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Interspecific oral rabies vaccine bait competition in the Southeast United States

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ABSTRACT

The United States Department of Agriculture's National Rabies Management Program (NRMP) has coordinated the use of oral rabies vaccination (ORV) to control the spread of raccoon rabies virus variant west of the Appalachian Mountains since 1997. Working with state and local partners, the NRMP deploys ORV baits containing a rabies vaccine, primarily targeting raccoon populations (*Procyon lotor*). Bait competition between raccoons and non-target species may limit the effectiveness of ORV programs, but the extent of bait competition remains poorly quantified, particularly in the southeastern United States. We placed placebo ORV baits in bottomland hardwood (n = 637 baits) and upland pine (n = 681 baits) habitats in South Carolina, USA during August–December 2019 and used remote cameras to examine bait competition between raccoons and non-target species. The estimated proportion of bait consumed by raccoons was $18.8 \pm 2.1\%$ in bottomland hardwood and $11.6 \pm 2.1\%$ in upland pine habitats. Vertebrate competition appeared to have a minimal effect on raccoon uptake as estimated consumption did not exceed 5% for any species or 8% of bait uptake events cumulatively. We estimated that raccoons were the primary consumer of baits in bottomland hardwood, whereas invertebrates were the primary consumer in upland pine ($26.7 \pm 1.3\%$ of baits). Our results indicate a need to closely consider the effects of invertebrates on bait consumption to minimize their potential impact on ORV bait uptake by target species. Uptake probabilities by raccoons were relatively low but not primarily driven by competition with vertebrates. As such, strategies to increase the specificity of raccoon uptake may be needed to enhance the effectiveness of ORV baiting programs.

1. Introduction

In the late 1980's, raccoons (*Procyon lotor*) replaced skunks (primarily the striped skunk, *Mephitis mephitis*) as the major wildlife reservoir for rabies virus in the United States (US) (Rupprecht et al., 1995). The shift coincided with an outbreak of the raccoon variant of the rabies virus in mid-Atlantic and northeastern states via infected raccoons translocated from southeastern states during the late 1970's (Rupprecht et al., 1995). Oral rabies vaccination (ORV) is the primary strategy used to control and eliminate rabies virus circulation in wildlife globally and

is a key tool to prevent westward expansion of and eliminate raccoon rabies virus in eastern North America (Elmore et al., 2017; Slate et al., 2009). Delivery of ORV to manage raccoon rabies occurs primarily by using fixed-wing aircraft to aerially deploy baits containing the vaccine (Elmore et al., 2017).

The effectiveness of ORV programs depends in large part on bait encounter and consumption by target wildlife populations, which is influenced by many factors. Competition in particular may have an important role and influence for bait uptake rates by target wildlife because baits are potentially available to an array of non-target animals

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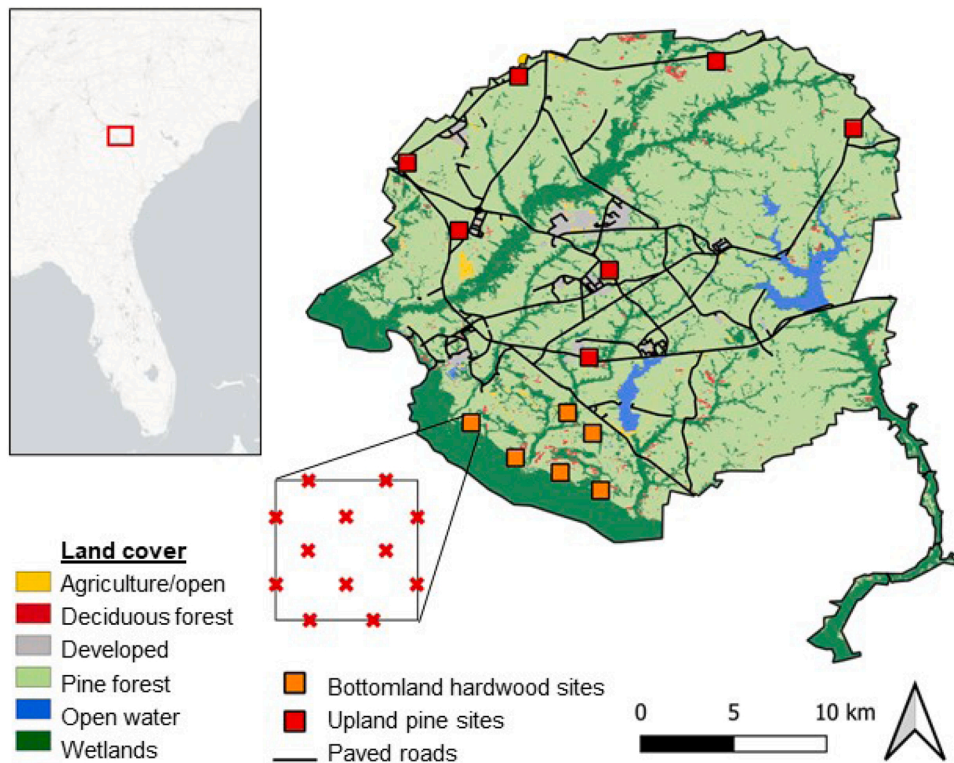


Fig. 1. A map of Savannah River Site with blue squares representing the six bottomland hardwood sites and red squares representing the seven upland pine sites (applicable for both the live and camera trapping projects). In 2019, one of the upland pine sites was clear cut, necessitating the creation of a replacement site. Therefore, only six upland pine sites were ever used at any one time as per protocol. The box with red crosses represents the offset grid of 12 cameras used to replicate the National Rabies Management Program's baiting density of 75 baits/km².

(Haley et al., 2019; Olson et al., 2000). Bait consumption by non-target species reduces the chance for raccoons to become vaccinated (Beasley et al., 2015; Smyser et al., 2010). Additionally, there are no benefits to the effectiveness of rabies management programs when baits are consumed by species which are neither vectors nor reservoirs of rabies virus (e.g., Virginia opossums [*Didelphis virginiana*] and wild pigs [*Sus scrofa*]). Understanding the diversity of species that consume ORV baits intended for raccoons can be used to inform decisions regarding baiting densities or to refine landscape-level baiting strategies to mitigate consumption by non-target animals.

Despite the recognized role of competition on the effectiveness of ORV programs, there remains a limited understanding of how competition influences raccoon bait uptake and how this varies across habitats. There are few recent studies of ORV bait competition in the southeastern US (but see Haley et al., 2019). We deployed placebo ORV baits across two southeastern US habitat types, upland pine and bottomland hardwood, and used remote cameras to estimate and compare bait uptake between raccoons and competitor species. Our objectives were to evaluate whether two focal habitats differed in terms of five characteristics related to bait consumption and/or competition: (1) the diversity of bait consumers (i.e., species diversity); (2) the probability of observing a bait consumer (i.e., observation probability); (3) the proportion of baits consumed by raccoons (the primary target species) and other secondary target or non-target species (i.e., uptake probability); (4) the effect of competitor visitation on the likelihood of raccoon bait uptake (i.e., indirect behavioral effects); (5) the probability of bait consumption of baits that were previously rejected by a raccoon (i.e., final consumer of rejected bait).

