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Not all surveillance data are created equal—A multi-method dynamic occupancy approach to determine rabies elimination from wildlife

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Not all surveillance data are created equal—A multi-method dynamic occupancy approach to determine rabies elimination from wildlife

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Abstract

1. A necessary component of elimination programmes for wildlife disease is effective surveillance. The ability to distinguish between disease freedom and non-detection can mean the difference between a successful elimination campaign and new epizootics. Understanding the contribution of different surveillance methods helps to optimize and better allocate effort and develop more effective surveillance programmes.
2. We evaluated the probability of rabies virus elimination (disease freedom) in an enzootic area with active management using dynamic occupancy modelling of 10 years of raccoon rabies virus (RABV) surveillance data (2006–2015) collected from three states in the eastern United States. We estimated detection probability of RABV cases for each surveillance method (e.g. strange acting reports, roadkill, surveillance-trapped animals, nuisance animals and public health samples) used by the USDA National Rabies Management Program.
3. Strange acting, found dead and public health animals were the most likely to detect RABV when it was present, and generally detectability was higher in fall–winter compared to spring–summer. Found dead animals in fall–winter had the highest detection at 0.33 (95% CI: 0.20, 0.48). Nuisance animals had the lowest detection probabilities (~0.02).
4. Areas with oral rabies vaccination (ORV) management had reduced occurrence probability compared to enzootic areas without ORV management. RABV occurrence was positively associated with deciduous and mixed forests and medium to high developed areas, which are also areas with higher raccoon (*Procyon lotor*) densities. By combining occupancy and detection estimates we can create a probability of elimination surface that can be updated seasonally to provide guidance on areas managed for wildlife disease.
5. *Synthesis and applications*. Wildlife disease surveillance is often comprised of a combination of targeted and convenience-based methods. Using a multi-method analytical approach allows us to compare the relative strengths of these methods, providing guidance on resource allocation for surveillance actions. Applying this multi-method approach in conjunction with dynamic occupancy analyses better

informs management decisions by understanding ecological drivers of disease occurrence.

KEYWORDS
dynamic occupancy, elimination, multi-method occupancy, rabies virus, raccoon, surveillance, wildlife disease

1 | INTRODUCTION

Knowing when elimination of a wildlife disease has been achieved is often difficult to assess as many wildlife diseases naturally persist at low prevalence (Nusser, Clark, Otis, & Huang, 2008; Rhyan & Spraker, 2010). Knowledge about the presence of wildlife diseases on a landscape is often further complicated by imperfect detection of the host species or disease of interest (Bailey, MacKenzie, & Nichols, 2014; Pepin et al., 2017), inconsistent or opportunistic surveillance (Artois et al., 2009; Duncan, Backus, Lynn, Powers, & Salman, 2008) and low reporting rates. Successful wildlife disease management is contingent on being able to distinguish true elimination from lack of detection of the disease (Anderson et al., 2013). If elimination is prematurely declared (Rosatte, Power, et al., 2007), and monitoring and management resources are shifted, a new epizootic could occur (Middel, Fehlner-Gardiner, Pulham, & Buchanan, 2017).

The elimination of wildlife disease can only be inferred through surveillance effort where no infected animals are detected (negative surveillance), and certainty of elimination is dependent on the amount of surveillance effort and the likelihood of detecting the disease by the surveillance methods employed. Surveillance of wildlife diseases often consists of opportunistic rather than random sampling methods (e.g. reported nuisance animals, roadkill; Duncan et al., 2008; Nusser et al., 2008), which cannot be described statistically (and thus have limitations in their scope of inference and likely result in biased estimates) but they are often the most common type of data available for wildlife disease surveillance and monitoring. Targeted wildlife disease sampling can be statistically rigorous but is often ephemerally applied and not practical for broad-scale surveillance (Martin, Cameron, & Greiner, 2007). Occupancy modelling, which simultaneously estimates occurrence and detection (MacKenzie et al., 2006), is well suited to answer questions about wildlife disease distribution, invasion dynamics and detectability, and is increasingly being applied to wildlife disease problems (Bailey et al., 2014; Lachish, Gopalaswamy, Knowles, & Sheldon, 2012; Pepin et al., 2017). By combining and evaluating multiple surveillance methods in a single occupancy framework, we can not only better estimate the epidemiological patterns of the disease of interest but we also can improve the probability of disease detection. Just as multiple diagnostic tests may be used to improve the accuracy of a diagnosis (Baker, 1995; Dendukuri & Joseph, 2001), multiple surveillance methods can be used to improve the accuracy of determining the status of a wildlife disease in an area of interest (Martin et al., 2007). In addition, by using multiple surveillance methods we have the ability to evaluate the probability a given method will detect the disease given it is present, and not simply estimate apparent prevalence of the disease within a given surveillance type (Pepin et al., 2017). Using occupancy modelling, we can estimate the probability of disease elimination (freedom from a disease—regardless of previous disease status) within a spatial area for a given time period based on sampling effort and occurrence patterns. This in turn allows us to plan surveillance such that we collect a sufficient number of samples across space and time to achieve a desired level of certainty about disease elimination from a defined area.

