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Evaluation of contingency actions to control the spread of raccoon rabies in Ohio and Virginia

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ABSTRACT

The raccoon (*Procyon lotor*) variant of the rabies virus (RRV) is enzootic in the eastern United States and oral rabies vaccination (ORV) is the primary strategy to prevent and control landscape spread. Breaches of ORV management zones occasionally occur, and emergency “contingency” actions may be implemented to enhance local control. Contingency actions are an integral part of landscape-scale wildlife rabies management but can be very costly and routinely involve enhanced rabies surveillance (ERS) around the index case. We investigated two contingency actions in Ohio (2017–2019 and 2018–2021) and one in Virginia (2017–2019) using a dynamic, multi-method occupancy approach to examine relationships between specific management actions and RRV occurrence, including whether ERS was sufficient around the index case. The RRV occupancy was assessed seasonally at 100-km^2 grids and we examined relationships across three spatial scales (regional management zone, RRV free regions, and local contingency areas). The location of a grid relative to the ORV management zone was the strongest predictor of RRV occupancy at the regional scale. In RRV free regions, the neighbor effect and temporal variability were most important in influencing RRV occupancy. Parenteral (hand) vaccination of raccoons was important across all three contingency action areas, but more influential in the Ohio contingency action areas where more raccoons were hand vaccinated. In the Virginia contingency action area, ORV strategies were as important in reducing RRV occupancy as a hand vaccination strategy. The management action to trap, euthanize, and test (TET) raccoons was an important method to increase ERS, yet the impacts of TET on RRV occupancy are not clear. The probability of detecting additional cases of RRV was exceptionally high (>0.95) during the season the index case occurred. The probability of detecting RRV through ERS declined in the seasons following initial TET efforts but remained higher after the contingency action compared to the ERS detection probabilities prior to index case incidence. Local RRV cases were contained within one year and eliminated within 2–3 years of each contingency action.

1. Introduction

Within the United States (US), specific variants of the rabies virus (RABV) circulate in wild carnivore populations (Rupprecht et al., 2011; Ma et al., 2023). The raccoon (*Procyon lotor*) rabies virus variant (RRV) underwent epizootic expansion, attributed to the movement of rabid raccoons from enzootic areas in Florida and Georgia to naïve populations of the mid-Atlantic states, during the late 1970 s (Nettles et al., 1979; Jenkins et al., 1988). In regions of the US where the RRV circulates, there are higher rates of post-exposure prophylaxis and there is the greatest burden of spillover RABV infections to domestic and wild mammals (Christian et al., 2009; Wallace et al., 2014).

The RRV is primarily managed using oral rabies vaccination (ORV) at a landscape scale. The US Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services (WS), National Rabies Management Program (NRMP) nationally coordinates an ORV program to prevent the spread of and locally eliminate RRV from the eastern US (Slate et al., 2008; Elmore et al., 2017). Coordinated ORV has been

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conducted in the eastern US since the 1990 s (Elmore et al., 2017; Fehlner-Gardiner, 2018), with a current geographic footprint from Maine west to Ohio and south to Alabama. ORV campaigns targeting RRV principally rely on bait delivery using fixed-wing aircraft across rural landscapes under management (Elmore et al., 2017). In areas with more human development, ORV deployment instead uses ground bait delivery methods (e.g., along roads from vehicles), rotary-wing aircraft, or bait stations (Elmore et al., 2017). The NRMP goal is to prevent the spread of, and eventually to eliminate RRV by strategically moving ORV zones eastward toward the Atlantic Ocean and southward away from the shared border with Canada. In the northeastern US, the ORV zone was shifted south from the US border with southern Québec, Canada based on evidence of local RRV elimination along the border (Davis et al., 2023).

The NRMP evaluates ORV program effectiveness primarily through enhanced rabies surveillance (ERS) to monitor RRV occurrence and help refine management (Kirby et al., 2017; Davis et al., 2021). ERS is active targeted surveillance and is conducted in and around ORV management zones in the US, as well as areas at high-risk of RRV spread. ERS is conducted to provide a more comprehensive estimate of RRV distribution for effective management, as a complement to public health surveillance data, which can be biased by human population density (Kirby et al., 2017). In North America, ERS can consist of a combination of surveillance methods, including public reporting of strange-acting and found dead animals, road kill surveys, surveillance-trapping, and removal of animals and nuisance sample collection, primarily sourced through robust cooperator networks. Sample collection for ERS is focused on "strange-acting" and "found dead" indicator animals as most informative for rabies surveillance (Kirby et al., 2017; Davis et al., 2021), along with indicator animals submitted for public health surveillance. The NRMP coordinates with WS field employees across ~20 states annually as well as state and local agencies to collect samples for ERS and characterize all positive cases. National public health rabies surveillance data, consisting of animals tested for RABV following a human or pet exposure by a network of laboratories across the US, are reported to and summarized annually by the Centers for Disease Control and Prevention (CDC). The national public health surveillance system, combined with virus characterization of cases, provides an additional means for detecting index cases and additional information on the distribution of the RRV (Ma et al., 2023), but not all positive cases may be characterized from this system (Pieracci et al., 2020). Given the demonstrated risks of epizootic expansion and burden of exposures associated with RRV, both public health and ERS surveillance systems are used for timely detection and response to breaches of the RRV management zone to prevent further spread to naïve populations of raccoons in eastern North America (Fehlner-Gardiner, 2018).

When a rabid animal infected with RRV is detected (by public health surveillance or ERS) beyond an ORV zone in the eastern US, it can pose a serious risk for epizootic spread through naïve raccoon populations if left unmanaged as observed from historical events. Additionally, there are public health concerns associated with the spread of RRV to naïve areas due to increased exposure risk to local human populations that lack awareness of the risks associated with RRV, along with the potential for spillover transmission to domestic and wild animals. For cases involving a potential ORV zone breach, the NRMP conducts a formal risk assessment to determine whether emergency management activities (hereafter, contingency actions) are needed in proximity to the index case. Contingency actions are meant to control and eliminate local RRV outbreaks occurring beyond management zones when and where breach events are detected (Slate et al., 2009; Slate and Rupprecht, 2012). In the US, all contingency actions are initiated with intensified ERS in the areas surrounding the index case (Chipman et al., 2023). We define intensified ERS for contingency actions as involving targeted outreach among local cooperator networks to increase collection and reporting of strange-acting or found dead indicator animals and increasing road kill surveillance within buffered areas surrounding an index positive case when practical. Intensified ERS may be initiated in part through surveillance-trapping and removal of animals (i.e., trap-euthanize-test – TET), which may reduce susceptible raccoon populations and mitigate the spread of RRV, consistent with guidelines for wildlife rabies prevention and control in the US (Brown et al., 2016). The switch from a reliance on more passive surveillance when an area is considered RRV free to more active surveillance following a positive case being found matches with the aims and strategies adjustments recommended by Thulke et al. (2009). Following intensified ERS, the combination of management strategies deployed in each contingency action may differ based on risk factors, local target host ecology, and logistical considerations. The types of management strategies associated with contingency actions include establishment of a new ORV zone or increasing the bait density and/or frequency of application within an existing ORV zone; and parenteral vaccination (hereafter, hand vaccination) of animals using trap, vaccinate, and release (TVR) methods independently or in conjunction with ORV and associated monitoring activities.

We evaluated three contingency actions in the central part of the RRV management zone in the eastern US in historically RRV free areas. In March 2017, a rabid raccoon was detected by ERS 8 km west of the ORV zone in Stark County, Ohio. In April 2017, a rabid raccoon was detected by public health surveillance 14 km west of the established ORV zone in Wise County, Virginia. In July 2018, a rabid raccoon was detected by ERS 27 km west of the existing ORV zone in Tuscarawas County, Ohio and 18 km southwest of the 2017 contingency action management area in Ohio. In each of these events, a combination of TET, increased ORV, and TVR in conjunction with post-ORV monitoring, were conducted along with locally intensified ERS.