2. Materials and methods

2.1. Study Area

We conducted this study at the Savannah River Site (SRS), an 800 km² site owned by the US Department of Energy. The SRS is bordered by the Savannah River on its western boundary and is approximately 40 km

southeast of Augusta, GA (Fig. 1). With an elevation between 20 and 130 m above sea level, the study area features gently rolling to flat topography ranging from xeric uplands to mesic swamp forests (Kilgo, 2005). Historically home to rural communities and agricultural activities, in the 1950's portions of this land were converted to industrial facilities to refine nuclear materials for manufacture of nuclear weapons (White and Gaines, 2000).

Since acquisition by the Department of Energy, pine forests have been planted across the SRS (Workman and McLeod, 1990) and consist of longleaf pine (*Pinus palustris*), loblolly pine (*Pinus taeda*), and slash pine (*Pinus elliotii*) (Workman et al., 1990). Bottomland hardwood forests are a mosaic of bald cypress (*Taxodium distichum*), water tupelo (*Nyssa aquatic*), black gum (*Nyssa sylvatica*) and numerous oak species (*Quercus* spp.), and typically feature both permanent and ephemeral bodies of water (Workman et al., 1990). The land area of SRS is composed of 57% pine forest, 21% hardwood forest, 6% mixed forest and 16% other (White et al., 2000). As habitat generalists, raccoons can be found across all habitats of the SRS and are sympatric with a number of potential bait competitors including opossums, wild pigs, coyotes (*Canis latrans*), and gray foxes (*Urocyon cinereoargenteus*) (Cothran et al., 1991). The springtime densities of raccoons at SRS are 5.44 ± 0.37 animals/km² in bottomland hardwood and 2.14 ± 0.23 animals/km² in upland pine (Hill et al., In Review). The springtime densities of opossums in the habitats we studied is 2.65 ± 0.45 animals/km² in bottomland hardwood and 1.44 ± 0.30 animals/km² in upland pine (Bernasconi et al., 2022).

2.2. Field methods

We carried out this study in two habitats on the SRS: bottomland hardwood and upland pine. Within both habitats, we established six grids separated from one another by a minimum of two kilometers. While the upland pine grids were dispersed across the SRS, the bottomland hardwood grids were clustered in the southwestern quadrant as bottomland hardwood habitat on SRS is restricted to this area (Fig. 1). Our minimum distance of two kilometers between grids was

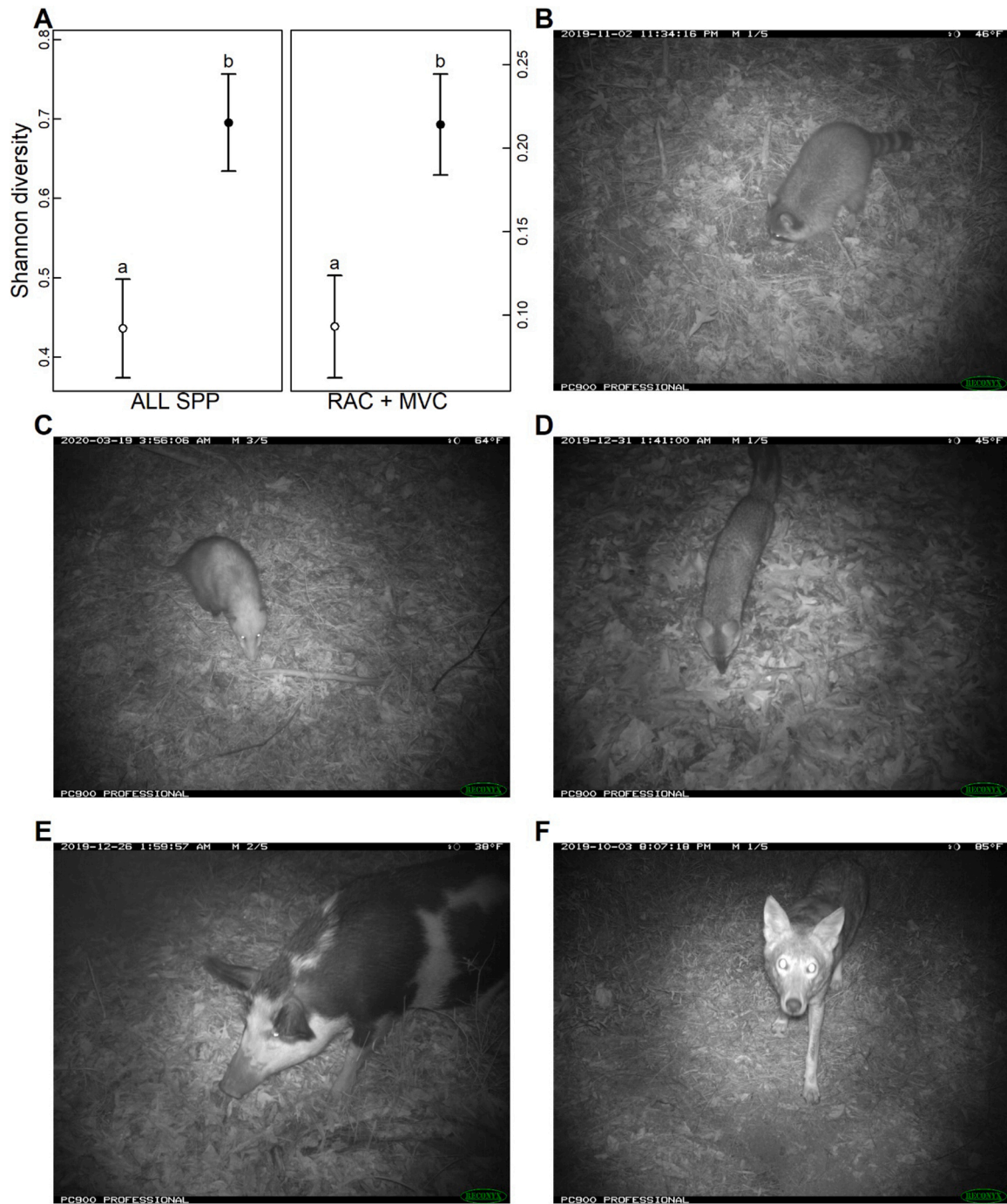


Fig. 2. (A) Shannon Diversity Index values of all observed species (ALL SPP) and raccoons combined with major vertebrate competitors (Raccoon + MVC) in upland pine habitat (open circle compared to bottomland hardwood (filled circle). Means followed by a common letter are not significantly different at $\alpha = 0.05$, and error bars represent the standard error of mean. (B – F) Camera images of the most common mammalian species taking vaccine bait during the camera trapping season of August–December 2019 at Savannah River Site, including: (B) raccoon (*Procyon lotor*); (C) Virginia opossum (*Didelphis virginiana*); (D) wild pig (*Sus scrofa*); (E) gray fox (*Urocyon cinereoargenteus*); (F) coyote (*Canis latrans*).

based on the maximum distance that could be maintained between grids within bottomland hardwood. Grid sites were static during the study except for cases of major disturbance (e.g., clear cutting), where we nominally shifted grid sites adjacent to the location of disturbance.

