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James L. Helton
University of Georgia

Jacob E. Hill
University of Georgia, jehill@uga.edu

David A. Bernasconi
University of Georgia

Wesley C. Dixon
University of Georgia,

Richard B. Chipman
USDA, APHIS, Wildlife Services, Concord, NH

See next page for additional authors

Authors
James L. Helton, Jacob E. Hill, David A. Bernasconi, Wesley C. Dixon, Richard B. Chipman, Amy Gilbert, James C. Beasley, Guha Dharmarajan, and Olin E. Rhodes Jr.

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Assessment of habitat-specific competition for oral rabies vaccine baits between raccoons and opossums

James L. Helton[1] | Jacob E. Hill[2] | David A. Bernasconi[1] | Wesley C. Dixon[1] | Richard B. Chipman[3] | Amy T. Gilbert[4] | James C. Beasley[1] | Guha Dharmarajan[5] | Olin E. Rhodes Jr.[6]

[1]Savannah River Ecology Laboratory, Warnell School of Forestry and Natural Resources, University of Georgia, Drawer E, Aiken, SC 29802, USA

[2]Savannah River Ecology Laboratory, University of Georgia, Drawer E, Aiken, SC 29802, USA

[3]National Rabies Management Program, USDA, APHIS, Wildlife Services, Concord, NH 03301, USA

[4]National Wildlife Research Center, USDA, APHIS, Wildlife Services, Fort Collins, CO 80521, USA

[5]School of Interwoven Arts and Sciences, Krea University, Sri City, AP, India

[6]Savannah River Ecology Laboratory, Odum School of Ecology, University of Georgia, Drawer E, Aiken, SC 29802, USA

Correspondence

Jacob E. Hill, Savannah River Ecology Laboratory, University of Georgia, Drawer E, Aiken, SC 29802, USA.
Email: jehill@uga.edu

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Abstract

Throughout the eastern United States, the National Rabies Management Program (NRMP) distributes oral rabies vaccine (ORV) baits to manage rabies virus circulation in raccoon (*Procyon lotor*) populations. The consumption of vaccine baits by non-target species including Virginia opossums (*Didelphis virginiana*) may reduce the effectiveness of ORV programs, but competition for baits remains poorly quantified in many areas of the southeastern United States. We distributed placebo ORV baits injected with a biomarker across 4 land cover types (bottomland hardwood, upland pine, riparian, isolated wetland) on the Savannah River Site in South Carolina, USA, 2017–2019. We then trapped and collected whiskers from 247 raccoons and 78 opossums to assess biomarker presence using fluorescent microscopy. Our data revealed greater bait uptake probability by raccoons (estimated $\bar{x}$ = 0.30, 95% CI = 0.19–0.44) compared to opossums (estimated $\bar{x}$ = 0.11, 95% CI = 0.05–0.23) across all cover types surveyed. Probability of bait consumption was not affected by cover type or the abundance of raccoons or opossums. Among raccoons, males were more likely to consume baits than females (estimated $\bar{x}$ = 0.28, 95% CI = 0.17–0.44 for males and 0.14, 95% CI = 0.05–0.31 for females) and probability of consumption increased by 0.08 with each additional day trapped during the 10-day trapping session. Uptake rates for raccoons were relatively low compared to other studies and not influenced by competition with opossums. These low consumption rates indicate that additional research addressing the roles of baiting season, bait density, and resource selection will be important to maximize ORV bait uptake by target species in these southeastern landscapes.

KEYWORDS

biomarker, *Didelphis virginiana*, disease ecology, ORV, *Procyon lotor*, rhodamine B

The National Rabies Management Program (NRMP), implemented in 1999, focuses on controlling the spread and eliminating specific variants of rabies virus from wildlife populations in the United States (Elmore et al. 2017). The NRMP is focused on the management of rabies virus in raccoon populations through the distribution of oral rabies vaccine (ORV) baits (Slate et al. 2020). The goal of ORV baiting is to reduce the likelihood of infections among wildlife by increasing herd immunity (Blancou et al. 2009). Most ORV delivery is accomplished by fixed-wing aircraft in rural areas, whereas helicopters, bait stations, and hand distribution are used to distribute baits in developed areas across an ORV zone that spans Maine to Alabama (Slate et al. 2009, Elmore et al. 2017).