There is interest and a financial need to improve and refine combinations of control strategies and advance our understanding of the relative impacts of different management actions to reduce and eliminate localized RRV outbreaks associated with contingency actions. Our study objectives were to determine the probability of RRV detection and local elimination during the three-year period(s) of contingency response and examine the relative impacts of specific management actions employed within and across these areas. We retrospectively examine local RRV dynamics prior to detection of index cases for each breach event, to assess whether sufficient ERS was occurring in these areas for detecting new cases beyond the index and to understand the broader impacts from RRV dynamics across managed landscapes.

2. Methods

2.1. Study area

We examined a study area that encompassed all three contingency actions and included areas both east of the ORV zones (i.e., enzootic for RRV) and west of the ORV zones (i.e., RRV free). The study area includes over 178,000 km^2 across eastern Ohio, western Pennsylvania, most of West Virginia, the eastern edge of Kentucky, and the western part of Virginia (Fig. 1). The study area is dominated by deciduous forest cover (58%), hay and pastureland (12%), development (11% cumulative; 0.4% high development, 1% medium development, 3% low development, and 6% open development), and 9% cultivated crops according to the 2011 National Land Cover Database (NLCD; Dewitz and U.S. Geological Survey, 2021). The elevation in the study area ranged from 152 to 1589 m, with an average of 418 m.

Habitat coverage varied across the three contingency action areas. The contingency action that started in Ohio in 2017 was north of the Ohio contingency action initiated in 2018, which we refer to as Ohio North and Ohio South, respectively. We used the contingency action ORV zone boundaries from the NRMP to identify the contingency action areas. The Ohio North contingency action area was ~1500 km^2 and was a mix of deciduous forest cover (28%), cultivated crop cover (25%), and hay and pastureland (21%), with open development area (11%) based on the 2011 NLCD. Ohio South was slightly larger at ~1800 km^2 and

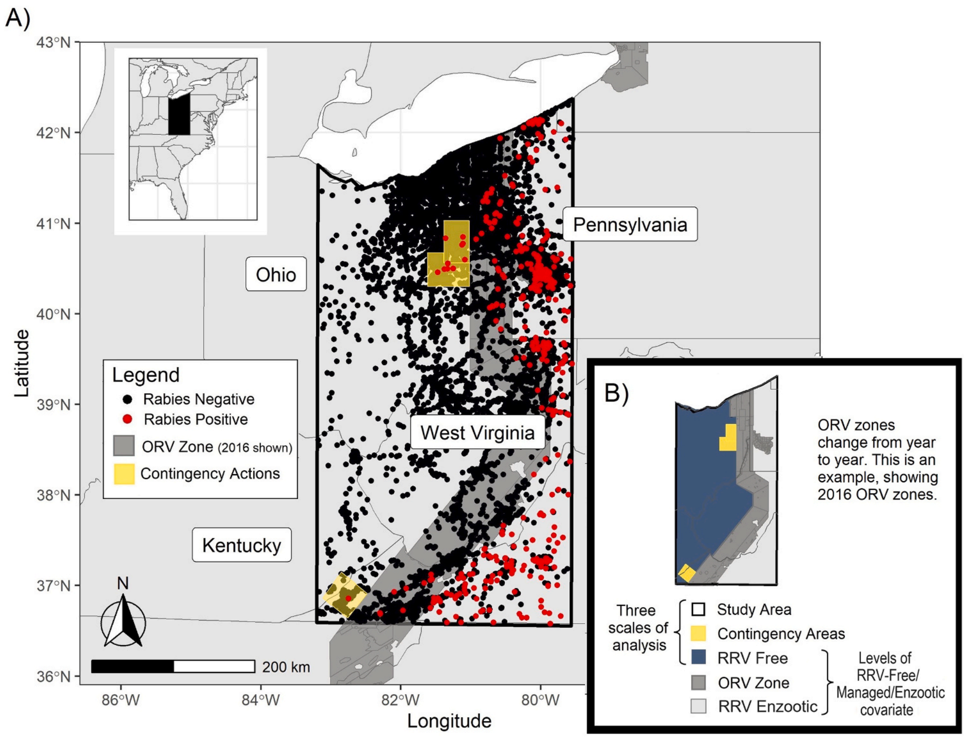

Fig. 1. A) Study area (outlined in black) used to examine raccoon rabies virus variant (RRV) occupancy. Contingency actions are shown as yellow polygons: two in Ohio (Ohio North, Ohio South) and one in Virginia. The locations of raccoon rabies surveillance samples from 2015 to 2021 are shown with negative samples as black dots and positive samples as red dots (positives are on top of negatives for clarity). Data include enhanced rabies surveillance and public health surveillance samples. To demonstrate how the contingency events were breaches of the oral rabies vaccination (ORV) zone, the ORV zone displayed is from 2016, prior to the breaches (dark grey polygon). B) The inset shows the three scales in the analysis: the study area, the contingency areas, and the RRV free area (west of the ORV zone; blue polygon). In the study area analysis, there is a covariate termed "RRV-Free/Managed/Enzootic" which includes the RRV free region, the ORV zone (managed for RRV), and the area where RRV is enzootic (east of ORV; light grey polygon).

had more deciduous forest cover (54%), but lower percent cover of cultivated crops (13%), hay and pastureland (16%), and open development (7%). The Virginia contingency action area was ~1600 km^2 and had the most deciduous forest cover (71%), no cultivated crop cover (0.0%), low hay and pastureland coverage (3%) and open development (5%) based on the 2011 NLCD. Each contingency action area had similar amounts of high development (0.2–0.5%), medium development (1–2%), and low development (2–6%). The Ohio North and South areas averaged 347 and 320 m in elevation respectively, whereas the Virginia area averaged 671 m in elevation. The Ohio South contingency action ORV zone overlapped with the southwestern portion of the Ohio North contingency action ORV zone by a width of ~8 km on the northeastern portion of the Ohio South area (Fig. 1). For analytical purposes, we assign overlap areas to Ohio North during 2015–2018 and to Ohio South during 2019–2021 to reflect the timing of management at these sites.

2.2. Surveillance data

The RRV surveillance data from 2015 to 2021 was derived from two sources: ERS and the public health National Rabies Surveillance System. We used data starting in 2015 to provide context for what was going on in the areas prior to the start of the first contingency case. For each animal record, the latitude and longitude, date, species, agency who collected the animal, animal encounter method (e.g., road kill, surveillance trapped), and field comments were recorded. The RABV diagnostic testing was conducted on brain tissue, either by WS using the direct rapid immunohistochemical test (Patrick et al., 2019) or by a diagnostic laboratory using the standard direct fluorescent antibody assay (Ronald et al., 2003). The RABV variant typing of index and ERS cases was conducted using discriminatory monoclonal antibody panels (Smith et al., 1984), or by real-time polymerase chain reaction – PCR (Szanto et al., 2011). The RABV variant typing was not conducted for all rabid animals detected within the study area by the public health surveillance system and uncharacterized cases in terrestrial species were assumed to be infected with the RRV.

The NRMP ERS system recognizes differences in the disposition of animals encountered or collected, using a point system to prioritize types of animals collected for ERS and to standardize efforts across years, with higher points assigned to indicator animals (Kirby et al., 2017; Davis et al., 2021). The NRMP surveillance categories are 1) animals reported as sick or strange-acting, 2) animals reported as found dead but not along roadways, 3) road-killed animals, 4) WS live-trapped animals specifically for ERS, 5) nuisance and other animals sampled not specifically collected for rabies surveillance (e.g., animals reported by the public as nuisance animals that were otherwise healthy, animals caught by the public during furbearer trapping) termed as 'other-known', and 6) samples for any unknown or unreported method of collection (Davis et al., 2021). In the occupancy model analysis employed in this and prior studies, we classify the national rabies public health surveillance data as a separate (7th) category ("public health").