Rabies is a viral zoonosis with a near global distribution in domestic animals and wildlife (Gilbert, 2018). The greatest human disease burden from rabies virus (RABV) globally is associated with transmission from domestic dogs (Hampson et al., 2015). However, RABV also circulates independently in diverse bat and carnivore wildlife reservoirs (Gilbert, 2018; Velasco-Villa et al., 2017), which are associated human exposures and prophylactic treatments (Christian, Blanton, Auslander, & Rupprecht, 2009), with economic costs (Sterner & Smith, 2006). Control of RABV circulation in domestic and wild carnivores focuses on the principle of preventive vaccination to reduce susceptible fractions of a target population to eliminate disease transmission. Wildlife vaccination against RABV relies principally on broadcast distribution of vaccine baits for consumption by target animals, a strategy known as oral rabies vaccination (ORV; Mähl et al., 2014; Rosatte, Tinline, & Johnston, 2007). ORV strategies have been used to eliminate RABV from red foxes (*Vulpes vulpes*) across large landscapes in Europe (Freuling et al., 2013; Müller et al., 2015), as well as a dog RABV variant from coyotes (*Canis latrans*) in the United States (Velasco-Villa et al., 2008). Since the mid-1990s, ORV has been used to work towards the elimination of and to prevent the spread of RABV in raccoons (*Procyon lotor*) in the eastern United States (Elmore et al., 2017). Surveillance is a key component of effective ORV and other disease management programmes, and is required to assess programme impact and disease elimination status (Cliquet et al., 2010; Freuling et al., 2013).

Surveillance of wildlife disease often leverages multiple sources of information that may be of unequal value for disease detection (Kirby et al., 2017). Understanding the relative strengths and weaknesses of different surveillance methods will help to prioritize resources and effort to maximize disease detection on the landscape. We used a dynamic occupancy approach to: (a) estimate local RABV elimination probability, (b) quantify the relative contribution of different surveillance methods for RABV detection, (c) estimate sample sizes needed across space and time to achieve a desired level of elimination certainty, and (d) identify seasonal and landscape variables that relate to the presence or absence of RABV in wild carnivores.

2 | MATERIALS AND METHODS

2.1 | Study area

Raccoon variant RABV is enzootic in raccoon populations along the east coast of the United States (Elmore et al., 2017). The United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services (WS) and National Rabies Management Program (NRMP; cumulatively hereafter generally referred to as NRMP), has been conducting ORV focused on preventing the spread of and eventually eliminating raccoon RABV from the United States. The ORV zone for raccoon RABV in the United States extends across 16 states from Maine in the north to Alabama in the south (Figure 1). NRMP has also implemented a comprehensive enhanced rabies surveillance (ERS) programme to monitor RABV incidence, especially in relation to management actions. ERS is complementary to public health surveillance (where animals are sampled following exposures to humans or pets), and involves efforts to collect and test samples that would not otherwise be tested through public health surveillance. As a result, high-priority ERS areas border the ORV zone (Figure 1).

To evaluate the value of different surveillance methods for RABV detection and to estimate elimination probabilities, we selected a region of the ORV zone and ERS area with a high concentration of animal samples to maximize our power to identify signals from these data. We focused on counties with at least 100 animals sampled within our 10-year study period in western Pennsylvania, eastern Ohio and northern West Virginia (Figure 1). This contiguous region largely consists of cultivated crops, pasture and hay fields surrounded by deciduous forests. The area (49,367 km^2) includes the city of Pittsburgh and its surrounding suburbs.

2.2 | Data

Data consist of individually sampled animals that are tested for RABV. Data include: location, date of collection, which agency collected the sample, how the animal was encountered (e.g. trapped, roadkill, incidental take, carcass collection), the fate of the animal (e.g. found dead, euthanized, non-WS sampled) and field comments. In 2016, NRMP developed six surveillance categories for classifying ERS collections for more strategic surveillance effort: strange acting, found dead, roadkill, surveillance-trapped, nuisance wildlife control officer (NWCO) collected/other (referring to nuisance reported animals, we have termed this "nuisance") and unknown (referring to the unknown behavioural state of the animal; Kirby et al., 2017). Prior to 2016, the data had not been similarly classified. We used the method of collection, fate data and comments to post-process the ERS data from 2006 to 2015 according to similar categories (see Appendix S1).

Brain tissue from each animal collected by the NRMP was initially tested for rabies using the direct rapid immunohistochemical test (dRIT; Rupprecht et al., 2014). All positive, indeterminate and 10% of negative dRIT samples were subject to confirmatory test by direct fluorescent antibody assay (DFA; Ronald et al., 2003). Where discrepant (<0.01% of samples), the results of the DFA test were considered final. All positive cases were genotyped to identify the RABV variant infecting the animal (Szanto, Nadin-Davis, Rosatte, & White, 2011). Public health surveillance data are reported annually by more than 130 state public health, veterinary, and university laboratories to the Centers for Disease Control and Prevention and include individual animals suspected of human or pet exposure which were tested using DFA to inform decisions about post-exposure prophylaxis for humans and animal quarantine (Brown, Slavinski, Ettestad, Sidwa, & Sorhage, 2016; Manning et al., 2008). A fraction (~10%) of the public health RABV cases are typed to variant, but most cases occurring in the eastern United States can be presumed to be infected with raccoon RABV (Wallace et al., 2014).