The effectiveness of ORV programs is contingent upon bait uptake by the target species (Smyser et al. 2010, Haley et al. 2019). Consequently, consumption of baits by non-target species can substantially reduce bait availability for target animals, limiting effectiveness of management programs (Smyser et al. 2010). The Virginia opossum (*Didelphis virginiana*) is a non-target species that is refractory to rabies and has been identified as the primary ORV bait competitor with raccoons (*Procyon lotor*) in the eastern United States between 27°N and 44°N latitude (Slate et al. 2020). Bait competition between raccoons and opossums is prevalent because they occupy similar ecological niches and are efficient scavengers (Ginger et al. 2003, Turner et al. 2017, Hill et al. 2018). In Florida, USA, for example, 30% of baits deployed at tracking stations were consumed by opossums, whereas 38% were taken by raccoons (Olson and Werner 1999). Another Florida study documented that 85% of opossums consumed baits, compared to 57% of raccoons (Olson et al. 2000). Furthermore, a biomarker study of bait competition in Indiana, USA, reported that the abundance of opossums had a significant negative effect on raccoon bait uptake rates (Smyser et al. 2010).

Bait uptake in free-ranging wildlife depends on the abundance and spatial ecology of target populations, especially in complex developed landscapes (Mainguy et al. 2012, McClure et al. 2020). However, the extent of competition between raccoons and opossums as a function of land cover type remains relatively unexplored, particularly in the southeastern United States (Haley et al. 2019). Several researchers have reported bait uptake in raccoons associated with experimental ORV field trials (Berentsen et al. 2018, Johnson et al. 2021), but these studies do not directly estimate the effect of bait competition from nontargets and there remains a limited understanding of how ecological and landscape factors interact to influence raccoon and opossum competition for ORV baits. Such information is important to increasing effectiveness of ORV baiting strategies across the United States.

In this study, we quantified ORV bait competition and uptake rates between raccoons and opossums across 4 land cover types in the southeastern Unites States. Our primary goal was to test whether bait uptake by raccoons and opossums was affected by cover type and local population density of both species. Additionally, we assessed how uptake by a single raccoon was influenced by these same variables in addition to its age, sex, and trapping area fidelity.

STUDY AREA

We conducted this study in 2017–2019 on the Savannah River Site (SRS), a 780-km^2 site owned by the United States Department of Energy in the upper Coastal Plain region of South Carolina, USA (33°19′N, 81°42′W; Figure 1). The SRS is primarily covered by evergreen forest (54%) and woody wetlands (24%), with other land cover types (e.g., developed, open water, mixed forest) collectively comprising 22% of the land area (Yang et al. 2018). In addition to raccoons and opossums, dominant megafauna on the SRS include coyotes (*Canis latrans*), wild pigs (*Sus scrofa*), wild turkey (*Meleagris gallopavo*), and American alligators (*Alligator mississippiensis*). The average elevation on the site is 200 m above sea level and annual rainfall averaged 120 cm during the study. The climate is subtropical with spring (Mar–May), summer (Jun–Aug), fall (Sep–Nov), and winter (Dec–Feb) temperatures averaging 17°C, 26°C, 18°C, and 9°C, respectively.