2.3. Analytical methods

To examine spatial and temporal patterns of RRV occurrence, we conducted a dynamic occupancy analysis (MacKenzie et al., 2017). Occupancy models estimate the biological process, here whether rabies is actually present in an area ('occupancy'), and the observation process, the probability that rabies would be detected if it were present ('detection'). Detection probability is conditional and can be thought of as: if rabies was present, how likely would we be able to detect it given our surveillance efforts (MacKenzie et al., 2002, 2017). We overlaid a 10 km by 10 km grid across the study area (to match the scale in which management is conducted, similar to: Davis et al., 2019a; Davis et al., 2021; Davis et al., 2023) and RRV occupancy was assessed within each grid cell (hereafter referred to as site). Dynamic models assume a period of closure (where occupancy status within a site does not change; primary period) and allows for changes in occupancy between periods of closure. We used astronomical seasons as our primary periods to account for the incubation time for RRV. We modeled RRV occupancy, and our methods of surveillance were targeted at raccoons and any other wild or domestic rabid animal infected with the RRV. The number of raccoons sampled and the number that were rabid within a given site and season were used to inform both the occupancy and the probability of detecting RRV. Any cross-species-transmission events were used to help inform the presence of RRV within a given site and season. We used a multi-method dynamic occupancy model (Davis et al., 2019a, 2019b) to estimate separate detection probabilities for each ERS category. If RRV was detected by any surveillance method, the model would indicate RRV was present in the grid during that site-season.

We fit the dynamic occupancy model using a Bayesian hierarchical approach custom coded in program R (R Core Team, 2021) code available on GitHub (https://github.com/AmyJDavis/RABV_DynamicOccupancy). Dynamic occupancy models model initial occupancy (ψ_1) and the transition rates of extinction (ε_t; the probability an occupied site will become unoccupied at the next time step $t+1$) and colonization (γ_t; the probability an unoccupied site will become occupied at the next time step). To account for variability in occupancy we fit models with management, habitat, spatial, and temporal covariates on the colonization process. Management covariates included the location of a site with respect to the ORV zone (if the site was west of the ORV zone in the RRV free region, within the ORV zone, or east of the ORV zone where RRV is enzootic; termed 'RRV-Free/Managed/Enzootic'; Fig. 1B), the duration of continuous ORV management (in years, termed 'Years of ORV'), an indicator of vaccine type either RABORAL V-RG® (hereafter, V-RG; Boehringer Ingelheim Animal Health USA Inc., Athens, Georgia, USA) or the Ontario Rabies Vaccine Bait (hereafter, ONRAB; Artemis Technologies, Inc., an indirect, wholly owned subsidiary of Ceva Sante Animale, S.A., Guelph, Ontario, Canada), an indicator for whether ORV was conducted in the preceding spring (two levels, yes/no) for a site-season, the number of animals hand-vaccinated by site (continuous), and the amount of TET by site (continuous). The footprint of ORV management may change from year to year and the areas considered RRV free, RRV managed, and RRV enzootic shift across years as a result. All ORV covariates are considered to have a year-long impact (e.g., a spring ORV event will impact occupancy for one calendar year starting in the spring and ending at the end of winter the following year). The habitat covariates we examined were the proportion of the site covered by cultivated crops, deciduous or mixed forest cover, evergreen forest cover, hay and pastureland, shrubland, medium or high development areas, and open or low development areas. We included a covariate for the average elevation of a site. We modeled a neighbor effect to account for the proportion of neighboring sites occupied (i.e., infected) with RRV. To address potential factors associated with case breaches into RRV free areas west of management zones, we modeled a covariate for the distance to the nearest ORV zone (km) and a distance to the nearest urban area (km). We calculated the distance to the nearest urban area by grid cell defining a grid with an urban area as one with more than 1% cover of medium or high development areas within the 100 km^2 grid. We allowed RRV occupancy to vary across time and included an interaction with site location with respect to the ORV zone to allow for different temporal patterns in the RRV free region, within ORV management areas, and within RRV enzootic areas. To account for temporal variability in the system, we fit models with a linear trend and with polynomial splines. We compared models with varying degrees of freedom based on Watanabe-Akaike information criteria – WAIC (Hooten and Hobbs, 2015), a metric similar to AIC, where lower values suggest a more parsimonious model. We examined the goodness of fit of the most supported model using the area under the curve (AUC) statistic adjusted for occupancy models (Zipkin et al., 2012).

As the dynamic occupancy model estimates occupancy itself as a derived parameter (a combination of the initial occupancy and the transition parameters), we used post-hoc analyses to examine factors relating directly to RRV occupancy at different spatial scales (Fig. 1B). One spatial scale of interest was the entire study area. Understanding broad scale factors that influence occupancy is important to get a general idea of the impacts of management and habitat on RRV. We were also interested in understanding high-risk factors associated with RRV spread to naïve areas; therefore, a second scale we examined was the RRV free region. A main objective was to examine the impacts of contingency actions on RRV occurrence, thus, a third spatial scale was focused on local buffered areas of each contingency action to examine factors relating to declines in occupancy resulting from management. We limited the scale of the local analysis to declines in RRV occupancy, to separate relationships between factors associated with management activities from the lagged and subsequent impacts of those activities. Declines in occupancy were determined from the differences between occupancy probabilities within a site from one seasonal time step to the next, only values less than zero were considered declines. We were interested in understanding the management and landscape drivers of RRV occupancy declines within these scales. We used random forest models to identify important covariates in our data (Breiman, 2001). We implemented these using the randomForestSRC package (Ishwaran and Kogalur, 2023). We used the tune function in the package to find the optimal mtry and nodesize to maximize the out-of-bag R-squared; out-of-bag data are set automatically within the function (Ishwaran and Kogalur, 2023). More important covariates are factors that explain a greater amount of the variation in the response data, i.e., RRV occupancy or decline in occupancy.

The occupancy model provides estimates of detection probability (p) by surveillance category k. The amount of surveillance and types of surveillance varied across site i and time t. To calculate the cumulative probability of detection at a site in time (θ_{it}), we used the detection probabilities by surveillance category (p_k) and accounted for the surveillance effort (e) employed by that surveillance method k, within that site i and time period t (Eq. 1). The probability that rabies is not present (local elimination) can be calculated based on the occupancy and detection probability information by site i and time period t (Eq. 2).

$$\theta_{it} = 1 - \prod_k (1 - p_k)^{e_{itk}} \tag{1}$$

$$P(elimination) = \frac{(1 - \psi_{it})}{(1 - \psi_{it}) + \psi_{it}(1 - \theta_{it})} \tag{2}$$

3. Results

3.1. Descriptive statistics

Across the entire study area from 2015 to 2021, 29,890 raccoons were sampled and 712 were rabid (2.4%). There were 176 animals from 13 other species confirmed to be infected with RRV (Table 1). At the start of each contingency action, raccoons were trapped, euthanized, and tested for ERS (per USDA SOP similar to: Rosatte et al., 2001; 2007; 2009; Fig. 2). A total of 1916 raccoons were removed: 1060 in Ohio North, 525 in Ohio South, and 331 in Virginia. Spring and autumn ORV was conducted for at least three years in each contingency action area (Fig. 2). Hand vaccination efforts were conducted routinely in conjunction with post-ORV sampling activities annually (Fig. 2). Additionally, some hand vaccination occurred within the broader study area apart from the contingency events. A total of 4716 raccoons were hand vaccinated across the entire study area: 1578 in Ohio North, 1362 in Ohio South, 536 in Virginia, and 1240 within the overall study area yet outside of the local contingency areas.

