Louis encephalitis virus epidemic in Florida. *J. Med. Entomol.* 36: 176–181.
- Day, J. F., and L. M. Stark. 1996. Transmission patterns of St. Louis encephalitis and eastern equine encephalitis viruses in Florida: 1978–1993. *J. Med. Entomol.* 33: 132–139.
- Day, J. F., and L. M. Stark. 1999. Avian serology in a St. Louis encephalitis epicenter before, during, and after a wide-

- spread epidemic in south Florida, USA. *J. Med. Entomol.* 36: 614–624.
- Day, J. F., and L. M. Stark. 2000. Frequency of Saint Louis encephalitis virus in humans from Florida, USA: 1990–1999. *J. Med. Entomol.* 37: 626–633.
- Dow, R. P., P. H. Coleman, K. E. Meadows, and T. H. Work. 1964. Isolation of St. Louis encephalitis viruses from mosquitoes in the Tampa Bay area of Florida during the epidemic of 1962. *Am. J. Trop. Med. Hyg.* 13: 462–474.
- Komar, N., S. Langevin, S. Hinten, N. Nemeth, E. Edwards, D. Hettler, B. Davis, R. Bowen, and M. Bunning. 2003. Experimental infection of North American birds with the New York 1999 strain of West Nile virus. *Emerg. Inf. Dis.* 9: 311–322.
- Marfin, A. A., and D. J. Gubler. 2001. West Nile encephalitis: an emerging disease in the United States. *Clin. Infect. Dis.* 33: 1713–1719.
- Reisen, W. K., R. E. Chiles, V. M. Martinez, Y. Fang, and E. N. Green. 2003. Experimental infection of California birds with western equine encephalomyelitis and St. Louis encephalitis viruses. *J. Med. Entomol.* 40: 968–982.
- Rutledge, C. R., J. F. Day, C. C. Lord, L. M. Stark, and W. J. Tabachnick. 2003. West Nile virus infection rates in *Culex nigripalpus* (Diptera: Culicidae) do not reflect transmission rates in Florida. *J. Med. Entomol.* 40: 253–258.
- Sardelis, M. R., M. J. Turell, D. J. Dohm, and M. L. O'Guinn. 2001. Vector competence of selected North American *Culex* and *Coquillettia* mosquitoes for West Nile virus. *Emerg. Inf. Dis.* 7: 1018–1022.
- Shaman, J., J. F. Day, and M. Stieglitz. 2002a. Drought-induced amplification of Saint Louis encephalitis virus, Florida. *Emerg. Infect. Dis.* 8: 575–580.
- Shaman, J., M. Stieglitz, V. Engel, R. Koster, and C. Stark. 2002b. Representation of stormflow and a more responsive water table in a TOPMODEL-based hydrology model. *Water Resources Res.* 38: 1156, doi:10.1029/2001WR000636.
- Shaman, J., J. F. Day, and M. Stieglitz. 2003a. St. Louis encephalitis virus in wild birds during the 1990 south Florida epidemic: the importance of drought, wetting conditions, and the emergence of *Culex nigripalpus* to arboviral amplification and transmission. *J. Med. Entomol.* 40: 547–554.
- Shaman, J., M. Stieglitz, S. Zebiak, and M. Cane. 2003b. A local forecast of land surface wetness conditions derived from seasonal climate predictions. *J. Hydromet.* 4: 611–626.
- Shaman, J., J. F. Day, M. Stieglitz, S. Zebiak, and M. Cane. 2004a. Seasonal forecast of St. Louis encephalitis transmission, Florida. *Emerg. Inf. Dis.* 10: 802–809.
- Shaman, J., J. F. Day, and M. Stieglitz. 2004b. The association of drought, wetting and human cases of St. Louis encephalitis virus in south-central Florida. *Am. J. Trop. Med. Hyg.* 71: 251–261.
- Shroyer, D. A. 1991. The 1990 Florida epidemic of St. Louis encephalitis: virus infection rates in *Culex nigripalpus*. *J. Fla. Mosq. Control Assoc.* 62: 69–71.
- Stieglitz, M., D. Rind, J. Famiglietti, and C. Rosenzweig. 1997. An efficient approach to modeling the topographic control of surface hydrology for regional and global climate modeling. *J. Climatol.* 10: 118–137.

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Appendix
Monthly percentage of sentinel chickens testing seropositive for WNV antibodies in 23 counties in southern Florida, 2001–2003.