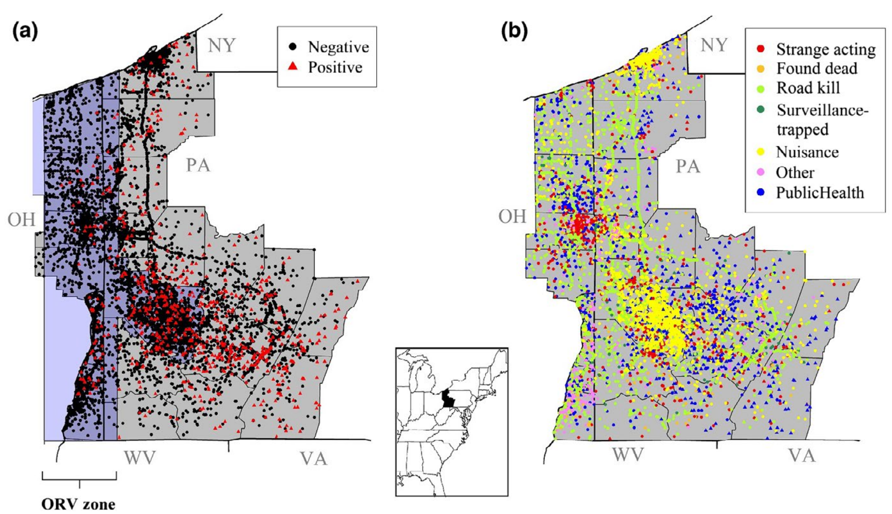

FIGURE 1 (a) Study area (shaded grey) with RABV-negative (black circles) and -positive (red triangles) raccoon rabies samples from 2006 to 2015. Positive samples are plotted on top of negative samples for ease of visualization. The oral rabies vaccination (ORV) zone is shown as a blue shaded region. (b) Surveillance sampling locations in the study area colour coded by surveillance method. The negatives are circles and the positives are triangles. The inset shows the location of the study area in the eastern United States (black)

2.3 | Occupancy model formulation

We used a dynamic occupancy approach (MacKenzie et al., 2006) to evaluate RABV occurrence spatially and temporally in our study area. Across the study area, we overlaid a 10 km by 10 km grid to process the data to a resolution that matches ERS sampling. Occupancy analyses assume that the occupancy status of rabies within a site does not change (i.e. closure) during a sampling occasion (termed the primary sampling period). The diagnostic tests for RABV detect infection during the infectious but not incubating phase. Since the incubation period for RABV ranges on average from 3 to 12 weeks (Tinline, Rosatte, & MacInnes, 2002), we used astronomical seasons as our primary sampling periods (where closure is assumed). This time period both reduces issues with potential closure violations, and also helps to increase the probability of detecting RABV status transitions as surveillance data are not routinely collected by sites to be able to document transitions.

Dynamic occupancy models can be expressed in a hierarchical framework. The hidden ecological state, z_{it}, indicates whether site i in primary sampling period t was occupied with RABV (regardless of whether it was detected). We used the number of rabies-positive samples, y_{ijt}, and number of total animals sampled, n_{ijt}, within site i, using sampling method j, and within a primary sampling period t, to estimate the observation process (p_j, detection probability for method j), given the hidden ecological process was occupied, z_{it} = 1. The observation process is modelled as a beta distribution by surveillance method and accounting for within-year variability in detection (j) using vague priors (Equation 2). Surveillance efforts are greater in the spring and summer compared to the fall and winter, which may correspond to different detection probabilities during these periods and they were modelled accordingly. A detection in any of the surveillance methods would suggest the site was occupied in that time step, and therefore would influence the probability of detection of all other surveillance methods (Nichols et al., 2008).

$$y_{ijt} \sim \text{Binomial}\left(z_{it} * p_j, n_{ijt}\right) \tag{1}$$

$$p_j \sim \text{Beta}\left(1,1\right) \tag{2}$$

We can explicitly model the ecological transition dynamics of colonization (the probability an uninfected site becomes infected, γ) and extinction (the probability an infected site becomes uninfected, ε). The conditional probability of the state of a site i in time t given the state in time t − 1 was modelled as a Bernoulli random variable with probability ψ_{it} (Equation 3). The initial occupancy probability, ψ_{i1}, was modelled as a function of covariates, X_ψ, with linear regression coefficients, β_ψ, Equation (4). Subsequent occupancy estimates (after the initial occupancy t = 1) were derived from the initial occupancy and the transition rates (Equation 5).

$$z_{it} | z_{it-1} \sim \text{Bernoulli}\left(\psi_{it}\right) \tag{3}$$

$$\text{logit}\left(\psi_{i1}\right) = X_\psi \beta_\psi \tag{4}$$

$$\psi_{it} = \left(1 - \varepsilon_{it-1}\right) * z_{it-1} + \gamma_{it-1}\left(1 - z_{it-1}\right) \tag{5}$$

The transition parameters, ε_{it} and γ_{it}, were modelled as combinations of covariates, X_ε and X_γ, with linear regression coefficients $\beta\varepsilon$ and $\beta\gamma$, in Equations (6) and (7). Extinction (ε_{it}) was modelled with a simple intercept only model. To understand the spatial and temporal variability in RABV occupancy in our study, covariates included spatial patterns (e.g. management effects, habitat effects and neighbour effect) and temporal patterns (e.g. seasonality and trends in RABV occurrence across years). Management effects were defined spatially by the ORV zone in the western quarter of the study area, where we included a covariate on colonization for grid cells within that ORV zone (modelled as a binary factor where over half of the grid cell must be in the ORV zone to be considered in the ORV zone). Habitat effects may influence animal host and rabies occurrence so we used covariates that may relate to raccoon densities and contact rates (Recuenco, Blanton, & Rupprecht, 2012). We evaluated three habitat coverage groupings derived from the National Land Cover Database 2011 (Homer et al., 2015). Additionally, the probability for colonization of grid cells with RABV may be related to the number of positive RABV cases in neighbouring sites in the previous time step (infection density). We also expect there to be temporal fluctuations, so we examined seasonal variability (modelled using a series of dummy covariates for the standard calendar seasons) and an annual trend in RABV occurrence. Equation (7) can be expanded to demonstrate how these covariates were modelled on colonization (Equation 8).