Table 1
Number of terrestrial (non-bat) animals that tested positive for raccoon rabies virus variant within the study area from 2015 to 2021 shown by species. Data include enhanced rabies surveillance and public health surveillance samples. A total of 29,890 raccoons were used in the analysis (29,178 were negative for rabies). To help inform raccoon rabies occupancy status, only raccoon rabies variant positives were used for non-raccoons (non-raccoon negatives were excluded).

Species	Scientific name	Positives
Beaver	*Castor canadensis*	1
Bobcat	*Lynx rufus*	4
Domestic cat	*Felis catus*	15
Cattle	*Bos taurus*	17
Coyote	*Canis latrans*	1
Dog	*Canis lupus familiaris*	4
Donkey	*Equus asinus*	1
Fox (red and gray)	*Vulpes vulpes and Urocyon cinereoargenteus*	30
Goat	*Capra aegagrus hircus*	2
Groundhog	*Marmota monax*	6
Horse	*Equus caballus*	1
Raccoon	*Procyon lotor*	712
Skunk	*Mephitis mephitis*	93
Yak	*Bos grunniens*	1

3.2. Occupancy results

We compared models of temporal variability in the data including a linear trend and polynomial splines with three to nine degrees of freedom (on time) in the model. The most supported model based on the WAIC statistic was a linear model (Table 2). The top occupancy model performed well based on the occupancy-adjusted AUC statistic (0.87). The probability of detecting RRV varied by surveillance category (Table 3). The highest probabilities of RRV detection were from ERS animals that were found dead, strange acting, or separately collected through the national rabies public health surveillance system. The lowest probabilities of RRV detection were live-trapped and other-known samples (e.g., nuisance reported animals). The largest number of samples across the entire study area came from the other-known category (e.g., nuisance reported animals), followed by public health samples, then road kill, strange acting, surveillance trapped, unknown, and found dead. Within the contingency action areas, intensified ERS involved increasing efforts of TET sample collection, categorized as surveillance-trapped were the majority of samples (Table 3). Surveillance-trapped samples had a low probability of detection (0.01, 95% CI 0.00, 0.02; Table 3). Three rabid individuals were sampled using this method across the entire study area but no positive cases were found using this approach in the contingency action areas (Table 3). The number of samples needed to reach a high cumulative RRV detection probability using only a single surveillance category varied with the detection probability for each category (Table 3).

The average cumulative RRV detection probability by site within ORV managed areas across the entire study period was 0.07 (95% CI: 0.00, 0.62), compared to 0.04 in the RRV free region (95% CI: 0.00, 0.35). Cumulative RRV detection probability within contingency action areas varied by site across time (Fig. 3B). Prior to index cases, the cumulative RRV detection probabilities in contingency areas were similar to or lower than the 0.04 average for RRV free regions. During the spring of 2017 in Ohio North and Virginia and during the summer of 2018 in Ohio South, ERS and cumulative detection probability increased within some, but not all, sites within the contingency action areas (Fig. 3B). In Ohio North the average cumulative detection probability increased from 0.04 (range: 0 – 0.27) prior to the contingency event to 0.15 (range: 0 – 0.98) during contingency management (spring 2017 through winter 2019), to 0.23 (range: 0 – 0.99) after contingency management. In Virginia the average cumulative detection probability increased from 0.003 (range: 0 – 0.23) prior to the contingency event to 0.05 (range: 0 – 0.92) during the contingency management (spring 2017 through winter 2019), to 0.02 (range: 0 – 0.32) after contingency management. In Ohio South, the average cumulative detection probability increased from 0.04 (range: 0 – 0.81) prior to the contingency event to 0.10 (range: 0 – 0.89) during the contingency management (summer 2018 through winter 2021). Our study period ended at the same time as the end of the Ohio South contingency action and thus there is no data post-contingency for this area in our study.

3.3. Elimination probability

Primary objectives of contingency action efforts are to contain local outbreaks to prevent the spread of RRV and to restore these local areas to a RRV free status. Therefore, we examined the probability that RRV was locally eliminated from an area. This is possible using information on the probability of occupancy and accounting for how much surveillance effort was employed in an area. The probability that RRV was locally eliminated in the contingency action areas was greater prior to the index case in Ohio South and Virginia, as expected (Fig. 3C). The probability of local RRV elimination remained lower than prior to initialized contingency actions for roughly two-three years in the contingency action

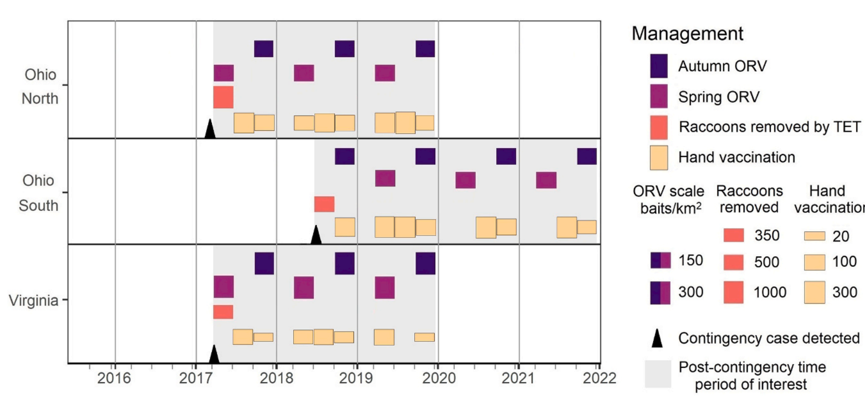

Fig. 2. Schedule of contingency action management actions shown by contingency area (Ohio North, Ohio South, Virginia) and scaled by intensity of management. Schedule blocks are by 3-month seasons (winter to fall) indicating if that management action occurred in that season. The dark purple and magenta bars are the autumn and spring oral rabies vaccination (ORV) actions, respectively. The scale for spring and autumn ORV is the same and blocks are discrete but increase in height as bait density increases (150 or 300 baits/km^2). The red bars are when raccoon removal (trap, euthanize, test – TET) took place. The scale is continuous ranging from 350 to just over 1000 animals removed by TET per contingency action area by season. The tan color indicates when hand vaccination (trap, vaccinate, release) efforts were implemented. The scale is continuous from 20 to 300 animals hand vaccinated per contingency action area by season. The time when the initial raccoon rabies virus variant case was detected which incited each contingency action is shown as a black triangle. The grey shaded regions show the periods of management that are of interest for the analyses in this study.

Table 2
Results for raccoon rabies virus (RRV) variant dynamic occupancy model to determine best fitting temporal model. All models except the intercept only model include habitat variables (proportions of: cultivated crops, deciduous and mixed forest cover, evergreen forest cover, hay and pasture cover, shrub, medium and high development areas), management impacts (RRV free regions, oral rabies vaccination [ORV] managed zones, or RRV enzootic areas; continuous years of ORV baiting; numbers of raccoons hand vaccinated; number of raccoons trapped, euthanized, and tested), impacts of lack of management (time since the last ORV and distance from the nearest ORV zone), and neighbor effects. The models compare the number of degrees of freedom for the splines to use on the temporal parameter compared to the linear time model and an intercept only model. Models are ranked by WAIC values, lower values are more parsimonious. The difference in WAIC from the top model is shown as the delta WAIC. K is the number of parameters. The occupancy adjusted AUC statistics are shown for each model, higher AUC indicates a better fit.

Model	k	Delta WAIC	WAIC	AUC
Linear trend	14	0.00	3146.62	0.87
bs(time, df=7)	31	66.62	3213.24	0.84
bs(time, df=4)	22	123.82	3270.44	0.86
bs(time, df=3)	19	189.91	3336.53	0.86
bs(time, df=6)	28	205.46	3352.08	0.87
bs(time, df=5)	25	235.05	3381.67	0.85
bs(time, df=8)	34	243.70	3390.32	0.85
bs(time, df=9)	37	502.47	3649.09	0.83
Intercept only	1	914.27	4060.89	0.67

areas, then returned to pre-contingency levels (Fig. 3C).