At each of 12 grid sites we established a 400×400 m camera array consisting of 12 tree-mounted cameras (Reconyx PC900 Hyperfire Professional IR; Reconyx, Holmen, WI) spaced 200 m apart. Cameras were installed on trees approximately 1.5 m from the ground and 2 m away from the baits using stainless steel camera mounts and were angled to

ensure the bait was in the center frame. Cameras were programmed to take a time lapse photo every hour as well as three motion-triggered, rapid-fire photos on a one second interval with no quiet period between motion-triggering events. These settings were chosen to capture as many images of animal-bait interactions as possible. The time-lapse images were used to document the status of the bait at hourly intervals.

We collected data continuously for 18 weeks during early August to late December 2019, which is the typical window for ORV deployment operations conducted by the National Rabies Management Program

Table 1

Comparisons of placebo oral rabies vaccination bait detection probability between raccoons and invertebrates (INV), secondary target species (ST: coyotes and gray foxes) and non-target species (NT: opossums and wild pigs) in bottomland hardwood and upland pine habitat at the Savannah River Site, South Carolina USA (Aug-Dec 2019). Last four rows are comparisons between habitats for each NT and ST species.

Contrast	Mean probability	Odds Ratio	Standard Error	P value
Bottomland	0.629 ± 0.064 vs.	3.054	0.533	> 0.001
INV–Bottomland NT	0.357 ± 0.064			
Bottomland	0.629 ± 0.064 vs.	1.093	0.189	0.605
INV–Bottomland raccoon	0.608 ± 0.064			
Bottomland	0.629 ± 0.064 vs.	25.621	6.612	> 0.001
INV–Bottomland ST	0.062 ± 0.064			
Bottomland INV–Pine	0.629 ± 0.064 vs.	0.619	0.247	0.230
INV	0.733 ± 0.064			
Bottomland	0.357 ± 0.063 vs.	0.358	0.062	> 0.001
NT–Bottomland raccoon	0.608 ± 0.063			
Bottomland	0.357 ± 0.063 vs.	8.389	2.151	> 0.001
NT–Bottomland ST	0.062 ± 0.063			
Bottomland NT–Pine	0.357 ± 0.063 vs.	4.586	1.916	> 0.001
NT	0.108 ± 0.063			
Bottomland raccoon	0.608 ± 0.065 vs.	2.365	0.934	0.029
–Pine raccoon	0.396 ± 0.065			
Bottomland	0.062 ± 0.019 vs.	0.043	0.011	> 0.001
ST–Bottomland raccoon	0.608 ± 0.019			
Bottomland ST–Pine ST	0.062 ± 0.019 vs.	0.481	0.219	0.109
	0.121 ± 0.019			
Pine INV–Pine NT	0.733 ± 0.057 vs.	22.612	5.298	> 0.001
	0.108 ± 0.057			
Pine INV–Pine raccoon	0.733 ± 0.057 vs.	4.175	0.792	> 0.001
	0.396 ± 0.057			
Pine INV–Pine ST	0.733 ± 0.057 vs.	19.912	4.544	> 0.001
	0.121 ± 0.057			
Pine NT–Pine raccoon	0.108 ± 0.030 vs.	0.185	0.041	> 0.001
	0.396 ± 0.030			
Pine NT–Pine ST	0.108 ± 0.030 vs.	0.881	0.222	0.614
	0.121 ± 0.030			
Pine ST–Pine raccoon	0.121 ± 0.033 vs.	0.210	0.045	> 0.001
	0.396 ± 0.033			
Fox: Bottomland–Pine	0.000 ± 0.000 vs.	0.000	0.000	0.998
	0.009 ± 0.000			
Coyote:	0.040 ± 0.026 vs.	1.145	1.129	0.891
Bottomland–Pine	0.035 ± 0.026			
Opossum:	0.152 ± 0.031 vs.	2.522	0.970	0.016
Bottomland–Pine	0.066 ± 0.031			
Pig: Bottomland–Pine	0.234 ± 0.049 vs.	6.529	3.010	> 0.001
	0.045 ± 0.049			

across the eastern US (Elmore et al., 2017). The 12 camera grids were divided into two groups of six grids within each habitat that were surveyed and baited in a consistent chronological order. Baiting was completed over the course of sequential 2-week sessions. Sessions alternated between the habitat groups such that one group was baited and one group was not baited within a habitat type, and then the group treatments were switched in the subsequent session. This ensured a two-week period where no baits were deployed between sequential sessions on a grid to limit habituation by bait consumers. During each session, we deployed a bait at each camera and rebaited the camera halfway through the session. Thus, we aimed for a total deployment of 1440 baits during the study (12 grids × 12 cameras per grid × 2 baits per camera × 5 sessions baited = 1440 baits).

During a baiting session, a single placebo ONRAB “Ultralite” rabies bait with a coating matrix consisting of hydrogenated vegetable fat,

wax, icing sugar, vegetable oil, vanilla flavor and dark-green food grade color was placed at each of the grids’ 12 camera locations (i.e., 12 baits/1600 m² grid) (Rosatte et al., 2009) to replicate the bait type and application density of 75 baits/km² used by the USDA to target raccoons (Slate et al., 2008). Any previously deployed baits still found at the cameras during mid-or-end session visits were removed to ensure no baits were present on a grid during the two-week resting period and that each camera station only had a single bait deployed at any given time during a baiting session.

We collected and examined all images from the cameras and recorded mammals to species level when possible based on the classification of Wilson and Reeder (2005). Bait uptake was defined when either of the following occurred: (1) confirmed oral contact with bait or (2) animal interaction with the bait followed by bait being chewed or missing in a subsequent time-lapse image. A rejected bait was classified when a vertebrate investigated the bait but did not interact with it orally. Invertebrate uptake was defined when invertebrates made contact with a bait followed by an estimated removal of approximately half or more of the bait matrix over subsequent days.

For analysis, we classified animals into groups that were related to uptake frequency and rabies epizootiology. These included (1) raccoons, (2) all vertebrate competitors (i.e., any vertebrate species documented consuming a bait), and (3) major vertebrate competitors (the subgroup of vertebrate species that were responsible for consumption of 95% of all baits not taken by raccoons or invertebrates). The separation of all vertebrate competitors and major vertebrate competitors was done to evaluate if there was a landscape level pattern of bait competition that differed if the minor competitors were ignored. For some analyses, we also distinguished between invertebrate and vertebrate competitors. Image analysis indicated that the subgroup of major vertebrate competitors were opossums, wild pigs, coyotes, and gray foxes. These species were further classified into two groups: secondary ORV targets that are rabies vectors or reservoirs (gray fox and coyote) versus true non-targets (opossum and wild pig). This was done to reflect the different management implications between bait competitor species that are secondary targets of ORV (i.e., gray fox and coyote) vs. species that have no role in the epizootiology of raccoon rabies virus (i.e., opossum and wild pig). Because we were unable to identify invertebrates to species, all species-level analyses were restricted to raccoons and/or vertebrate competitors, whereas invertebrates were pooled together as one entity for analysis.