We studied bait competition across 4 prominent land cover types on the SRS: upland pine, isolated wetland, bottomland hardwoods, and riparian. Upland pine is characterized by mature stands of loblolly (*Pinus taeda*) and longleaf pine (*Pinus palustris*) cover. Since 1951, much of the SRS has been managed for timber harvest and upland pine is

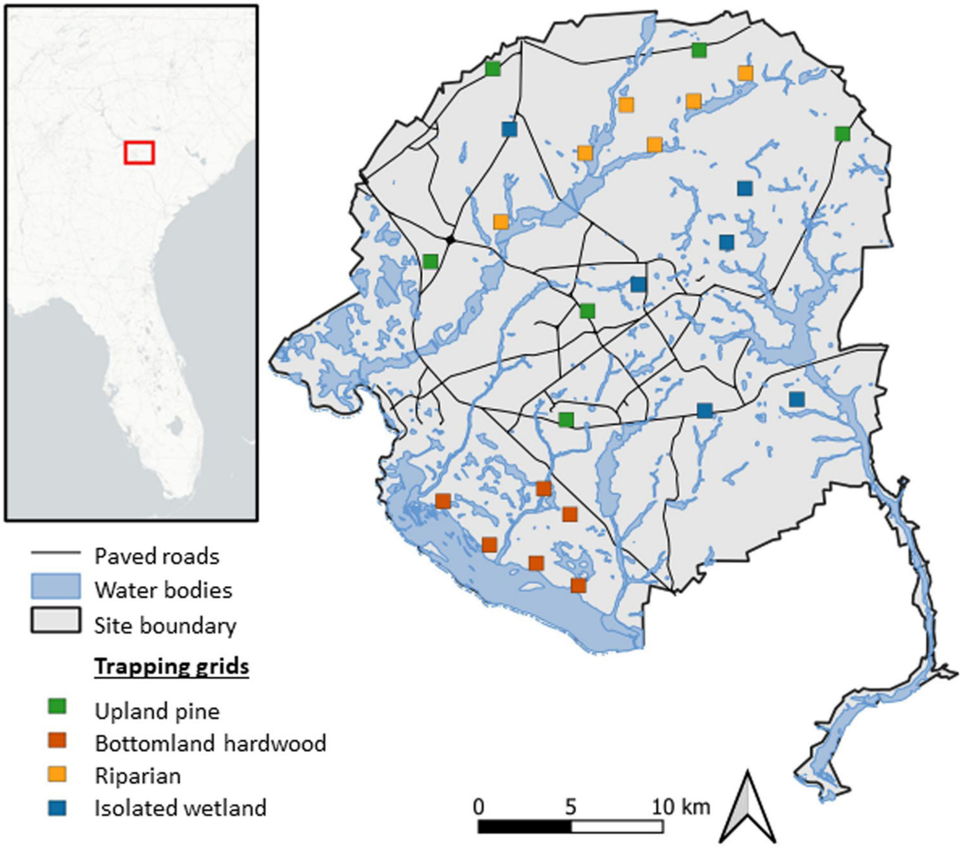

FIGURE 1 The Savannah River Site, South Carolina, USA, 2017–2019, with boxes indicating locations of the 24 grids where we trapped raccoons and opossums divided among 4 land cover types.

harvested on a rotating basis and subject to management practices such as thinning and prescribed burning (White and Gaines 2000). Isolated wetlands are natural shallow ovoid or elliptical-shaped depressions that form ephemerally and are usually surrounded by pine (*Pinus* spp.) or oak (*Quercus* spp.) trees (Workman and McLeod 1990, White and Gaines 2000). Bottomland hardwoods are confined to the lower southwest portion of the site along the Savannah River and consist of seasonally flooded cypress (*Taxodium distichum*)-tupelo (*Nyssa aquatica*) forests, with oak and hickory (*Carya* spp.) scattered throughout (White and Gaines 2000). Riparian areas have similar vegetation as bottomland hardwoods, but bottomland hardwood is largely one contiguous cover type on the SRS, whereas riparian areas are more dispersed across the site, existing in relatively narrow corridors along smaller rivers and creeks.