3.4. Random forest results

Random forest analyses explained a considerable amount of variability in RRV occupancy across the study area (out of box R^2= 0.99) and for RRV free regions (out of box R^2 = 0.96). Random forest results revealed that the location of a site relative to the ORV zone (termed RRV-Free/Managed/Enzootic) was one of the strongest explanatory variables of RRV occupancy across the entire study area (Fig. 4A). Temporal variability and the neighbor effect (proportion of neighboring sites that was occupied with RRV) were important across all scales of analysis (Figs. 4A and 4B). The RRV occupancy probability declined over time in the managed areas and was lowest in RRV free regions and conversely greatest in the unmanaged RRV enzootic area (Fig. 5A). As the proportion of neighboring sites infected with RRV increased, the probability a given site would be infected increased as well (Fig. 5B). In the RRV free region, the neighbor effect was the most important predictor, then temporal variability, and then the number of years since ORV management had occurred (Fig. 4A). The distance to the nearest urban area (termed DistToCity) was not important at explaining ORV occupancy probability at our grid scale of 100 km^2 (Fig. 4A).

Within the contingency action areas, respectively, the random forest analyses explained a majority of the RRV occupancy variability (out of the box R^2 = 0.51 for Ohio North, 0.67 for Ohio South, and 0.55 for Virginia respectively). In the context of controlling RRV outbreaks as part of contingency actions, the neighbor and temporal variability effects were important in explaining variability around declining RRV occupancy as expected (Fig. 4B). Within both Ohio contingency action areas, the hand vaccination effort was the most important factor explaining declines in RRV occupancy (Fig. 4B). Hand vaccination was also important in Virginia, along with several other factors, in explaining declining RRV occupancy (Fig. 4B). Hand vaccination efforts were more successful in both Ohio contingency areas compared to Virginia. All areas showed a more rapid decline in RRV occupancy as the number of animals hand vaccinated increased from a zero baseline up to 50 raccoons per km^2 (Fig. 6A). Hand vaccination of more than 50 raccoons per km^2 still resulted in RRV occupancy declines, but the decay rate was slower (Fig. 6A). In Virginia, the years of cumulative ORV baiting, vaccine type (V-RG compared to none in this area), bait density (300 baits/km^2 compared to none), and spring ORV baiting were other important factors in explaining declining RRV occupancy (Fig. 4B).

The number of years of cumulative ORV and spring ORV were important across all contingency actions, although the relative importance of either factor varied by contingency action area and both factors were relatively more important in Virginia (Fig. 4B). The first few years of ORV resulted in the greatest RRV occupancy declines across all contingency action areas (Fig. 6B). RRV occupancy declined when spring ORV was conducted in addition to autumn campaigns, but the impact was greatest in Virginia (Fig. 6C). The occupancy of RRV tended to decline with raccoon removals (i.e., TET) in the previous seasonal timestep (Fig. 4B and Fig. 6D). There were two vaccine types used for ORV (V-RG and ONRAB) and two application densities used in the contingency action areas (150 and 300 baits per km^2) but ONRAB only at 150 baits per km^2 was the only ORV deployment in both Ohio contingency areas and V-RG at 300 baits per km^2 was the only deployment in the Virginia contingency action areas. The average decline associated with ONRAB at 150 baits/km^2 (at Ohio North and Ohio South) was −0.06 (95% CI: −0.2.–0.01). The average decline associated with V-RG at 300 baits/km^2 (in Virginia only) was −0.07 (95% CI: −0.12, −0.02). Caution is warranted for interpretation of specific bait types or densities associated with declines in RRV occupancy given the lack of treatment controls and uneven replication of treatment factors across areas.

Table 3
Probability of rabies detection by surveillance category. The 95% credible interval (CI) for each detection probability is provided. The number of samples from each category are shown by region: the entire study area (excluding the contingency areas), and the three contingency action areas: Ohio North, Ohio South, and Virginia with the numbers of raccoon rabies variant (RRV) positive values shown in parentheses. Data are from 2015 to 2021. Additionally, the number of samples required for each surveillance category to reach a cumulative detection probability of 0.5, 0.8, and 0.95 per site and season is shown.

			Number of samples collected in each region (number of positives)				Samples needed to reach cumulative detections of:		
Category	Detection Probability	95% CI	Study Area	OH North	OH South	VA	0.50	0.80	0.95
Strange acting	0.14	(0.12–0.16)	2565 (157)	137 (3)	40 (1)	14 (2)	5	11	20
Found dead	0.16	(0.09–0.25)	240 (13)	21 (0)	11 (0)	1 (0)	4	10	17
Road kill	0.05	(0.03–0.06)	4251 (41)	273 (0)	191 (2)	16 (0)	15	34	64
Surveillance trapped	0.01	(0.00–0.02)	116 (3)	1063 (0)	530 (0)	344 (0)	86	201	373
Other-known	0.01	(0.01–0.01)	10840 (56)	18 (0)	17 (1)	8 (0)	63	147	274
Unknown	0.05	(0.02–0.08)	408 (10)	2 (0)	0 (0)	1 (0)	15	53	65
Public health	0.13	(0.11–0.14)	8391 (418)	225 (1)	121 (4)	46 (0)	5	12	22