2.3. Data analysis

Our objectives were to evaluate whether two focal habitats differed in terms of the following five characteristics related to bait consumption and/or competition:

- (1) *Species diversity*: To evaluate the diversity of bait consumers we measured using the Shannon diversity index with the R package VEGAN (Oksanen, 2013). We estimated diversity separately for all vertebrates and for major vertebrate competitors.
- (2) *Observation probability*: to evaluate the probability of observing a bait consumer we used a binary variable representing whether a specific animal taxon was observed on camera.
- (3) *Uptake probability*: to evaluate the proportion of baits consumed by a specific animal taxon we used a binary variable representing whether the bait was consumed by that taxon.
- (4) *Indirect behavioral effects*: to evaluate the effect of competitor visitation on the likelihood of raccoon bait uptake we used a

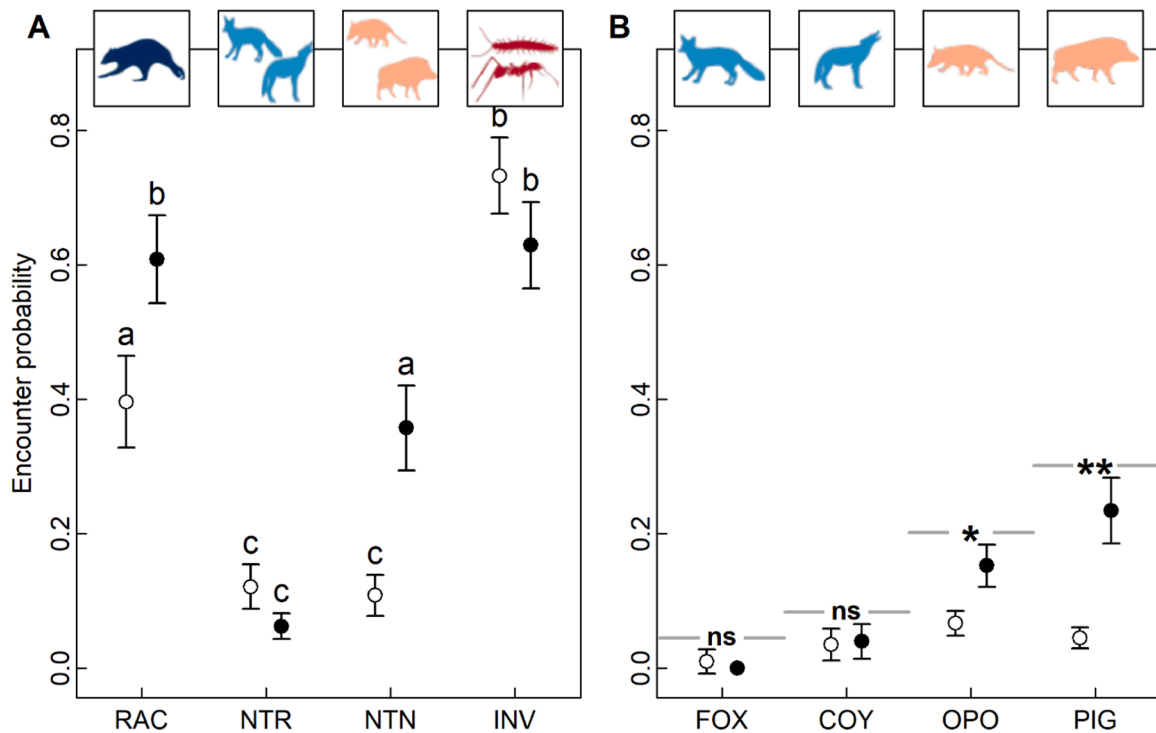


Fig. 3. (A) Detection probability for raccoons (Raccoon), secondary targets (NTR: gray fox and coyote), non-targets (NTN: opossum and wild pig), and invertebrates (INV) (B) and each major competitor (see Fig. 2) separately in upland pine habitat (empty circles) and bottomland hardwood habitat (filled circles). When multiple points in a single panel are from a single model, means followed by a common letter are not significantly different at $\alpha = 0.05$ (A). Alternatively, when multiple points in a single panel are from multiple models (B), only results from the same model are compared, with means not differing significantly at $\alpha = 0.05$ indicated by “ns” while those differing significantly at $\alpha = 0.05$ by a single asterisk, and those differing significantly at $\alpha = 0.01$ by a double asterisk. Error bars represent the standard error of mean.

binary variable representing whether a raccoon consumed a bait previously visited by another animal taxon.

- (5) *Final consumer of rejected bait*: to evaluate the probability of bait consumption of baits that were previously rejected by a raccoon we used a binary variable representing whether baits previously rejected by a visiting raccoon were consumed subsequently by raccoons or another animal taxon.

We analyzed the response variables mentioned above using linear mixed effect models (for species diversity; Objective 1) and generalized linear mixed effects models with a binomial error distribution and logit link (for the other variables; Objectives 2–5) with the package lme4 (Bates et al., 2007) in program R (R Core Team, 2022). All models included session as a random effect, and camera within grid as a nested random effect (Table S1). For each objective we ran a null model (intercept-only model with all random effects), as well as a model which incorporated habitat type (bottomland hardwood or upland pine) as a fixed effect. Additionally, for the observation and uptake probability models (Objectives 2 and 3), we also included species category (raccoon, invertebrate, secondary targets, or non-targets) which signified the species that detected/consumed the bait as a fixed effect to compare these metrics between the groups. Finally, given that we found significant differences in bait uptake rates for the different animal taxa (Objective 3), we also tested if the time to bait uptake differed between these animal taxa by fitting flexible parametric mixture models for times to competing events using the R package FLEXSURV (Jackson, 2016).

In the indirect behavioral effects model (Objective 4), we included three variables representing presence or absence of invertebrates, secondary targets and non-targets and included their interactions with habitat. The model for uptake of rejected baits (Objective 5) included the species category and habitat interaction.

We ranked models based on AIC values, choosing that with the

lowest AIC as the best supported model and making inferences from this top model (Burnham and Anderson, 2002). We plotted regression model results using the least-square means, as implemented in the package EMMEANS (Lenth et al., 2019). We used odds ratios (OR) to report the strengths of contrast effects, and uncertainty of the model-predicted statistical estimates are reported as mean \pm SE.

3. Results

During the study we deployed 1318 placebo ORV baits (637 and 681 baits in bottomland hardwood and upland pine, respectively). We were unable to deploy 122 of the baits planned due to site access restrictions (e.g., explosive ordinance testing or hunting season) and personnel limitations. We collected and analyzed 771,896 images from 19,992 trap nights, and a combination of 56,078 motion-trigger images were identified to contain vertebrate taxa with representation from amphibians, reptiles, birds, and mammals. Vertebrate species detected on camera included: raccoon, wild pig, Virginia opossum, coyote, gray fox, nine-banded armadillo (*Dasypus novemcinctus*), white-tailed deer (*Odocoileus virginianus*), bobcat (*Lynx rufus*), dog (*Canis familiaris*), domestic cat (*Felis catus*), eastern gray squirrel (*Sciurus carolinensis*), southern fox squirrel (*Sciurus niger niger*), eastern cottontail (*Sylvilagus floridanus*), woodrat (*Neotoma spp.*), mouse (*Peromyscus spp.*), southern toad (*Anaxyrus terrestris*), black rat snake (*Pantherophis obsoletus*), eastern box turtle (*Terrapene carolina carolina*), and wild turkey (*Meleagris gallopavo*). Additionally, 55,602 time-lapse images were identified to contain invertebrate activity on the deployed baits.