METHODS

Field methods

We established 6 trapping grids in each of the 4 land cover types (Figure 1). Trapping grids were separated by ≥5 km to maintain spatial independence. At each grid, we placed 25 live-capture box traps (model 108SS; Tomahawk®, Hazelhurst, WI, USA) at intervals of 100 m in either a 5 × 5 square or 6 × 4 + 1 rectangular configuration. We placed whole kernel corn on the ground adjacent to the trap and plaster tabs soaked in fish oil inside the traps as a lure (Webster and Beasley 2019). We replaced the tabs after capture events and halfway through the trapping sessions. We replaced corn as needed on daily checks of traps.

We carried out our study concurrently with a mark-recapture study focused on estimation of abundances of raccoons and opossums in each of the 4 land cover types. Each year, we divided the 24 grids into 3 groups of 8 that were randomized with respect to land cover type. We trapped 8 grids concurrently during 3 consecutive 10-day sessions and following a minimum of 14 days, we trapped them again in the same order. We trapped each of the 24 grids twice annually in 2017–2019. The concurrent studies used capture data from both sessions in each year to derive abundance estimates (Helton 2021, Bernasconi et al. 2022), but we used only individuals trapped in the second sessions to assess bait uptake because we deployed baits between the 2 sessions.

We examined bait uptake using placebo ONRAB® Ultralite baits (Artemis Technologies Inc., Guelph, ON, Canada) filled with a non-toxic biomarker, Rhodamine B (RB; Sigma-Aldrich, St. Louis, MO, USA). Rhodamine B is a fluorescent dye that has been used to assess bait uptake through collection of hair, whiskers, and other keratinized tissues (Fisher 1999, Smyser et al. 2010, Beasley et al. 2015). Ultralite baits consist of an oval blister pack measuring 30 × 14 × 10 mm with a rectangular lip extending to 40 × 20 mm encased in a waxy coating filled with water during manufacturing. We used a syringe to extract 1 mL of water from the blister pack. We then injected 1 mL of fish oil containing RB at a concentration of 150 mg/mL. We retained wax fragments from the external coating of the bait and later melted and used fragments to seal the puncture hole. Fourteen days before the start of the second trapping session, we distributed 12 baits by hand along transects in each 0.16-km^2 grid to mimic a density of 75 baits/km^2, the standard density used by the NRMP in rural areas of the eastern United States (Elmore et al. 2017).

We immobilized all raccoons and opossums upon capture using intramuscular injection of Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA) at a dosage of 5 mg/kg of estimated body mass (Gehrt et al. 2001, Beasley and Rhodes 2008, Smyser et al. 2010). At initial capture of an animal, we marked it with a pair of matching uniquely coded ear tags (1 in each ear; Monel 3, National Band and Tag Company, Newport, KY, USA), then weighed, sexed, and aged animals based on tooth eruption and wear (Grau et al. 1970). For all animal captures in the second sessions within each grid, we also pulled 2 whiskers from each side of the face to evaluate evidence of bait uptake. We pulled whiskers so that the entire whisker was retained for analysis, as fluorescent bands from recent RB consumption are at the proximal whisker end. We placed all whiskers in sealed plastic bags in dry dark storage until microscopic analysis for presence of RB.

For microscopic analysis, we soaked whiskers in distilled water for 10 minutes and then allowed them to dry at ambient conditions for 15 minutes. We thoroughly cleaned dried whiskers with Kimwipes (Kimberly-Clark, Irving, TX, USA) and isopropyl alcohol to remove dirt and debris, always handling them with nitrile gloves and forceps. We placed all 4 whiskers from an individual animal onto a single microscope slide with Fluoromount Aqueous Mounting Medium (Sigma-Aldrich) and covered them with a cover slip. We applied tape at the base of each slide to mask written data, and gave each slide a random number to avoid potential observer bias. We analyzed slides using an Olympus BX 61 fluorescent microscope (Olympus Corporation, Shinjuku, Tokyo, Japan) with a tetramethylrhodamine isothiocyanate (TRITC) filter set (e.g., narrow-band excitation and red-shifted emission filters) under 4x and 10x magnification. If ≥1 of the 4 whiskers from an animal displayed fluorescent marker bands consistent with RB presence, we scored the sample as positive for bait uptake. Two observers scored all whiskers independently and when they recorded contradictory scores, a third independent observer scored them for a final determination (Smyser et al. 2010).