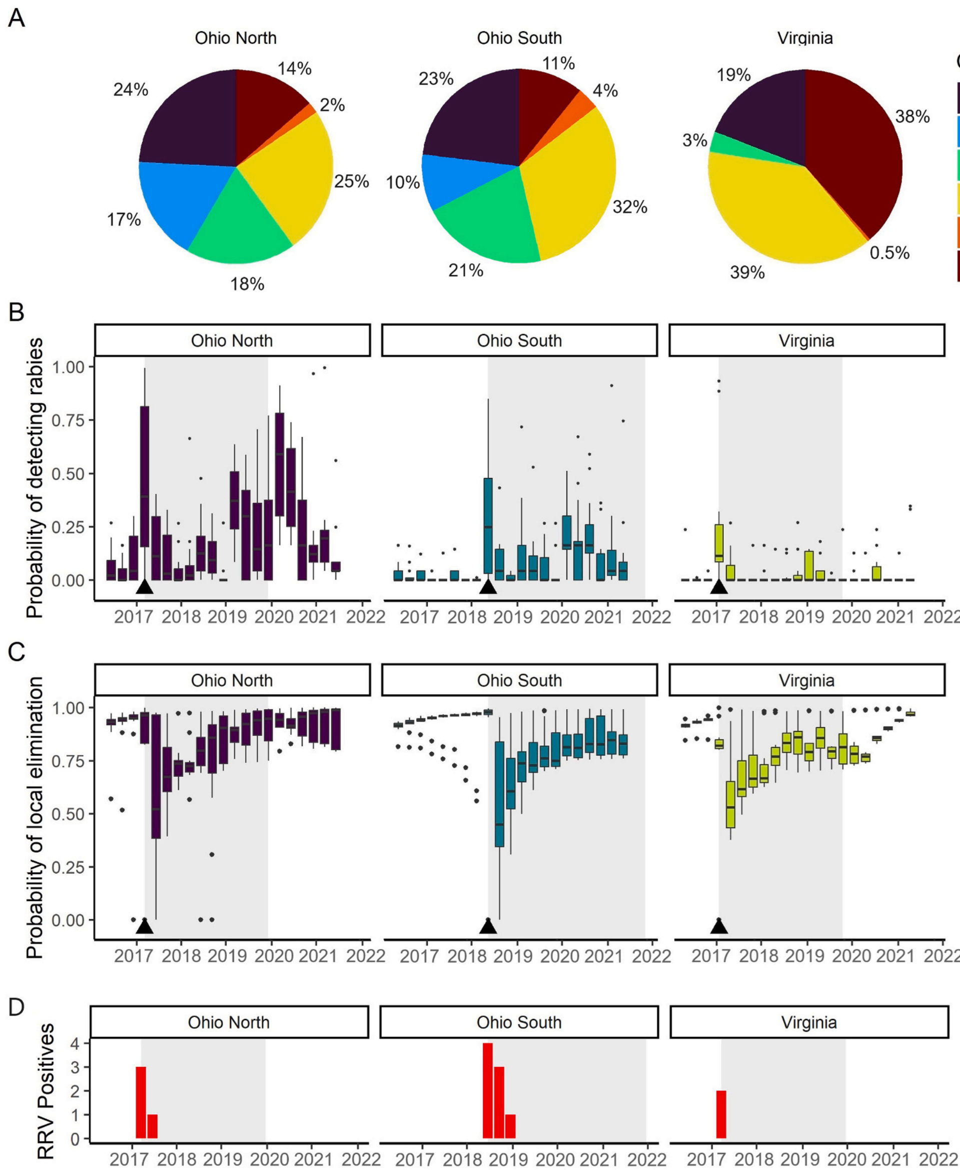

Fig. 3. A) The proportion of the cumulative probability across time that is contributed by each surveillance category shown by contingency action area: Ohio North, Ohio South, and Virginia. B) Cumulative probability of detecting rabies by season based on the surveillance effort employed and the probability of detection for each surveillance category. C) The probability that rabies was locally eliminated from each site in the contingency action areas based on the probability of occupancy and the detection probability (Eq. 2). D) Bar plot showing the number of raccoon rabies variant (RRV) positives across time and region. Boxplots in B and C show the median (horizontal line), interquartile range (box), 1.5 times the interquartile range (vertical line), and data outside that range (dots). The boxplots show the distribution of detection probabilities for each site within each contingency action area, there were 10 sites in Ohio North and Virginia, and 12 sites in Ohio South. Probability of local elimination was zero when there was a RRV positive in a site. The time when the index RRV case was found which incited each contingency action is shown as a black triangle. The grey shaded regions in B, C, and D show the periods of management that are of interest for the analyses in this study.

4. Discussion

Contingency actions often involve expensive and intensive management and surveillance efforts to ensure that breaches of ORV zones are detected and addressed rapidly for efficient RABV control (Slate and Rupprecht, 2012; Gilbert and Chipman, 2020). The probability of RRV occupancy spiked in the contingency areas following index cases being detected. However, within one year from the index case(s), the RRV occupancy in local contingency areas was comparable to other areas managed with ORV, and the probabilities that RRV was locally eliminated within the contingency areas was relatively high within 2–3 years following the index case. This underscores the importance of a multi-year approach to management targeting local RABV elimination as reported elsewhere (e.g., Baker et al., 2019; Acheson et al., 2023). Furthermore, no new RRV cases were detected after a year from the index case across all three local areas examined in this study. These results suggest that contingency action management efforts can rapidly and effectively control RRV breaches of ORV zones and locally eliminate RRV.

The probability that RRV was locally eliminated from the contingency action areas depends both on the probability of RRV occupancy and the amount of surveillance in the area. If RRV is not detected in an area, this could either be due to RRV being locally eliminated from that area, or RRV was present but not detected in that area. ERS was intensified surrounding contingency action index cases, primarily through TET efforts conducted immediately following each index case. In the site where the index case occurred, RRV detection probability was often above 90%, suggesting if additional rabies cases were present during the

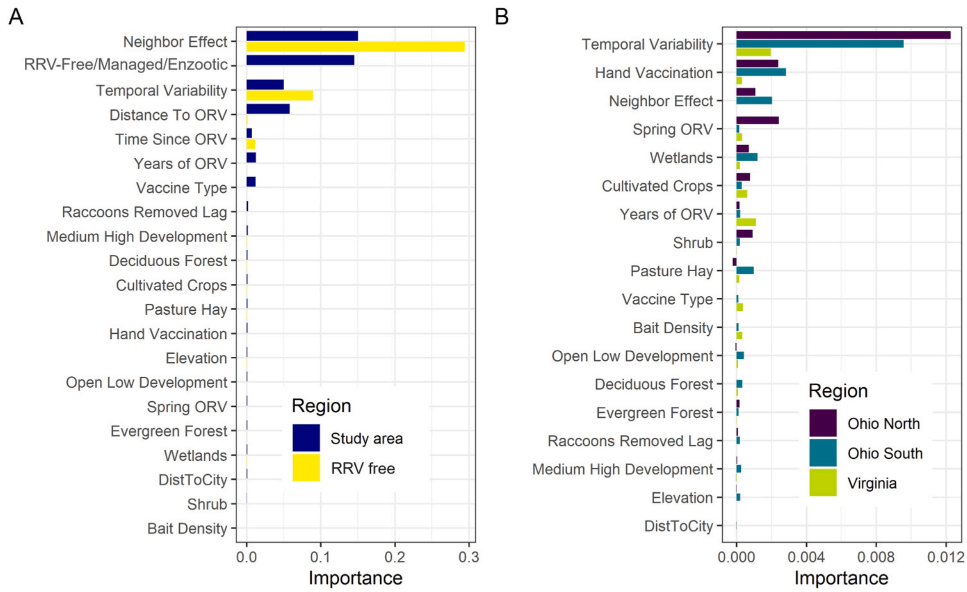

Fig. 4. Variable importance plot from random forest analyses on A) raccoon rabies virus variant (RRV) occupancy across the entire study area (blue) and just the RRV free areas (yellow) and B) on declines in RRV occupancy within the three contingency action areas: Ohio North (purple), Ohio South (teal), Virginia (light green). The variables are sorted by the most important to the least. Larger values of importance suggest the covariate was important for explaining variability in RRV occupancy or declines in RRV occupancy.

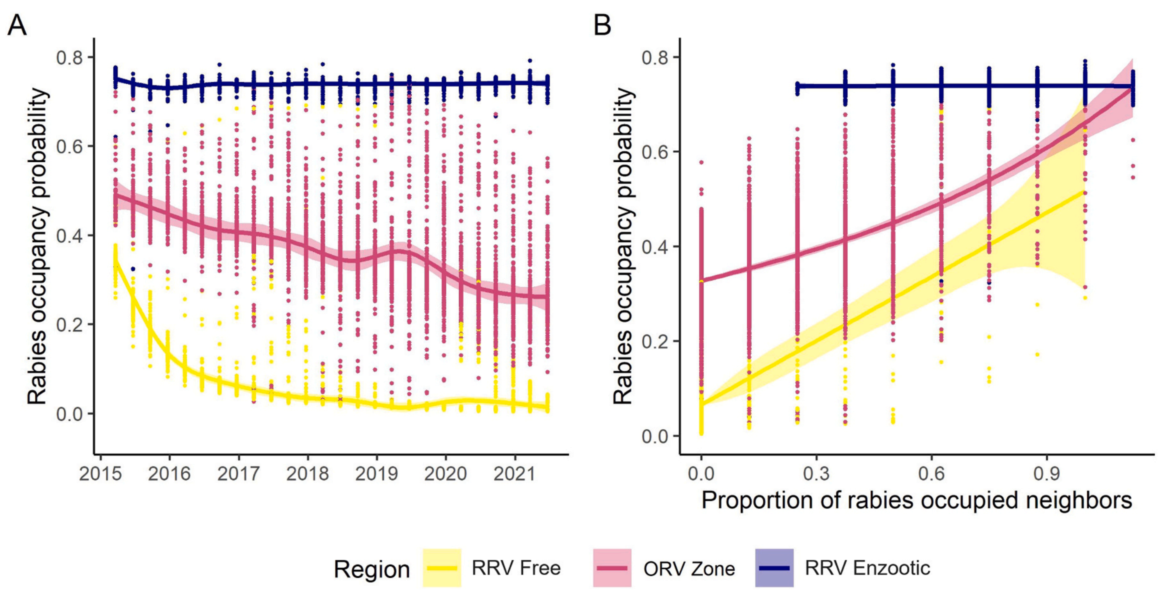

Fig. 5. Marginal plots from the random forest model on the entire study area showing the relationship between raccoon rabies virus variant (RRV) occupancy and A) time and B) proportion of neighboring sites that were occupied by RRV. Each plot shows the results by general region: RRV enzootic area (navy), oral rabies vaccination (ORV) zone (magenta), and RRV free (yellow). The shaded region represents the variability in the relationship for the marginal plot. The points are the realized rabies occupancy probabilities from the most supported model from the occupancy analysis. The initial rabies occupancy in RRV free regions was higher than expected (A) likely due to lower sampling in this area.