For the overall vertebrate community diversity model, the top ranked model included habitat (Table S1) and indicated greater community diversity in bottomland hardwood than in upland pine (0.695 ± 0.061 vs. 0.436 ± 0.061 , $p = 0.008$; Fig. 2). For major vertebrate competitor only model of community diversity, the top ranked model

Table 2

Comparisons of estimated proportion of placebo oral rabies vaccination baits consumed between raccoons and invertebrates (INV), secondary target species (ST: coyotes and gray foxes) and non-target species (NT: opossums and wild pigs) in bottomland hardwood and upland pine habitat at the Savannah River Site, South Carolina USA (Aug-Dec 2019).

Contrast	Mean proportion of baits consumed	Mean difference	Standard Error	P value
Bottomland INV–Bottomland NT	0.092 ± 0.013 vs. 0.076 ± 0.013	0.016	0.018	0.362
Bottomland INV–Bottomland ST	0.092 ± 0.013 vs. 0.015 ± 0.013	0.076	0.014	> 0.001
Bottomland INV–Bottomland raccoon	0.092 ± 0.013 vs. 0.188 ± 0.013	-0.097	0.024	> 0.001
Bottomland INV–Pine INV	0.092 ± 0.013 vs. 0.267 ± 0.013	-0.176	0.030	> 0.001
Bottomland NT–Bottomland ST	0.076 ± 0.012 vs. 0.015 ± 0.012	0.060	0.013	> 0.001
Bottomland NT–Bottomland raccoon	0.076 ± 0.012 vs. 0.188 ± 0.012	-0.113	0.024	> 0.001
Bottomland NT–Pine NT	0.076 ± 0.012 vs. 0.029 ± 0.012	0.046	0.014	0.001
Bottomland ST–Bottomland raccoon	0.015 ± 0.005 vs. 0.188 ± 0.005	-0.173	0.021	> 0.001
Bottomland ST–Pine ST	0.015 ± 0.005 vs. 0.050 ± 0.005	-0.035	0.012	0.004
Bottomland raccoon–Pine raccoon	0.188 ± 0.021 vs. 0.116 ± 0.021	0.072	0.027	0.007
Pine INV–Pine NT	0.267 ± 0.028 vs. 0.029 ± 0.028	0.238	0.029	> 0.001
Pine INV–Pine ST	0.267 ± 0.028 vs. 0.050 ± 0.028	0.217	0.030	> 0.001
Pine INV–Pine raccoon	0.267 ± 0.028 vs. 0.116 ± 0.028	0.151	0.032	> 0.001
Pine NT–Pine ST	0.029 ± 0.008 vs. 0.050 ± 0.008	-0.021	0.013	0.118
Pine NT–Pine raccoon	0.029 ± 0.008 vs. 0.116 ± 0.008	-0.087	0.018	> 0.001
Pine ST–Pine raccoon	0.050 ± 0.011 vs. 0.116 ± 0.011	-0.066	0.020	0.001

also included habitat (Table S1) and indicated greater diversity in bottomland hardwood than in upland pine (0.214 ± 0.030 vs. 0.093 ± 0.030 ; $p = 0.013$).

There was a greater observation probability of raccoons in bottomland hardwood compared to upland pine habitats (0.608 ± 0.065 vs. 0.396 ± 0.065 ; Table S1, Table 1, Fig. 3). Observation probability of secondary targets and non-targets was lower compared to raccoons in bottomland hardwood and upland pine habitats. There was no difference in detection probability between invertebrates and raccoons in bottomland hardwood habitat but invertebrates were detected more

frequently than raccoons in upland pine habitat (0.733 ± 0.057 vs. 0.396 ± 0.057). Among the major vertebrate competitors, there was a higher observation probability in bottomland hardwood compared to upland pine for both opossums (0.152 ± 0.031 vs. 0.066 ± 0.031) and wild pigs (0.234 ± 0.049 vs. 0.045 ± 0.049), but no difference in observation probability between bottomland hardwood and upland pine for coyotes or gray foxes (Fig. 3).

Similar to animal observation probability, the top model for bait uptake probability included the interaction between species category and habitat type (Table S1). We thus fit a bait survival model to evaluate the proportion of bait consumed by the different taxa in a seven-day period as well as median time to bait consumption by each taxon. We found the proportion of bait taken in a seven-day period was significantly higher in bottomland hardwood vs. pine habitats for both raccoons (0.188 ± 0.021 vs. 0.116 ± 0.021) and non-targets (0.076 ± 0.012 vs. 0.029 ± 0.012 ; Table 2, Fig. 4). Conversely, proportion of baits consumed was lower in bottomland hardwood compared to upland pine habitats for secondary targets (0.015 ± 0.005 vs. 0.050 ± 0.005) and invertebrates (0.092 ± 0.013 vs. 0.267 ± 0.013). Invertebrates took fewer baits than raccoons in bottomland hardwood (0.092 ± 0.013 vs. 0.188 ± 0.013), but more baits than raccoons in upland pine (0.267 ± 0.028 vs. 0.116 ± 0.028).

Our analysis of time to bait uptake by different animal taxa reinforced the data on taxon-specific differences in bait consumption rates between habitats. Specifically, we found that raccoons found and consumed baits faster in bottomland vs. pine sites (4.530 ± 0.472 vs. 7.485 ± 0.472 days; Fig. 4, Fig. S1). However, while time to bait consumption did not differ for secondary targets, the time was significantly shorter in bottomland vs. pine in non-targets (3.734 ± 0.402 vs. 9.019 ± 0.402 days, Table 3). Most interestingly, we found that invertebrate taxa found and consumed bait significantly slower in bottomland vs. pine habitats (16.977 ± 2.088 vs. 7.100 ± 2.088 days; Fig. 4, Fig. S1).

The top model for indirect behavioral effects included presence of invertebrates and non-targets (Table S1). Raccoon bait uptake probability was reduced when the bait had been previously visited by invertebrate competitors as compared to naive baits (0.403 ± 0.052 vs. 0.535 ± 0.052 , $p = 0.034$). Although bait uptake probability by raccoons was reduced when the bait had been previously visited by non-target taxa as compared to naive baits, this effect was not statistically significant (0.390 ± 0.112 vs. 0.535 ± 0.112 ; $p = 0.170$; Fig. 5).

Uptake of rejected baits was influenced by the interaction between species group and habitat type (Table S1). There was no difference in the proportion of initially rejected baits that were ultimately consumed by raccoons in bottomland hardwood compared to upland pine (Table 4, Fig. 5). The proportion of raccoon rejected bait consumed by invertebrate competitors was significantly lower in bottomland hardwood vs. upland pine (0.090 ± 0.025 vs. 0.277 ± 0.025 ; Fig. 5). In bottomland hardwood, fewer rejected baits were taken by secondary targets (0.017 ± 0.010 vs. 0.205 ± 0.010), non-targets (0.107 ± 0.027 vs. 0.205 ± 0.027) and invertebrate competitors (0.090 ± 0.025 vs. 0.205 ± 0.025), compared to raccoons. Similarly, in upland pine, fewer rejected baits were taken by secondary targets (0.061 ± 0.031 vs. 0.199 ± 0.031) and non-targets (0.030 ± 0.022 vs. 0.199 ± 0.022). However, there was no significant difference in proportion of rejected bait consumed by invertebrate competitors and raccoons in upland pine habitat.