$$\text{logit}\left(\varepsilon_{it}\right) = X_\varepsilon \beta_\varepsilon = 1 * \beta_{\varepsilon 0} \tag{6}$$

$$\text{logit}\left(\gamma_{it}\right) = X_\gamma \beta_\gamma \tag{7}$$

$$\begin{aligned} \log\text{it}\left(\gamma_{it}\right) = {} & \beta_{\gamma 0} + \beta_{\gamma 1} * \%\text{cultivated} + \beta_{\gamma 2} * \%\text{forest cover} \\ & + \beta_{\gamma 3} * \%\text{open low development} + \beta_{\gamma 4} * \text{ORV} \\ & + \beta_{\gamma 5} * \text{trend} + \beta_{\gamma 6} * \text{trend} * \text{ORV} + \beta_{\gamma 7} * \text{winter} \\ & + \beta_{\gamma 8} * \text{spring} + \beta_{\gamma 9} * \text{summer} + \beta_{\gamma 10} * \text{infection density} \end{aligned} \tag{8}$$

To calculate the posterior distributions for this model we used a Markov Chain Monte Carlo algorithm with Metropolis–Hastings steps custom coded in Program R (R Core Team, 2017). We used 200,000 iterations with a 100,000 run burn-in and five chains. We assessed distribution convergence and mixing using visual diagnostics and Gelman–Rubin statistics (Gelman et al., 2013). The full posterior distribution and conditional distributions are provided in Appendix S2.

2.4 | Posterior analyses

Using posterior estimates of occupancy and detection probabilities, we calculated the effective probability of detection, $p*$, accounting for all sampling methods, J, and sampling effort by method e_j (Equation 8). Using the effective detection probability, $p*$, we can calculate the probability of elimination for each site at each time point (Equation 9; Nichols et al., 2008). By rearranging Equations (9) and (10), we can calculate the sample size (e) needed for a single surveillance method to achieve a given certainty of elimination under a specific occupancy probability for a particular grid cell at a given time step (Equation 11).

$$p^* = 1 - \prod_{j=1}^{J} (1 - p_j)^{e_j} \tag{9}$$

$$P(\text{elimination}) = \frac{(1 - \psi_{it})}{(1 - \psi_{it}) + \psi_{it} * (1 - p^*)} \tag{10}$$

$$e_j = \log\left(\frac{(1 - \psi_{it})\,(1 - \text{Prob}(\text{elim}))}{\text{Prob}(\text{elim}) * \psi_{it}}\right) \Big/ \log(1 - p_j) \tag{11}$$

Only the initial occupancy estimate was modelled directly, the occupancy estimates for the remaining time steps were derived from the initial occupancy and the transition rates (Equation 5). Therefore, covariate relationships were modelled on the transition rates (extinction and colonization). However, we were ultimately interested in how occupancy changed with respect to the spatial and temporal covariates. Therefore, we conducted post hoc beta regression analyses (conducted in Program R, package 'betareg', which uses maximum likelihood to fit regression models to beta distributed data; Gruen, Kosmidis, & Zeileis, 2012) using the occupancy estimates from the model as the response and habitat covariates including the percent coverage of: cultivated crops, deciduous and mixed forests, evergreen forests, pasture lands, open space and low developed areas, medium and high developed areas, and wetlands; and categorical seasonal effects, and annual trend effect as the predictors. We also looked at an interaction between the spatial and temporal effects and the ORV zone to determine if spatial and temporal patterns were consistent across management areas (within and to the east of the ORV zone).

2.5 | Validation and surveillance method bias comparison

We evaluated model fit using Bayesian *p*-values with deviance as our test statistic (Broms, Hooten, & Fitzpatrick, 2016; Gelman, Meng, & Stern, 1996). Values close to 0.5 suggest good fit, whereas values greater than .95 or less than .05 suggest poor fit (Broms et al., 2016). We used an area under the curve (AUC) statistic suggested by Zipkin, Grant, and Fagan (2012) to assess sensitivity and specificity of occupancy estimates by models using single surveillance types compared to the estimated occupancy status (z_{it}) from the full dataset. We also visually compared estimates of occupancy to observed positive and negative data. Due to imperfect detection with our data, high probabilities of occupancy in areas where only negative samples were observed could be expected. We also examined how the model performs at prediction. We withheld the last 2 years of data (eight time steps) and fit the model to the data without these years of data. Additionally, we compared the number of sites where we would declare elimination with 95% probability with the proportion of those sites that became occupied during the next time step using the dataset withholding the last 2 years.

We used multiple surveillance methods to estimate elimination probability and evaluate detection probability for each method in our study. The objective of using multiple methods was to reduce the bias inherent with any individual method. We compared the estimates using the full dataset (with all surveillance types) to estimates using each method of surveillance separately, to examine the relative biases of the different surveillance types. Since positive samples from any method are true representations of the positive status of a grid cell in a given time period (i.e. there are no false positives), this method of assessing bias highlighted spatial or temporal patterns of particular methods that failed to detect positive RABV cases observed by other methods.