Statistical analysis

We modeled the probability of bait uptake of individual animals using a generalized linear mixed effects regression with a binomial error distribution and a logit link using the package lme4 (Bates et al. 2015) implemented in Program R version 4.0.4 (R Core Team 2022). The response variable was presence or absence of RB in the sample from each animal. Fixed effects included species and land cover type (bottomland hardwood, upland pine, riparian, or isolated wetlands). We also included the estimated raccoon and opossum abundance in each grid as fixed effects, derived from the concurrent mark-recapture study (Table S1, available in Supporting Information; Bernasconi et al. 2022; J. E. Hill, University of Georgia, unpublished data). We included year as a random effect to account for interannual variation in bait uptake.

We used a similar modeling approach to examine variables that influenced bait consumption in only raccoons. Fixed effects included land cover type, sex, age (≤2 yr = juvenile, >2 yr = adult), and grid-specific raccoon and opossum abundance. Because bait consumption may be related to the amount of time an individual spends on the trapping grid, we also included a residency index for each individual, defined as the number of times each raccoon was caught on the grid in the trapping session the sample was taken (Smyser et al. 2010). The model also included year as a random effect.

In our last model, we examined bait uptake at the population level using the proportion of raccoons captured on each grid that tested positive for RB. For this grid-specific model of RB prevalence, we used a linear mixed effects model with the response variable being the proportion of raccoons testing positive for RB on each grid in each year. We weighted each case by the number of raccoons in the sample (i.e., number of raccoons trapped during the second session on that grid in that year) so that samples with very few animals did not have an overly large contribution to models (range of raccoons caught per grid per year = 1–16). The fixed effects were land cover type, raccoon abundance, and opossum abundance, with year as a random effect.

For all models, we examined collinearity between continuous variables by calculating the correlation coefficient between predictors, considering variables to be correlated when $|r|>0.70$ (Dormann et al. 2013). For the raccoon-only model, we also determined correlation between residency index and both sex and age using a point-biserial correlation (rpb) to account for the possibility of sex- or age-dependent residency (Tate 1954). We ranked all possible model combinations based on sample-size corrected Akaike's Information Criterion (AIC_c), considering the model with lowest AIC_c to be the top model. We assessed the relative support for the top model by comparing models within 2 AIC_c units of the top model. If land cover type was included as a parameter in the top model(s), we used the odds ratio to test for pairwise comparisons with a significance level of 0.05. We assessed the fit of the top model by calculating its marginal and conditional R^2 (Nakagawa and Schielzeth 2013).

RESULTS

We obtained whiskers from 78 opossums and 247 raccoons. Among these, 9 opossums (12.0%) and 69 raccoons (27.9%) were positive for RB (Table S1). We used data from all 325 individuals in the 2-species model, whereas the raccoon-only model was based on 237 individuals (10 were excluded because of missing sex or age information; Table 1). There was no indication of correlation between continuous variables ($|r|<0.70$ for all comparisons) in either model, or between sex and residency (rpb = 0.049, $P = 0.458$) or age and residency (rpb = −0.011, $P = 0.864$) in the raccoon-only model.

In the top 2-species model, raccoons were about 3 times more likely to test positive for RB than opossums (model estimated $\bar{x}$ probability = 0.30, 95% CI = 0.19–0.44 for raccoons and 0.11, 95% CI = 0.05–0.23 for opossums; marginal $R^2 = 0.07$, conditional $R^2 = 0.14$; Table 2; Table S2, available in Supporting Information). A second competitive model included species and land cover type ($\Delta AIC_c = 1.05$). None of the odds ratio comparisons between cover types were significant ($P > 0.05$ for all pairwise comparisons; Table S3, available in Supporting Information), indicating no substantial role of cover type in bait uptake probability among individual raccoons and opossums. We were unable to incorporate the interaction between land cover type and species in this model because of convergence issues, but raw proportions of raccoons testing positive for the biomarker were higher than for opossums in every cover type (bottomland hardwood: 0.26 vs. 0.09; upland pine: 0.36 vs. 0.13; riparian: 0.20 vs. 0.07; isolated wetland 0.34 vs. 0.20).