4. Discussion

We documented ORV bait consumption by several vertebrate species

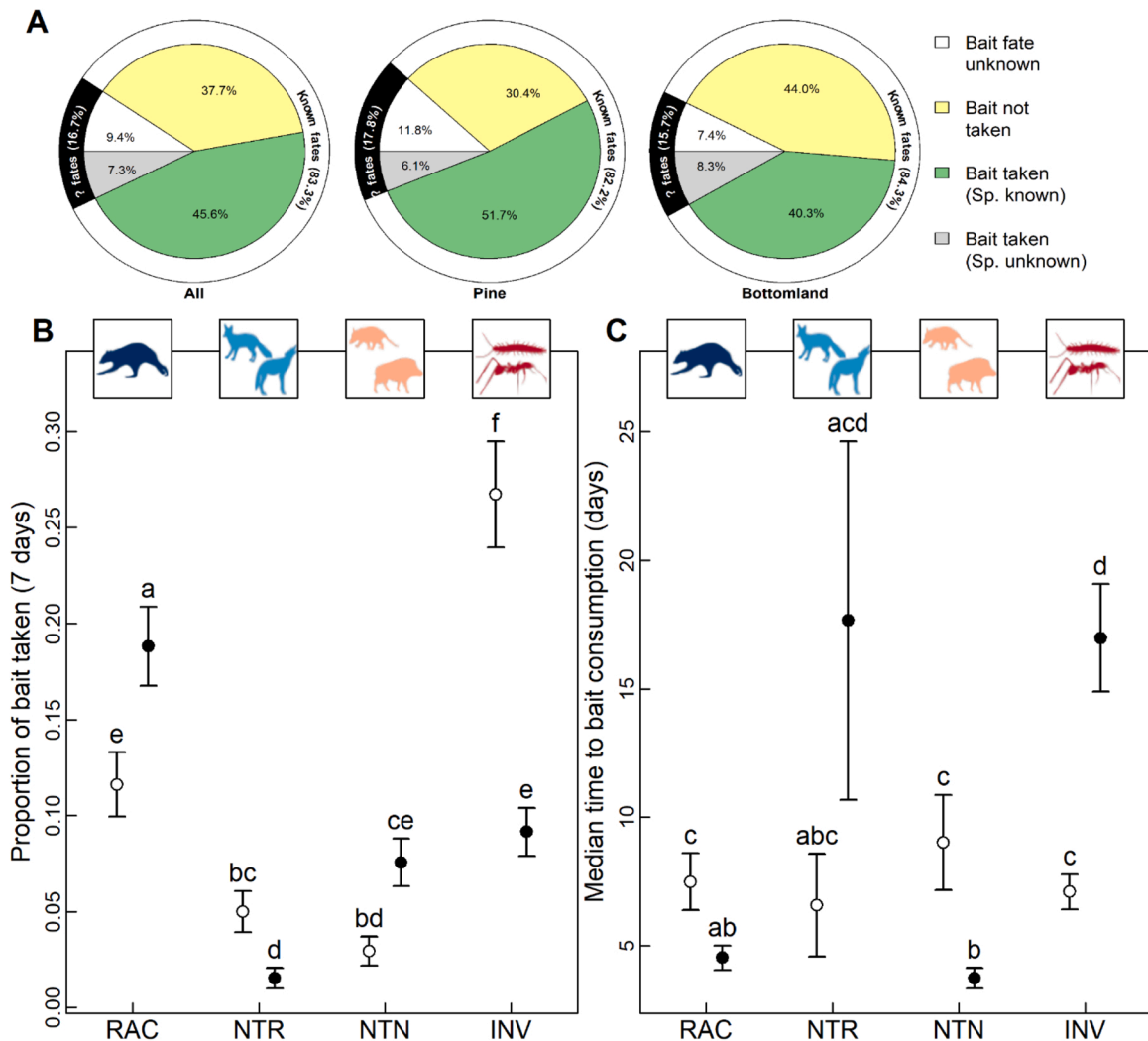


Fig. 4. (A) Percentages of known and unknown bait fates in both habitat types combined (i.e., All), upland pine and bottomland hardwood. Known fates were categorized by “Bait not taken” (i.e., the bait was not consumed by any animal and was “viable” when collected at the end of the session) and “Bait taken (Sp. known)” (i.e., the bait was consumed by an animal whose taxa was identified). Unknown fates were categorized by “Bait fate unknown” (i.e., Unable to see or determine the bait’s fate due to a variety of reasons: bait was out of frame, covered by leaves, ground was flooded, camera died prematurely etc.) and “Bait taken (Sp. unknown)” (The bait was suddenly missing or visibly chewed between subsequent, hourly time-lapse images but there were no images of the animal that took the bait). (B) Proportions of baits taken by raccoons (Raccoon), secondary targets (NTR: gray fox and coyote), non-targets (NTN: opossum and wild pig) and invertebrates (INV) separately in upland pine habitat (empty circles) and bottomland hardwood habitat (filled circles) (C) proportions of baits taken by each major vertebrate competitor (gray fox, coyote, opossum and wild pig) separately in upland pine habitat (empty circles) and bottomland hardwood habitat (filled circles). When multiple points in a single panel are from a single model, means followed by a common letter are not significantly different at $\alpha = 0.05$ (B). Alternatively, when multiple points in a single panel are from multiple models (C), only results from the same model are compared, with means not differing significantly at $\alpha = 0.05$ indicated by “ns” while those differing significantly at $\alpha = 0.05$ by a single asterisk, and those differing significantly at $\alpha = 0.01$ by a double asterisk. Error bars represent the standard error of mean.

as well as invertebrates across two habitats in the southeastern US. Despite the presence of vertebrate competitors in our study, their presence and visitation of baits had a minimal effect on uptake by raccoons. However, invertebrates seem to play a role in bait uptake by both primary and secondary target species. In both bottomland hardwood and upland pine habitats, the estimated bait consumption by secondary target and non-target vertebrates did not exceed 5% for a single species or 8% of bait uptake events cumulatively. Nontarget uptake of this magnitude is not likely to substantially affect immunization rates of raccoons (Linhart et al., 2002). Additionally, raccoons were the dominant vertebrate consumer of baits in both habitats, consuming more

baits than either secondary targets or non-targets, and neither group consumed more rejected baits than raccoons in either habitat. Similarly, studies in Ohio, Georgia, and Florida, USA all reported raccoons as the primary consumer of ORV baits (Linhart et al., 2002; Olson and Werner, 1999). Furthermore, coyotes and gray foxes, two of the major bait competitors in this study, are secondary targets of ORV to manage raccoon rabies (Sidwa et al., 2005; Slate et al., 2009). Therefore, bait uptake by these species is considered beneficial from a management perspective by helping to reduce the circulation of raccoon rabies in key wildlife populations.

Our results indicate that when vertebrate bait competition occurs, it

Table 3

Comparisons of mean time to placebo oral rabies vaccination bait consumption between raccoons and invertebrates (INV), secondary target species (ST: coyotes and gray foxes) and non-target species (NT: opossums and wild pigs) in bottomland hardwood and upland pine habitat at the Savannah River Site, South Carolina USA (Aug-Dec 2019).