3 | RESULTS

During the 10-year period of our study there were 23,635 raccoons sampled, of which 787 were rabid (3.3%). Public health and nuisance animals represented the largest proportions of all of the samples collected (8,982/23,635 = 38.0% and 7,249/23,635 = 30.7% respectively; Table 1).

3.1 | Rabies occurrence

The mean probability of RABV occupancy in a grid cell within a season in the ORV management area was 0.34 (95% credible intervals, CI: 0.22, 0.49) and east of the ORV management area was 0.55 (95% CI: 0.47, 0.62; Figure 2a,b). Occupancy probabilities declined over time in the ORV management area ($\beta_{\text{trend in ORV}}$ = −.10, 95% CI: −0.16, −0.04) but remained relatively constant across years east of the ORV management area ($\beta_{\text{trend east of ORV}}$ = .03, 95% CI: −0.03, 0.08; Figure 2a). Occupancy probability varied seasonally during our study (Figure 2a). Two habitat effects had consistent relationships with occupancy both within the ORV zone and east of the ORV zone. Deciduous and mixed forest cover and medium to high developed areas were positively associated with RABV occupancy (Appendix S3, Table 1). The probability of local RABV colonization of grid cells increased with the number of RABV-positive cases in neighbouring sites (i.e. infection density; β = .30, 95% CI: 0.15, 0.46; covariate estimates for colonization Appendix S3, Table 2).

TABLE 1 Enhanced rabies surveillance surveillance methods and sample distributions of RABV-negative and -positive samples from 2006 to 2015 in western Pennsylvania, eastern Ohio and northern West Virginia

Surveillance method name	# Negatives	# Positives	Total
Strange acting	1,254	84	1,338
Found dead	413	24	437
Roadkill	3,256	101	3,357
Surveillance trapped	691	9	700
Nuisance	7,177	72	7,249
Other	1,550	22	1,572
Public health	8,507	475	8,982
Total	22,848	787	23,635

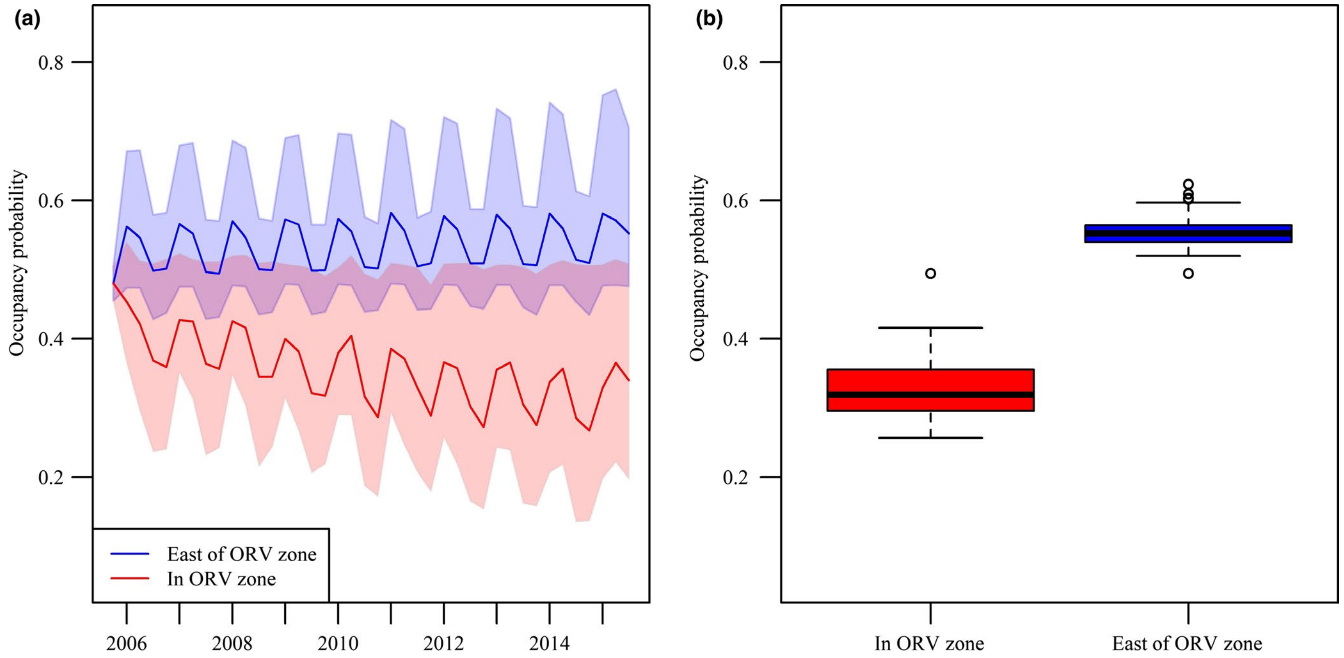

FIGURE 2 (a) Temporal pattern of mean RABV occupancy in the oral rabies vaccination (ORV) zone (red) and east of the ORV zone (blue) during 2006–2015 in western Ohio, eastern Pennsylvania and northern West Virginia, with 95% credible intervals shown by shaded region. (b) Box plots of RABV occupancy estimates in the fall of 2015 among grid cells managed by ORV and unmanaged grid cells averaged across time. The box plot shows the median (horizontal line), interquartile range (IQR; box), 1.5*IQR (whiskers) and extreme values (dots) of the posterior distributions