initial season of surveillance, they would likely be detected. After the initial season, ERS efforts declined across all contingency areas but remained higher than pre-contingency action levels. ERS in Ohio remained higher than in Virginia following the contingency action response, and thus conditions of local RRV elimination were realized sooner in Ohio areas compared to Virginia. Additional ERS in Virginia might have resulted in a shorter time to be confident of local RRV elimination; however, further intensification of ERS requires additional program costs and the economic cost-benefit ratios considered for determining how intensive ERS response should be for a localized RRV outbreak could be conducted (Anderson et al., 2019; Bastille-Rousseau et al., 2024), but was beyond the scope of this study.

The ERS detection probability for RRV is known to vary with surveillance category (Kirby et al., 2017; Davis et al., 2021). Targeted removal efforts (e.g., TET) for ERS at the start of contingency actions help to identify the scope of a potential ORV zone breach or outbreak, i.e., to gauge how long RRV was present in the area before detecting the index case (Slate et al., 2008). In the context of ERS, TET samples are considered surveillance-trapped and mostly are comprised of healthy-appearing animals. The surveillance-trapped samples were the most common surveillance category within localized contingency action areas and contributed substantially to the high cumulative RRV

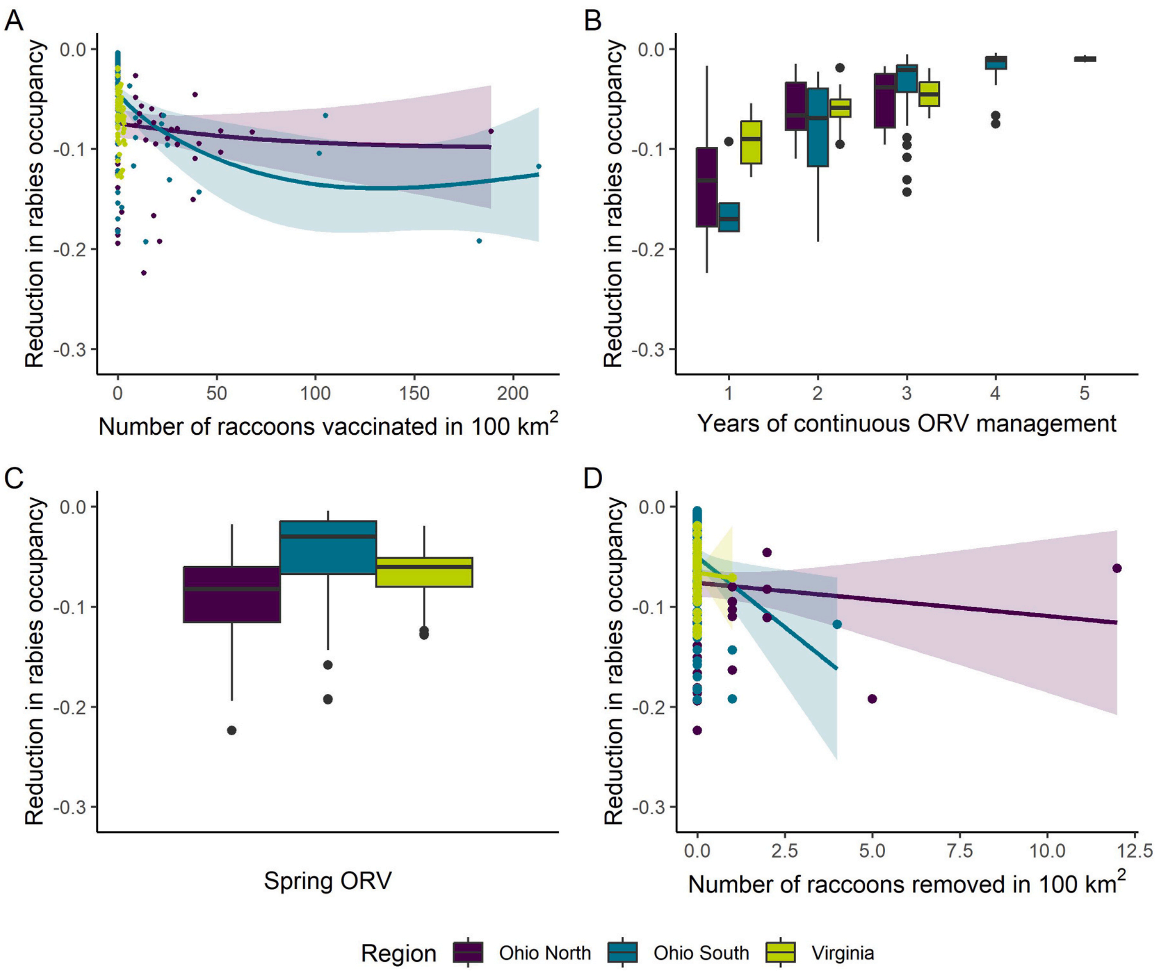

Fig. 6. Marginal plots from the random forest models on the declines in raccoon rabies virus variant (RRV) occupancy shown for the three contingency action areas: Ohio North (purple), Ohio South (teal), Virginia (light green). Patterns are shown for A) number of raccoons hand vaccinated within a 100 km^2 area, B) number of years of cumulative oral rabies vaccination (ORV) baiting, C) declines associated when spring ORV was conducted, and D) the number of raccoons removed by trap, euthanize, and test within a 100 km^2 area. Line plots show the smoothed marginal relationships with 95% confidence intervals. Boxplots show the median (horizontal line), interquartile range (box), 1.5 times the interquartile range (vertical line), and data outside that range (dots).

detection probabilities surrounding the initiation of contingency actions which played a critical role in planning and establishing the ORV zones (Fig. 3A&B). The substantial contribution of TET samples to the overall detection probability (Fig. 3A), despite the lower probability of detecting rabid animals from TET samples compared to other categories (Table 3), suggests that surveillance trapping and removal as part of intensified ERS is an important component of contingency action surveillance to plan and design effective rabies control interventions with ORV. A different modeling approach would be needed to further explore and optimize *in silico* strategies for strategic use of TET during contingency responses to RABV outbreaks. The scale of the local RRV outbreak and timing of TET is likely to be of the utmost importance given that some studies suggest that local population reduction may disrupt social interactions and enhance the movement, contact rates, and dispersal of animals remaining in the local populations, which could increase RRV spread (McDonald et al., 2008; Beasley et al., 2013; Chipman et al., 2023; Viana et al., 2023). The impacts of TET for RRV control were difficult to tease apart in our study, given that TET was only conducted immediately following when an index case was detected, which only corresponded to periods of time when RRV occupancy was locally increasing. We examined a lag effect of TET which was weakly associated with declines in RRV occurrence. Simulation-based modeling could be used to further evaluate the potential impacts of varying levels of local removal effort, along with ORV management, and timing of animal removal in the context of contingency action responses to limit RRV spread and to enhance the time needed for effective outbreak control (McClure et al., 2020). Simulation modeling combined with genetic analysis of RRV outbreaks might help inform how rapidly the index case is found and what management actions may be most effective in a contingency action.