Contrast	Mean time to consumption	Mean difference	Standard Error	P value
Bottomland	16.977 ± 2.088	13.243	2.126	> 0.001
INV–Bottomland	vs. 3.734			
NT	± 2.088			
Bottomland	16.977 ± 2.088	-0.677	7.282	0.926
INV–Bottomland	vs. 17.653			
ST	± 2.088			
Bottomland	16.977 ± 2.088	12.447	2.140	> 0.001
INV–Bottomland	vs. 4.530			
raccoon	± 2.088			
Bottomland	16.977 ± 2.088	9.877	2.196	> 0.001
INV–Pine INV	vs. 7.100			
	± 2.088			
Bottomland	3.734 ± 0.402	-13.920	6.988	0.046
NT–Bottomland ST	vs. 17.653			
	± 0.402			
Bottomland	3.734 ± 0.402	-0.796	0.620	0.199
NT–Bottomland	vs. 4.530			
raccoon	± 0.402			
Bottomland NT–Pine	3.734 ± 0.402	-5.286	1.901	0.005
NT	vs. 9.019			
	± 0.402			
Bottomland	17.653 ± 6.977	13.124	6.993	0.061
ST–Bottomland	vs. 4.530			
raccoon	± 6.977			
Bottomland ST–Pine	17.653 ± 6.977	11.078	7.259	0.127
ST	vs. 6.575			
	± 6.977			
Bottomland	4.530 ± 0.472	-2.956	1.200	0.014
raccoon–Pine	vs. 7.485			
raccoon	± 0.472			
Pine INV–Pine NT	7.100 ± 0.681	-1.920	1.979	0.332
	vs. 9.019			
	± 0.681			
Pine INV–Pine ST	7.100 ± 0.681	0.525	2.116	0.804
	vs. 6.575			
	± 0.681			
Pine INV–Pine	7.100 ± 0.681	-0.386	1.297	0.766
raccoon	vs. 7.485			
	± 0.681			
Pine NT–Pine ST	9.019 ± 1.858	2.444	2.733	0.371
	vs. 6.575			
	± 1.858			
Pine NT–Pine	9.019 ± 1.858	1.534	2.161	0.478
raccoon	vs. 7.485			
	± 1.858			
Pine ST–Pine raccoon	6.575 ± 2.004	-0.910	2.287	0.691
	vs. 7.485			
	± 2.004			

is likely from species that are ecologically similar to raccoons: medium to large-sized generalists with flexible, omnivorous diets (Ginger et al., 2003). This could explain not only their presence across habitat types, but also the capacity to consume a novel food item such as an ORV bait (Beatty et al., 2013; Swingen et al., 2015). In contrast, species with more specialized diets, such as bobcats (an obligate carnivore), white-tailed deer (an obligate herbivore), and nine-banded armadillos (strongly insectivorous), displayed little interest in ORV baits and had no documented consumption (Riley, 2006; Rooney and Waller, 2003; Sikes et al., 1990). Consumption of baits by other human commensals, especially nontargets such as opossums, may pose challenges to ORV programs because the same ecological factors leading to elevated densities

of raccoons may also result in high densities of their competitors (e.g., Bernasconi et al., 2022).

Although opossums are suspected to be a key competitor for ORV baits (e.g. Pedersen et al., 2019; Pedersen et al., 2018; Slate et al., 2020), this was not observed at our study site. A study in Ohio, also carried out on a restricted access site without human development or agricultural land use, reported equally low take by opossums (Linhart et al., 2002). The density of opossums in the habitats we studied is relatively low during the breeding season (Bernasconi et al., 2022) and in such rural areas, opossums may not be abundant enough to encounter and take substantial quantities of ORV baits. An analysis across land use types during spring in Florida found opossums to consume more baits than raccoons in developed areas, but found the opposite pattern in undeveloped areas (Olson et al., 1999). Thus, there is likely a high degree of variability in the extent to which opossums impact bait consumption by raccoons, which is probably related to season, landscape attributes and opossum abundance.

In contrast to vertebrates, invertebrate uptake of ORV baits was greater than expected and they appear to be the primary competitor for baits at our study site. Invertebrates took more baits than any major vertebrate competitor in either habitat type and took the highest proportion of baits in upland pine of any species including raccoons. Additionally, raccoons were less likely to consume baits that had been visited by invertebrates. Previous studies have generally not addressed bait consumption by invertebrates, yet most studies have either used tracking plates to document visits to bait stations (e.g. Haley et al., 2019; Olson et al., 1999) or biomarkers to assess uptake in animals (e.g. Olson et al., 2000; Smyser et al., 2010), neither of which adequately document invertebrate activity. As such, it remains unclear whether invertebrate bait uptake in our study is actually greater than other studies or whether our results reflect key methodological differences. Bachmann et al. (1990) documented bait consumption by insects in Ontario, Canada, but at a much lower frequency than we observed, whereas Berentsen et al. (2014) reported fire ant infestations at 20% of baits intended for small Indian mongoose (*Herpestes auro-punctatus*) in Puerto Rico. Future work should incorporate techniques to detect and identify invertebrate uptake of ORV baits, as our results suggest they may be an important bait competitor.

Bait uptake by invertebrates varied across habitats and was approximately three times greater in upland pine compared to bottomland hardwood. This difference may result from the lower observation probability of raccoons in upland pine, suggesting that the reduced rates of bait uptake by raccoons may increase uptake opportunities for invertebrates. Invertebrates tended to slowly consume bait attractant over multiple days, whereas vertebrates generally consume the entire bait during a single visitation event. Alternatively, the greater bait uptake by invertebrates in upland pine may be related to higher invertebrate abundance in this habitat. Fire ants (*Solenopsis invicta*), for example, were documented consuming baits and at SRS their abundance increases with levels of habitat disturbance (Todd et al., 2008). Pine forests at SRS are routinely subject to management including clear-cutting and thinning, whereas these practices occur less frequently in bottomland hardwoods, possibly contributing to greater abundance of and ORV bait uptake by fire ants in upland pine habitat. The comparative role of invertebrate abundance and vertebrate competition on bait uptake by invertebrates has implications for ORV baiting programs. If the former has a larger role, the numerical abundance of invertebrates may be facilitating bait interference with raccoons, reducing effectiveness of baiting. However, if the latter is more prevalent, insects are merely consuming baits that target species would not have consumed anyway, having a negligible effect on the effectiveness of ORV programs. Thus, an