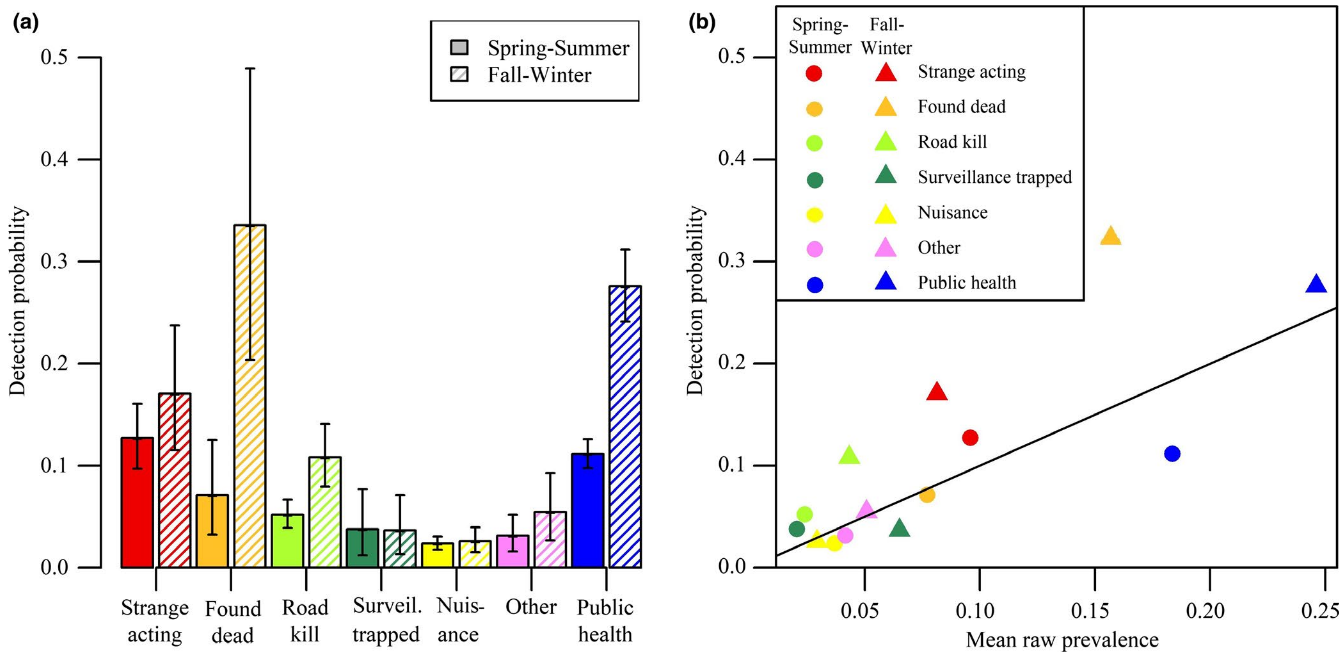

FIGURE 3 (a) Estimates of detection probability shown by bar height (with 95% CIs) by surveillance method and by spring and summer (solid) and by fall and winter (striped). (b) Comparison of the mean raw prevalence (number of RABV-positive samples/total number of samples per grid cell and season) and the estimates of detection probability by surveillance method and season (spring–summer and fall–winter). The black line shows the 1:1 line, estimates below the line have a lower detection probability than expected based on the raw prevalence and estimates above the line have a higher detection probability than expected by the raw prevalence

3.2 | Surveillance results

Generally, the strange acting, found dead and public health surveillance methods had the highest RABV detection probabilities (Figure 3a). The detection probabilities for found dead, roadkill and public health surveillance methods were considerably higher in fall–winter compared to spring–summer (Figure 3a). The other methods were less variable across seasons. The highest RABV detection probability was among found dead animals in fall–winter at 0.33 (95% CI: 0.20, 0.48). The lowest RABV detection probability was among nuisance animals at any time of year at 0.02 (95% CI: 0.01, 0.04). Strange acting, found dead and roadkill surveillance methods had higher detection probabilities than their raw prevalence would suggest (Figure 3b). However, nuisance and public health methods had lower detection probabilities than their raw prevalence would suggest (Figure 3b).

3.3 | Elimination probability and surveillance planning

The probability of elimination was estimated for each season and represented the probability that a given grid cell was free of RABV infection during that season. In the last time step of this study (fall of 2015), the probability of RABV elimination was highest in the ORV management zone (Figure 4a). There were nine grid cells infected with RABV in the last time step and by definition had a probability of elimination equal to zero. There was greater uncertainty about the RABV elimination status in areas in the north within the ORV management area and in the southern part of the enzootic area in the last season (Figure 4b). Uncertainty was lower in grid cells with more samples, areas without samples had a mean standard error of 0.09 (95% CI: 0.07, 0.19), areas with one sample had a mean standard error of 0.05 (95% CI: 0.01, 0.12), an area with 10 samples had a mean standard error of 0.02 (95% CI: 0.017, 0.047).

Surveillance data provide information about the state of the system and certainty about that system state. The number of negative samples needed to have a desired probability of RABV elimination can be calculated for a given set of conditions. This number is dependent on the probability of occupancy, the surveillance method used and the probability of elimination desired (Equation 11). For instance, the number of negative found dead animals that need to be collected during fall–winter would be two if the occupancy probability is .1 and a 95% probability of elimination is desired (Table 2).