Contingency actions are labor intensive and costly compared to routine management operations (Rosatte et al., 2001); therefore, it is valuable to understand the relative impacts of varying ORV and hand-vaccination management strategies in local control of RRV outbreaks (Bastille-Rousseau et al., 2024). In North America, the primary management tools associated with contingency actions include ERS, ORV (often deployed in the spring and autumn), and hand vaccination (Sterner et al., 2009). All three management tools were deployed at each contingency action analyzed in this study; for that reason, our results must be considered as part of an integrated strategy and cannot be interpreted as impacts from individual strategies as stand-alone management strategies. In that context, hand vaccination of raccoons was the most effective management tool associated with declining RRV occupancy across all three contingency actions (Fig. 4B). In general, hand-vaccinating around 50 raccoons per 100 km^2 was related to the most rapid declines in RRV occupancy. This result is similar to findings on the impact of hand vaccination at a landscape scale and used in conjunction with ORV reported from studies in the northeastern US and

Québec, Canada (Davis et al., 2019b, 2023). Considerably more raccoons were hand-vaccinated in the two Ohio contingency action areas compared to the Virginia contingency action area. However, this may be due to the presumed differences in raccoon population densities in the Ohio areas compared to the Virginia contingency area, where lower raccoon population densities are predicted to occur in the higher elevation forested landscapes of Virginia compared to the lower elevation, forested-agricultural landscapes in Ohio (Slate et al., 2020).

The first few years of continuous ORV baiting led to more dramatic declines in RRV occupancy within the contingency areas. The rate of decline in RRV occupancy slowed after a few initial years of ORV baiting in the contingency action areas as RRV was effectively controlled. Declines were still observed as more years of continuous ORV baiting was conducted, but the rates of decline were not as profound during later years (Fig. 6B), similar to other findings (Mähl et al., 2014). Potentially as fewer animals were hand-vaccinated in Virginia, the ORV variables vaccine type, bait density, spring ORV, and years of ORV were relatively more important compared to hand-vaccination in Virginia. The bait density employed in the Virginia contingency action (300 baits/km^2) was greater compared to either of the Ohio contingency action areas and to date is used only for localized or emergency needs (Rosatte et al., 2011; Bigler et al., 2021; Johnson et al., 2021; Chipman et al., 2023). Deployments of V-RG at 300 baits/km^2 have been found to increase seroprevalence over bait densities of 75 baits/km^2 (Sattler et al., 2009), but no differences were documented in comparing applications of 75–150 baits/km^2 in rural Virginia (Pedersen et al., 2019) and suggest that impacts to target population vaccination coverage from increasing bait density are non-linear. A relatively high ORV bait density, coupled with the low raccoon abundance observed in rural Virginia, may jointly explain why the impacts of ORV compared to hand vaccination were relatively more important in the Virginia contingency area compared to the Ohio contingency areas. However, there may be interplays between the different management tools that we have yet to uncover, and those questions may be better suited for alternative *in silico* modeling approaches.

Across the broader study area, the spatial distinction of being in a RRV free region, within the ORV zone, or in the RRV enzootic area was the most important factor explaining local RRV occurrence. The RRV free regions had very low probability of RRV occurrence, whereas RRV enzootic areas exhibited very high probability of RRV occupancy (Fig. 5A). Areas managed using ORV had moderate RRV occupancy probabilities, with declining occupancy over time in these areas (Fig. 5A). As reported previously, the years of continuous ORV management were important at broad spatial scales, supporting the need for multi-year programs to control and locally eliminate RRV. Similarly, other studies have found that ORV management has been successful at controlling and eliminating RABV from mesocarnivore reservoir populations (Sidwa et al., 2005; Slate et al., 2005; Freuling et al., 2013). Despite the contingency action events in Ohio and Virginia, the trend in RRV occurrence in both the ORV zone and the RRV free regions has continued to decline at broad landscape scales, as described from the northeastern US (Davis et al., 2023).

Habitat covariates explained less variation in the RRV occupancy data compared to management actions, temporal variability, and neighbor effects at the broad spatial scale (Fig. 4A). Deciduous forest cover was the most important habitat variable in our study which is well supported by raccoon habitat preferences from other studies (Leberg and Kennedy, 1988; Rosatte et al., 2010; Slate et al., 2020). At the spatial scale of local contingency actions, habitat metrics were not very variable nor informative in explaining RRV occurrence (Fig. 4B). Within our study areas and local scales examined, the management, spatial and temporal variables (neighbor effects and seasonal and annual variability) were more influential in explaining RRV occurrence than habitat.

We sought to understand spatial landscape factors associated with ORV zone breaches. We explored whether the risk of RRV occurrence increased positively with distance from the nearest ORV zone, if previously managed areas had higher risks of RRV occurrence, whether RRV occurrence risk was greater in areas with increasing time elapsed since the last ORV campaign, and if distance to urban areas increased risk of ORV zone breaches (i.e., as a proxy for nuisance animal translocation risks from urban areas), yet none were strong indicators of RRV occurrence. The most important explanatory variable for RRV free regions was the neighbor effect (the relationship with the proportion of neighboring sites with RRV). The CDC recognizes the importance of spatial disease pressure and have used the status of neighboring sites in their definition for RABV elimination (Kunkel et al., 2023). The importance of the neighbor effect relative to the distance to the nearest ORV zone suggests that distance to ORV is more important at the local (site level) scale. In our study the grids (sites) were 100 km^2, which is considerably larger than raccoon home range sizes in rural and agricultural areas (Prange et al., 2004; Totton et al., 2004; Bozek et al., 2007). The three contingency action index cases in this study were within 20 km of the nearest ORV zone. To better understand the risks of RRV breach events across the ORV zone, it would help to know from where the index animals originated and whether translocation was a possibility. However, the host and RABV molecular epidemiological analyses were not available from the events studied here. Coupling host and RRV genetic information would give a better picture of where breaches are coming from and possibly the movement pathways to new (breach and outbreak) areas (Biek et al., 2007; Trewby et al., 2017; Nadin-Davis et al., 2018; Hopken et al., 2023). These types of investigations should be coupled with contingency management to better understand, mitigate, and prevent risks of RRV colonization in naïve areas.

5. Conclusion

Timely and targeted contingency actions are an integral part of effective RRV management and control. Understanding the value of different management and surveillance activities for contingency responses, as well as the risks of new contingency events, across management zones and areas can be difficult, as each area may have a complex tapestry of management history, habitats, and raccoon population dynamics. Our results suggest that the importance of different management strategies varied across the three contingency actions and across spatial scales of investigation, but other general patterns emerged. Hand vaccination was particularly useful at reducing RRV occurrence at local scales. Spring ORV was helpful in reducing RRV occupancy, particularly at higher bait densities. The intensified ERS (i.e., TET) efforts seemed to be more important as a critical component of surveillance and ORV planning, but additional work is needed to optimize the use of TET to prevent or control RRV outbreaks.

CRediT authorship contribution statement

Amy J. Davis: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Richard B. Chipman:** Conceptualization, Project administration, Writing – review & editing. **Kathleen M. Nelson:** Conceptualization, Writing – review & editing. **Betsy S. Haley:** Data curation, Writing – review & editing. **Jordona D. Kirby:** Data curation, Writing – review & editing. **Xiaoyue Ma:** Data curation, Writing – review & editing. **Ryan M. Wallace:** Data curation, Writing – review & editing. **Amy T. Gilbert:** Conceptualization, Project administration, Writing – review & editing.

Declaration of Competing Interest

None.

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