In the raccoon-only analysis, the top model included sex and residency index, with estimated bait uptake probability increasing by 0.08 with each additional day trapped (marginal $R^2 = 0.08$, conditional $R^2 = 0.16$; Figure 2; Table S4, available in Supporting Information). Male raccoons were about twice as likely to uptake baits compared to females (estimated $\bar{x}$ = 0.28, 95% CI = 0.17–0.44 for males and 0.14, 95% CI = 0.05–0.31 for females; Table 2). Land cover type was included in the second ranked model ($\Delta AIC_c = 0.03$), but none of the pairwise comparisons between cover types were significant (Table S3).

TABLE 1 Number of raccoons testing positive for Rhodamine B (RB) in whisker samples (indicating placebo oral rabies vaccine bait consumption) at the Savannah River Site, South Carolina, USA, 2017–2019.

Sex	Age	Number of RB positive samples	Total number of samples	% RB positive
Female	Adult	4	27	15
	Juvenile	3	18	17
Male	Adult	38	119	32
	Juvenile	22	73	30
Total		67	237	28

TABLE 2 Parameter estimates and standard error for top models of Rhodamine B (RB) presence in whiskers collected from raccoons and opossums on the Savannah River Site, South Carolina, USA, 2017–2019.

Model	Parameter	Estimate	SE	*P*-value
Interspecific model (raccoons and opossums)	Intercept	−2.109	0.458	<0.001
	Species: raccoon	1.25	0.389	0.001
Raccoons only	Intercept	−2.319	0.584	<0.001
	Residency	0.328	0.116	0.005
	Sex: male	0.906	0.456	0.047
Proportion raccoons positive for RB	Intercept	−0.988	0.402	0.014

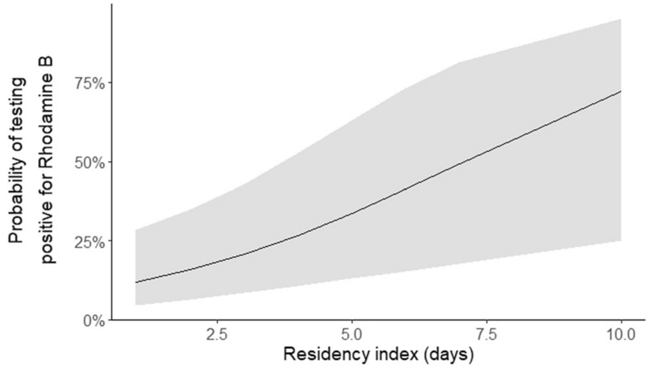

FIGURE 2 Predicted probability of Rhodamine B presence in raccoon whisker samples collected from the Savannah River Site, South Carolina, USA, 2017–2019, as a function of residency (number of days an individual was caught on a grid during a trapping season). Shaded area = 95% confidence interval.

The top model for the population-level biomarker prevalence analysis was the null intercept only model (conditional $R^2 = 0.51$; Table S5, available in Supporting Information), whereas a competitive model included raccoon abundance as a covariate, with a positive relationship between this variable and population level RB prevalence ($\Delta AIC_c = 1.45$). This model estimated a 0.62% increase in proportion of animals testing positive for RB with every one animal increase in raccoon abundance.