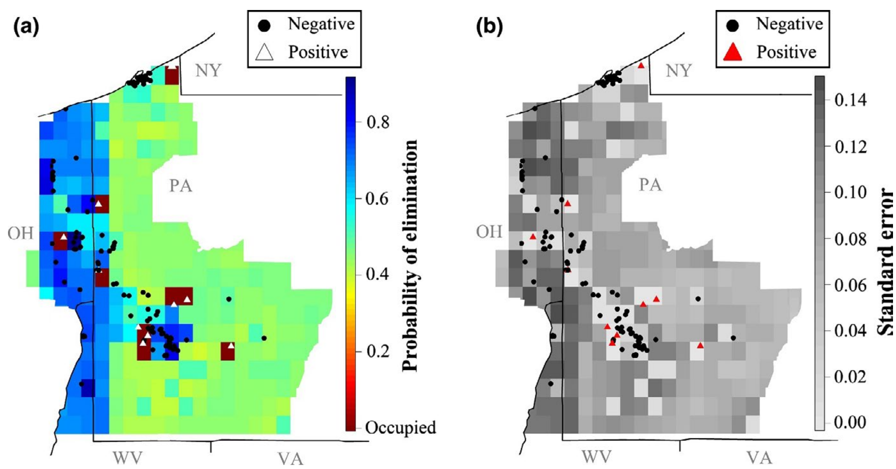

FIGURE 4 (a) Probability of elimination (grid cell freedom from infectious RABV cases) in the fall of 2015 (end of study). (b) Standard error of occupancy estimates by grid in the fall of 2015. Black dots are negative samples and triangles (white in (a) and red in (b)) are positive samples in this time step

TABLE 2 Number of negative samples needed, within a grid cell (100 km^2) within a season, by surveillance method and time of year ('S' = spring–summer and 'W' = fall–winter) to have a 95% probability of elimination (freedom from infectious rabies cases in a grid cell in a given season) for two occupancy probabilities (.1 and .5)

	For sites with an occupancy probability of .1		For sites with an occupancy probability of .5	
Surveillance Method	Sample size	95% CI	Sample size	95% CI
Strange acting-S	5	(4, 7)	21	(16, 28)
Strange acting-W	4	(3, 6)	16	(11, 24)
Found dead-S	9	(5, 20)	36	(20, 80)
Found dead-W	2	(1, 3)	7	(4, 12)
Roadkill-S	13	(10, 18)	51	(40, 69)
Roadkill-W	6	(5, 9)	25	(19, 35)
Surveillance trapped-S	17	(8, 54)	68	(32, 214)
Surveillance trapped-W	20	(10, 54)	77	(40, 213)
Nuisance-S	31	(24, 42)	124	(95, 167)
Nuisance-W	30	(19, 52)	118	(77, 203)
Other-S	13	(8, 26)	51	(31, 101)
Other-W	13	(8, 27)	52	(30, 108)
Public health-S	8	(7, 9)	30	(26, 36)
Public health-W	3	(2, 3)	11	(10, 14)

In contrast, 31 negative nuisance animals would need to be collected at any time to have the same elimination confidence under the same conditions. However, if the occupancy probability was .5 we would need seven negative found dead samples in fall–winter or 124 negative nuisance samples in spring–summer to have a 95% probability of elimination (Table 2).

3.4 | Validation and bias

The Bayesian p-value for our model with the full dataset was .33, suggesting model adequacy (Royle, Kéry, Gautier, & Schmid, 2007). The AUC comparing the estimated occupancy status with the occupancy probabilities for the model with all surveillance types was 0.88 (Appendix S4, Table 1). We also used a visual comparison to assess model fit across surveillance methods (Appendix S4, Figure 1). The visual assessment makes clear that the use of only one surveillance type independently does a poor job of capturing the overall picture of occupancy on the landscape. The results show that model prediction one time step beyond the available data performed reasonably well, but patterns in seasonality and trends were not well captured the further out in time that predictions were made (Appendix S4, Figure 2). During the study, there were 14 site/time combinations where elimination would be declared, one of those was found to be occupied in the next time step, for an error rate of 7.1%.

In general, we found that individual surveillance occupancy estimates were overestimated in the ORV management area compared to the full dataset (Appendix S5), suggesting that to guide management on elimination probabilities, no individual surveillance method provides a full picture, and the estimates from the full dataset are more informative than simply the sum of the different components. Individual surveillance approach largely had worse model fits (Bayesian p-values; Appendix S4, Table 1) and lower AUC values (Appendix S4 Table 1) than the full dataset.

4 | DISCUSSION

By combining data on wildlife disease occurrence and the probability of detection given sampling effort, we can estimate the probability of elimination (i.e. freedom of RABV) for every grid cell at every time point in our study. When a disease is detected, the probability of elimination is logically zero. When a disease is not detected, an increasing number of negative surveillance samples improves certainty that a site is free from that disease and decreases the standard error associated with the probability estimates. The elimination probability surface can help provide guidance for effective surveillance efforts by identifying areas where greater management or monitoring is needed. ORV programmes have proved a useful tool for controlling, and in some cases, eliminating RABV in wildlife reservoir species (Freuling et al., 2013; Sidwa et al., 2005; Slate et al., 2005). Indeed, we found lower occurrence of RABV in the ORV-managed areas in our study area when compared with unmanaged areas where RABV is enzootic in the raccoon population, suggesting that ORV management is effective in reducing RABV transmission among raccoons. Additionally, the probability of occupancy decreased with time in the ORV managed area compared to the occupancy remaining relatively constant in the enzootic area, providing support that continued ORV management can increase the likelihood of eliminating RABV. We observed greater uncertainty in grid cells without samples near areas of current or recent RABV detections. If we wanted to increase certainty in these areas, we can use the elimination probability surface to provide guidance on where increased sampling would provide the most benefit.