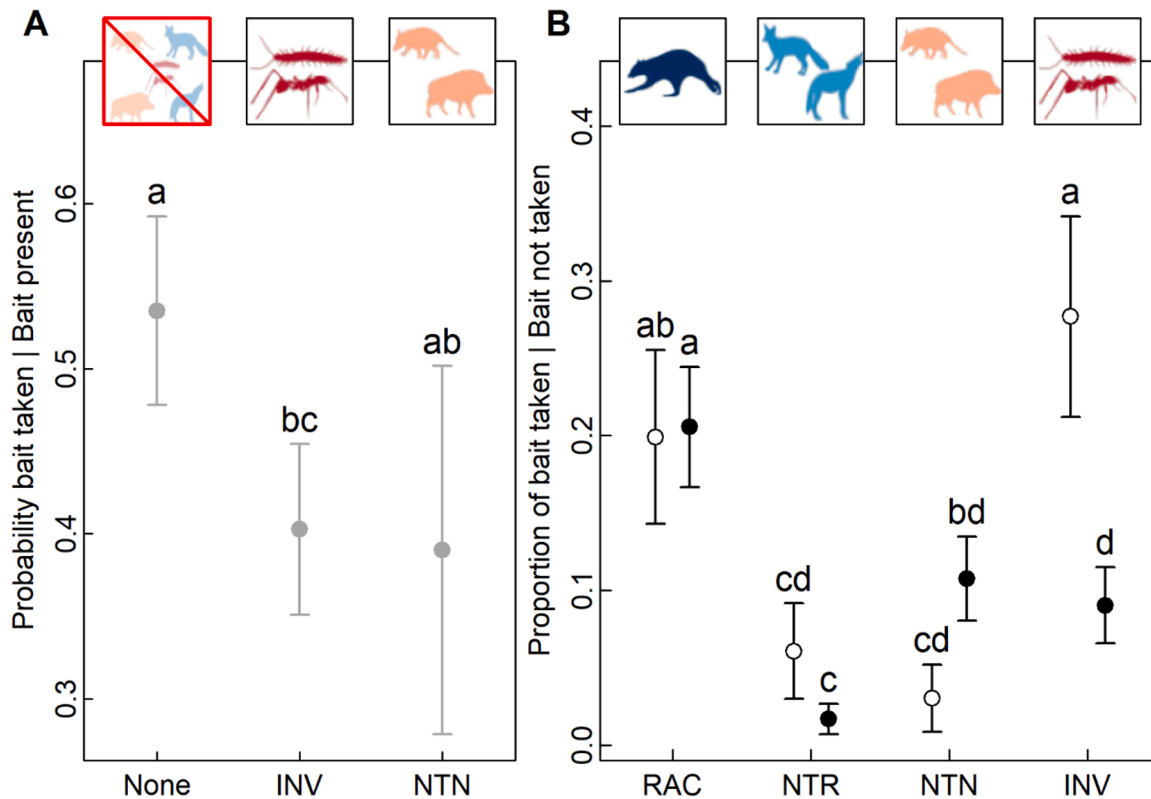


Fig. 5. Effects of competitor presence and raccoon behavior on raccoon bait uptake. (A) Probability that a raccoon will consume a viable bait when camera station was previously visited by no major competitor (None), invertebrate competitors (INV) or non-targets (NTN: opossum and wild pig). (B) Proportion of bait taken by each competitor type for each viable bait that had been previously visited and rejected by a raccoon in upland pine habitat (empty circles) and bottomland hardwood habitat (filled circles). Estimated probabilities followed by a common letter are not significantly different at $\alpha = 0.05$, and error bars represent the standard error.

important component of future work will be to identify how invertebrate abundance and vertebrate competition interact to impact bait attractiveness and palatability by invertebrates.

If invertebrates are competing substantially with raccoons across habitats targeted for ORV (i.e., deciduous and mixed forest habitats [Slate et al., 2020](#)), there may be a need to alter the bait matrix to deter invertebrate consumption. The ONRAB contains a sweet attractant matrix, but other products may potentially be less attractive to insects. In Puerto Rico, fire ants also consumed baits intended for mongoose that had savory flavor attractants ([Berentsen et al., 2014](#)). Because our experimental design was aimed at detection of medium-sized vertebrates, we lacked the image resolution to make fine-scale taxonomic identifications of invertebrates. However, determining the invertebrate species primarily responsible for bait consumption will be an important step for future research. There is likely geographic variation in invertebrate diversity and abundance, which may influence the degree of interference with ORV programs.

Across both habitats, the higher densities of raccoons compared to opossums likely contributes to greater uptake by raccoons ([Bernasconi et al., 2022](#)). Although raccoons were more likely to consume baits than opossums, uptake probability was low overall, with less than 20% of baits being consumed by raccoons in either habitat. Similarly, a study based on biomarker presence in spring at SRS in the same habitats found that 31% of raccoons and 11% of opossums consumed placebo ORV baits ([Helton et al., In Review](#)). These levels of bait consumption likely fall

below the vaccination thresholds required to eliminate raccoon rabies ([Rees et al., 2013](#); [Robbins et al., 1998](#)). Collectively these studies suggest that bait uptake by raccoons is relatively low at our site, but not substantially influenced by vertebrate competition.

Considering the minimal ORV bait consumption by vertebrate competitors, deterring consumption by these species may be less important than encouraging bait uptake by raccoons to increase seroprevalence. Strategies to achieve this goal may include refining the bait matrix to make it more attractive to raccoons, carrying out baiting programs in seasons of greater raccoon food limitation to encourage bait acceptance, or carrying out baiting during seasons when there is less invertebrate activity and competition. In southeastern US habitats such as those in this study, techniques that increase bait acceptance by raccoons and reduce invertebrate competition when necessary may augment the effectiveness of ORV baiting programs and reduce the prevalence of rabies in wildlife populations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Table 4

Comparisons of uptake probability of placebo oral rabies vaccination baits previously rejected by raccoons between raccoons and invertebrates (INV), secondary target species (ST: coyotes and gray foxes) and non-target species (NT: opossums and wild pigs) in bottomland hardwood and upland pine habitat at the Savannah River Site, South Carolina USA (Aug-Dec 2019).

Contrast	Mean probability	Odds Ratio	Standard Error	P value
Bottomland	0.090 ± 0.025 vs.	0.825	0.296	0.592
INV–Bottomland NT	0.107 ± 0.025			
Bottomland	0.090 ± 0.025 vs.	5.817	3.721	0.006
INV–Bottomland ST	0.017 ± 0.025			
Bottomland	0.090 ± 0.025 vs.	0.384	0.124	0.003
INV–Bottomland raccoon	0.205 ± 0.025			
Bottomland INV–Pine	0.090 ± 0.025 vs.	0.259	0.115	0.002
INV	0.277 ± 0.025			
Bottomland	0.107 ± 0.027 vs.	7.053	4.458	0.002
NT–Bottomland ST	0.017 ± 0.027			
Bottomland	0.107 ± 0.027 vs.	0.465	0.144	0.013
NT–Bottomland raccoon	0.205 ± 0.027			
Bottomland NT–Pine NT	0.107 ± 0.027 vs.	3.853	3.046	0.088
	0.030 ± 0.027			
Bottomland	0.017 ± 0.010 vs.	0.066	0.040	0.000
ST–Bottomland raccoon	0.205 ± 0.010			
Bottomland ST–Pine ST	0.017 ± 0.010 vs.	0.264	0.214	0.100
	0.061 ± 0.010			
Bottomland	0.205 ± 0.039 vs.	1.040	0.442	0.926
raccoon–Pine raccoon	0.199 ± 0.039			
Pine INV–Pine NT	0.277 ± 0.065 vs.	12.256	9.453	0.001
	0.030 ± 0.065			
Pine INV–Pine ST	0.277 ± 0.065 vs.	5.923	3.481	0.002
	0.061 ± 0.065			
Pine INV–Pine raccoon	0.277 ± 0.065 vs.	1.540	0.644	0.302
	0.199 ± 0.065			
Pine NT–Pine ST	0.030 ± 0.022 vs.	0.483	0.428	0.411
	0.061 ± 0.022			
Pine NT–Pine raccoon	0.030 ± 0.022 vs.	0.126	0.098	0.008
	0.199 ± 0.022			
Pine ST–Pine raccoon	0.061 ± 0.031 vs.	0.260	0.157	0.026
	0.199 ± 0.031			

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.applanim.2023.105897](https://doi.org/10.1016/j.applanim.2023.105897).

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