DISCUSSION

Raccoons were more likely than opossums to consume baits deployed during spring across all land cover types sampled at the SRS and years of study. Despite similar ecological niches and dietary breadth between the species, the low uptake probability by opossums suggests a minimal influence of this non-target competitor on raccoon bait uptake. Opossums exist at relatively low spring-time densities across the cover types we studied on the SRS, ranging from to 1.14 ± 0.26 (SE) animals/km^2 in isolated wetlands to 2.65 ± 0.45 animals/km^2 in bottomland hardwoods (Bernasconi et al. 2022). At these densities during spring, opossums may not occur in high enough numbers to outcompete raccoons for baits. While spring-time raccoon densities are similarly low on the SRS (range varied from 2.14 ± 0.23 animals/km^2 in upland pine to 5.44 ± 0.37 animals/km^2 in bottomland hardwoods; J. E. Hill, unpublished data), they are more abundant than opossums across every land cover type, which may result in greater competitive advantage. Low densities of raccoons and opossums across the site may also account for the absence of either species' abundance in the top model for any analysis.

Variation in interspecific bait competition between this study and previous works may reflect the level of human landscape disturbance and its effect on ecology of these species. For example, a study in forest fragments interspersed among agriculture in Indiana reported that opossums directly limited bait consumption by raccoons (Smyser et al. 2010). In that landscape, both species were confined to the forest fragments, which resulted in elevated competition. By contrast, cover types on the SRS are comparatively less fragmented, which does not force animals into relatively small areas of suitable habitat, resulting in less spatial overlap and reduced competition.

Additionally, our study site does not include certain land cover types that support higher densities of these species such as agricultural or developed areas (Prange et al. 2003, Bateman and Fleming 2012, Slate et al. 2020). A study in Ohio, USA, with a similar landscape as ours also reported levels of raccoon bait consumption around 30% (Linhart et al. 2002). Studies showing opossums as major bait competitors have generally been in areas with substantial human influence, whereas those reporting greater consumption by raccoons tend to be in less-developed landscapes (Olson and Werner 1999, Olson et al. 2000, Smyser et al. 2010). Thus, there appears to be a land cover type and fragmentation component to interspecific bait competition. As landscapes transition from more natural to more anthropogenically modified, opossum density increases, which leads them to compete more substantially with raccoons for ORV baits compared to more rural areas.

Generally, larger home ranges correlate with an increased likelihood of encountering components of the environment such as seeds (Kuprewicz 2013), parasites (Vitone et al. 2004), and certain mortality sources (Schwab and Zandbergen 2011), a principle that may also apply to ORV baits. Home range size also tends to increase as a function of body mass (Tucker et al. 2014) and because raccoons in our study were on average 1.78 times heavier than opossums, their home ranges may have been larger. Although we did not test this, in Oklahoma, USA, raccoons had larger home ranges than opossums within the same cover type (Ginger et al. 2003), thus higher bait uptake by raccoons in our study may be a function of space use.

The role of movement on uptake is further supported by the greater bait consumption of male raccoons compared to females. Male raccoons typically have larger home ranges than females as the result of divergent resource requirements and mating habits (Gehrt and Frttzell 1997, Chamberlain et al. 2003, Beasley et al. 2007). Additionally, we carried out this study in the breeding season (Feb–May for raccoons in the southeastern U.S.; Chamberlain et al. 2003) when males tend to further expand their home ranges to maximize access to females for mating, resulting in more pronounced intraspecific differences in space use (Gehrt and Frttzell 1997). Therefore, the higher uptake rate of males may be especially prominent during these months and it is unclear whether female uptake would be greater during autumn, when annual baiting campaigns are carried out in the eastern United States (Gilbert et al. 2018).