Understanding epidemiological patterns of wildlife disease facilitates management planning and surveillance. RABV occurrence increased in areas with greater deciduous and mixed forest cover and in areas characterized as medium to high development. These habitats correspond to areas that raccoons select (Beasley, DeVault, Retamosa, & Rhodes, 2007; Bozek, Prange, & Gehrt, 2007); therefore, the increase in RABV occurrence may be a simple proxy for raccoon habitat selection. We also found a cyclic-seasonal pattern in rabies occurrence, consistent with a prior related study addressing RABV circulation in striped skunk populations (Pepin et al., 2017). Seasonal rabies incidence has also been described in bats (George et al., 2011) relating to variation in host contact rates, susceptibility, survival and life history (e.g. synchronized parturition). These factors may also relate to seasonal variation in RABV occurrence observed in raccoons (Duke-Sylvester, Bolzoni, & Real, 2011; Hirsch, Reynolds, Gehrt, & Craft, 2016). Understanding such patterns can help optimize management strategies by vaccinating animals prior to the predicted occurrence of seasonal epizootics. Modifications in the ORV strategy in response to habitat-associated patterns of rabies incidence may be one way to adapt management practices for maximal effect (but see Beasley et al., 2015). Habitat-targeted ERS has also been proposed for optimal detection of infected animals (Rees, Bélanger, Lelièvre, Coté, & Lambert, 2011).

Wildlife disease sampling often relies on passive sampling, convenience sampling or targeted sampling but on a limited spatial or temporal scale (Duncan et al., 2008; Mörner & Beasley, 2012). Some methods of surveillance may poorly represent a broader area of interest or might be seasonally variable. In our data, nuisance animals are more heavily concentrated around urban and suburban areas and interestingly showed negative biases in occupancy in these areas. When RABV is present in developed areas it is less likely to be detected by nuisance reports than by other surveillance methods. There is considerable literature on biases of road-based surveys (Keller & Scallan, 1999; Roberts et al., 2006). We found that occupancy estimates from road-killed samples alone were biased compared to occupancy estimates from all samples particularly in the ORV managed areas, suggestive of differences in road coverage, road speed or surrounding habitats across managed and unmanaged areas. Although roadkilled samples had a higher probability of RABV detection than methods such as surveillance-trapped or nuisance sample collection, there are drawbacks to exclusive use of this surveillance method. Therefore, to use just one surveillance type may result in spatial or temporal biases in occupancy estimation and using a combination of methods is generally recommended to be more robust for estimating disease presence.

Approximately 70% of all surveillance samples were collected in the spring and summer, likely reflective of periods of increased movement and higher likelihoods of people and their pets encountering raccoons in the warmer months (Glueck, Clark, & Andrews, 1988; Hirsch, Prange, Hauver, & Gehrt, 2013). However, the probability of detecting RABV was generally higher in the fall and winter for several surveillance methods. This seasonal effect was particularly strong for surveillance methods of found dead and roadkill animals. Although the overall number of samples from these categories is lower in fall–winter, the detection of rabid animals was higher. This may reflect how an increase in aberrant behaviour due to RABV (Hubbard, 1985; Jenkins & Winkler, 1987) is more detectable during periods of lower host population activity. The largest seasonal difference was observed among found dead samples, in which samples collected during fall–winter were over four times more likely to detect RABV than samples collected during spring–summer. Thus, samples that are found dead in fall–winter should be prioritized over found dead samples from other seasons, and these samples should be prioritized for testing.

To eliminate RABV, we need to understand patterns of RABV occurrence to inform optimal management efforts, monitoring, and ERS. By using a combination of surveillance methods we aimed to better understand the relative contribution of each method and achieve more robust estimation. Our approach of a multi-surveillance method, dynamic occupancy model is well suited to simultaneously evaluate spatial and temporal influences on occurrence, while accounting for and evaluating detection probabilities for multiple surveillance methods. Given that there are no false positives, any detection of RABV by any surveillance method constitutes a site that is truly occupied. Thus, reduced models (i.e. with single stream surveillance data) that failed to detect RABV underestimate RABV. By combining approaches we can gain strengths from each individual surveillance method without necessarily also being restricted by the caveats of each method. The full surveillance model also reduces the overall uncertainty around estimates which give us greater power to detect when RABV is truly eliminated and not just that there was a failure to detect it—a critical distinction for achieving long-term management objectives. This approach is particularly useful for monitoring of wildlife disease in general, as many wildlife disease surveillance make us of a combination of opportunistic, convenience and targeted sampling approaches.

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AUTHORS' CONTRIBUTIONS

A.J.D., C.T.W., A.T.G., T.X. and K.M.P. conceived the ideas. J.D.K., R.B.C., K.M.N., J.B. and R.W. compiled the data. A.J.D. analysed the data with inputs from C.T.W., A.T.G. and K.M.P. All authors provided edits to the manuscript.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.v23517k (Davis et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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