	1/01	2/01	3/01	4/01	5/01	6/01	7/01	8/01	9/01	10/01	11/01	12/01	1/02	2/02	3/02	4/02	5/02	6/02	7/02	8/02	9/02	10/02	11/02	12/02	1/03	2/03	3/03	4/03	5/03	6/03	7/03	8/03	9/03	10/03	11/03	12/03	
Brevard	-	-	-	-	0	0	0	0	0	3.1	0	-	0	-	0	0	0	1.9	10.9	27.6	22.2	31.7	0	-	-	-	-	0	0	0	0	1.7	8.5	9.7	6.8	10.7	-
Charlotte	-	-	-	-	0	0	0	0	0	0	0	-	-	-	-	-	0	0	15.8	26.6	27	2.8	8.8	0	-	-	0	0	3.3	3.7	52.8	51.6	14.3	4.3	17.4	-	
Citrus	-	-	-	-	0	0	0	0	2.4	5.7	-	-	-	-	-	-	-	0	2.8	2.8	27	24.3	3.3	-	-	-	-	-	-	0	0	0	21.6	16.7	18.4	3	7.7
Collier	-	-	-	-	0	0	0	0	0	20	0	-	-	-	-	-	0	0	0	3	45.5	48.5	9.5	26.7	-	-	-	0	3.7	16.7	22.9	22.4	20	33.3	15.2	11.5	-
Dade	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	5.6	0	4.8	15.8	12.9	0	-	-	
Desoto	-	-	-	-	-	-	0	0	0	0	0	-	-	-	-	-	-	-	-	-	0	9.5	0	0	-	-	-	-	-	-	-	-	-	-	-	-	
Hendry	0	-	-	-	-	0	0	0	0	0	0	-	-	-	-	-	-	0	0	35.7	14.3	9.1	0	-	-	-	-	-	0	5.1	8.1	37.8	32	24.1	13.6	7.1	
Hillsborough	0	0	0	0	0	0	0	0	2.9	1.3	0	0	0	0	0	0	0	0	17.8	29.2	17.2	11.6	15.8	0	0	0	0	0	0	0	0	1.7	21.6	9.6	7.1	12.3	1.6
Indian River	-	-	-	-	0	0	0	0	0	6.3	0	0	0	0	0	0	0	0	18	13.5	21.1	0	14.3	2.1	0	0	0	0	7.3	6	0	17.6	7.6	14.5	15	1.6	-
Lee	0	0	0	0	0	0	0	0	0	3.9	1.4	0	0	0	0	0	0	0	1.2	16.4	23.6	16.3	3.1	7.1	1.6	0	0	3.4	0	1.2	21.3	32	32.6	8.2	5.1	2.9	
Manatee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5	28.2	13.3	25.4	10.4	9.8	2.8	0	1.4	0	2.9	0	1.4	34.3	14.6	13.6	8.7	3.6	
Martin	-	-	-	-	0	0	0	0	10	15.2	0	0	-	-	-	-	-	0	3.1	6.5	27.8	39.5	6.7	-	-	-	0	0	0	0	11.8	15.4	33.3	9.1	3.1	-	
Okeechobee	-	-	-	-	-	0	0	0	0	11.1	0	-	-	-	-	-	-	-	0	5.6	19	38.1	6.7	11.1	-	-	-	-	-	-	0	17.4	27.3	4.8	5.6	10	
Orange	0	0	0	0	0	0	0	0	0	0	2.5	0	0	0	0	0	0	1.6	5.6	22.4	17.5	15.3	1.3	9.6	0	0	0	0.8	-	0.8	2.1	9.9	4.8	10.9	5.1	7.3	
Osceola	-	0	0	0	0	0	0	0	3.4	0	0	-	0	-	0	-	0	0	6.8	10.2	17.7	23.8	4.3	13.6	0	2.9	3	0	0	0	0	6.3	9	4.1	4.2	4.7	
Palm Beach	-	-	0	0	0	0	2	5.6	0	0	0	0	1.5	0	0	0	0	0	1.7	3.1	21.1	25.4	3.9	22.2	0	0	0	0	0	0	9.1	40.3	28.4	22.5	5.3	3.9	
Pasco	-	-	-	-	0	0	0	0	5.3	0	0	0	0	0	0	0	0	0	3.2	24.3	56.7	0	2.9	2.9	0	0	0	0	0	0	0	0	2.7	0	11.1	0	0
Pinellas	-	-	-	-	0	0	0	0	1.6	1.6	0	0	0	0	0	0	0	11.5	0	5.4	3.6	11.9	1.8	8.3	1.8	0	0	0	0	1.7	3.6	3.4	9.7	0	0	0	
Polk	-	-	-	-	0	4.2	2.6	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Sarasota	-	-	-	-	-	0	0	0	2.8	0	0	0	-	0	0	0	0	0	1.8	23.3	31.1	33.9	5.4	19.4	0	0	1.5	0	0	0	1.5	26.9	26.6	13	17.1	8.8	
Seminole	-	-	-	-	0	0	0	0	3.1	0	0	0	0	0	0	0	0	0	3.3	14.3	21.6	6.1	0	6.7	-	-	-	0	0	0	0	12.5	0	3.2	0	0	
St. Lucie	-	-	-	-	0	0	0	0	0	0	0	0	0	-	-	-	8.3	0	0	4.2	8.3	25	11.5	0	0	0	0	0	0	0	3.2	11.4	17.1	6.3	0	0	
Volusia	-	-	-	-	0	0	0	0	0	0	0	3.3	0	0	0	0	4.3	10.3	42.9	22.8	20.3	14.8	3.4	11.1	8.6	0	1.7	0	0	0	2	9.6	2.1	3.8	5.4	1.9	