A greater number of captures for an individual raccoon was correlated with an increased probability of consuming a bait. More captures likely reflect higher intensity use of the area encompassing the trapping grid (Gil-Sánchez et al. 2011), but alternatively may reflect trap-happy individuals. Raccoons often make long range movements to food resources and their home ranges can be several times larger than the core area of use (Chamberlain et al. 2003). Thus, baits were likely consumed by animals whose core area contained the trapping grid and by those whose home ranges encompassed the trapping grid on its periphery. More concentrated use of the baited landscape could result in individuals consuming multiple baits, but we could not detect this with our methodology (whisker fluorescence is identical regardless of number of baits consumed). Multiple bait consumptions would not be desirable from a management perspective, as there is little benefit to repeated consumption. Therefore, another potential area of research is to examine multiple bait consumption using baits that contain different biomarkers (e.g., iophenoxic acid biomarkers in blood; Ballesteros et al. 2013). Expanding the area of the baited landscape, even potentially at a reduced bait density, may reduce repeated individual consumption and increase the number of individual raccoons that encounter baits.

We did not find evidence that land cover type influenced bait consumption in any of our models. In contrast, a study using cameras to examine bait competition on the SRS during fall reported higher raccoon probability of uptake in bottomland hardwood than in upland pine (Dixon 2021). Estimated bait consumption probability by species in that study was also low, with estimated uptake of approximately 18% for raccoons and 5% for opossums. Unlike our study, the previous work used cameras to detect all bait competitors, whereas we could only detect bait consumption by the species we trapped. Only 8% of all bait uptake events documented were the result of other vertebrate species, so it is unlikely that there was substantial bait loss to other species that we did not trap. The previous study documented considerable bait consumption by invertebrates, which may have contributed to the low uptake rates by raccoons we observed. As such, research addressing invertebrate consumption of ORV baits is needed to further understand their influence on uptake by target species.

Bait consumption in the landscapes we studied may be correlated with space use, with more movement leading to higher bait detection and consumption; however, the relative spacing of individuals on the landscape and the manner in which home range and core areas sizes influence such spacing has not been examined. In this landscape, probability of bait uptake by raccoons may be highly related to the presence of the baits in core areas, which are dispersed across the landscape, rather than overlapping as they are in the limited patches of forest found in the agricultural landscapes of the

Midwest (Smyser et al. 2010). Understanding how resource selection influences space use and core area size may be another important factor to determine the appropriate scale and foci for bait distribution.

Strategies to maximize bait uptake by raccoons in these southeastern landscapes are likely necessary, as our estimated 30% probability bait consumption by raccoons during spring would fall short of the theoretical vaccination rate of 60% required to eliminate raccoon rabies (Robbins et al. 1998, Rees et al. 2013). These thresholds have mostly been recommended based on suburban and urban raccoon populations, whereas there is a paucity of research in landscapes such as ours where raccoon densities and the incidence of rabid raccoons may be lower. As a result, target vaccination rates in these landscapes remain undefined (Berentsen et al. 2018), precluding an understanding of how much our bait consumption rates must be augmented to effectively reduce rabies circulation in this area.

MANAGEMENT IMPLICATIONS

Bait uptake by raccoons in the southeastern landscape we studied was likely insufficient to eliminate rabies and this low uptake was not substantially affected by competition with opossums. As such, baiting strategies should focus on techniques to maximize uptake by raccoons, but deterring opossum consumption should not be a major priority. Across the land cover types we examined, there is a similar probability of bait consumption by raccoons, diminishing the likelihood that land cover-targeted baiting at this scale would substantially increase seroprevalence. Potential methods of maximizing raccoon uptake include altering the bait matrix to make it more attractive to raccoons or carrying out baiting during seasons of greater food limitation to promote bait acceptance by raccoons. Future work that addresses the roles of baiting season, bait density, and resource selection of target animals will be important to provide a more comprehensive understanding of the factors governing ORV bait uptake by target species and increase the effectiveness of rabies management strategies in these southeastern landscapes.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflict of interests.

ETHICS STATEMENT

All animal trapping and handling activities were conducted in accordance with the University of Georgia Animal Care and Use Guidelines under Animal Care and Use Protocol A2018 06-024-A12.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Jacob E. Hill http://orcid.org/0000-0003-2761-8786
David A. Bernasconi http://orcid.org/0000-0002-2936-0566

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