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Research Article

Rabies Management Implications Based on Raccoon Population Density Indexes

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ABSTRACT An estimate or index of target species density is important in determining oral rabies vaccination (ORV) bait densities to control and eliminate specific rabies variants. From 1997–2011, we indexed raccoon (*Procyon lotor*) densities 253 times based on cumulative captures on 163 sites from Maine to Alabama, USA, near ORV zones created to prevent raccoon rabies from spreading to new areas. We conducted indexing under a common cage trapping protocol near the time of annual ORV to aid in bait density decisions. Unique raccoons ($n = 8,415$) accounted for 68.0% of captures ($n = 12,367$). We recaptured raccoons 2,669 times. We applied Schnabel and Huggins mark-recapture models on sites with ≥3 years of capture data and ≥25% recaptures as context for raccoon density indexes (RDIs). Simple linear relationships between RDIs and mark-recapture estimates supported application of our index. Raccoon density indexes ranged from 0.0–56.9 raccoons/km^2. For bait density decisions, we evaluated RDIs in the following 4 raccoon density groups, which were statistically different: (0.0–5.0 [$n = 70$], 5.1–15.0 [$n = 129$], 15.1–25.0 [$n = 31$], and >25.0 raccoons/km^2 [$n = 23$]). Mean RDI was positively associated with a higher percentage of developed land cover and a lower percentage of evergreen forest. Non-target species composition (excluding recaptured raccoons) accounted for 32.0% of captures. Potential bait competitors accounted for 76.5% of non-targets. The opossum (*Didelphis virginiana*) was the primary potential bait competitor from 27°N to 44°N latitude, north of which it was numerically replaced by the striped skunk (*Mephitis mephitis*). We selected the RDI approach over mark-recapture methods because of costs, geographic scope, staff availability, and the need for supplemental serologic samples. The 4 density groups provided adequate sensitivity to support bait density decisions for the current 2 bait density options. Future improvements to the method include providing random trapping locations to field personnel to prevent trap clustering and marking non-targets to better characterize bait competitors. © 2020 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS non-target, opossum, oral rabies vaccination, population density index, rabies management, raccoon, skunk.

Wild carnivores and insectivorous bats emerged as reservoirs for unique rabies virus variants following successful control in domestic dogs in the United States around 1960 (Centers for Disease Control and Prevention [CDC] 1997). Since the early 1990s, wild animals have accounted for >90% of the approximately 5,000–9,000 cases annually reported to the CDC (Monroe et al. 2016). The raccoon (*Procyon lotor*) has been responsible for 30–50% of those cases and was the primary species reported from the early 1990s through 2014 (Monroe et al. 2016). Raccoons are often common along

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the human-wildlife interface (Riley et al. 1998, Prange et al. 2003), resulting in an elevated risk of human exposure to rabies, with increased risks to domestic and other wild animals (Blanton et al. 2008, Wallace et al. 2014).

Since the late 1970s, rabies management has included oral rabies vaccination (ORV) as a method to control rabies variants in specific reservoir species (Steck et al. 1982, Sidwa et al. 2005, Rosatte et al. 2007, Rupprecht and Slate 2012). Oral rabies vaccination has been applied at the landscape level to control or eliminate rabies in red foxes (*Vulpes vulpes*) from areas in western Europe (Freuling et al. 2013) and southern Ontario, Canada (MacInnes et al. 2001), and in gray foxes (*Urocyon cinereoargenteus*) and coyotes (*Canis latrans*) from Texas, USA (Sidwa et al. 2005).

Raccoons are a ubiquitous ecological generalist and as a result rabies elimination is more challenging for this species (Slate et al. 2009). Better success has been realized in Ontario (Rosatte et al. 2009) and Quebec, Canada (Mainguy et al. 2012) in eliminating raccoon rabies that spread north through ORV zones in the United States. These outbreaks represented relatively small foci compared to the broader geographic distribution of raccoon rabies in the United States. Early detection and intervention that integrated ≥2 methods (i.e., population reduction, trap-vaccinate-release, ORV with 2 different vaccine baits) has been attributed to their successes (Rosatte et al. 2009). Since December 2015, a new incursion of raccoon rabies in the vicinity of Hamilton, Ontario remains a target for elimination through the integration of trap-vaccinate-release and ORV (Middel et al. 2017).

An estimate or index of target species density is often a prerequisite to establish and evaluate wildlife population management goals. The goal for ORV is to create sufficient immunity within the population of a target species in a specified area to break the rabies transmission cycle among conspecifics (Thulke and Eisinger 2008). Bait attributes, vaccine effectiveness, bait distribution patterns, baiting frequency, seasonal timing of baiting, habitat characteristics, and other factors such as weather and non-target species competition may affect bait uptake and the immune response in the population (Rosatte et al. 2007, Sattler et al. 2009, Smyser et al. 2010). To meet rabies management goals, estimates or indices of population density for rabies reservoir species in areas under consideration for ORV is fundamental (Rupprecht et al. 1995, Mainguy et al. 2012) among all variables to help address the optimal bait density and distribution patterns to achieve population immunity necessary for rabies control and elimination.

The basis for our most commonly applied bait densities can be traced to the range of bait densities suggested for raccoons in earlier studies (Johnston et al. 1988, Roscoe et al. 1998, Sattler et al. 2009). Bait densities have remained largely limited to 2 options: 75 baits/km^2, or when raccoon densities are known or suspected to be high or there is a generally poor immune response, bait density has been increased to 150/km^2 in an attempt to increase population immunity (Slate et al. 2009, 2014). Bait density as high as 300/km^2 has been evaluated (Sattler et al. 2009, Pedersen et al. 2018) and bait density of 37/km^2 is currently being evaluated for an ORV immune response where raccoon densities are low.

These factors along with cost, staff availability, and the necessity to collect sera to supplement roadside sampling largely influenced the decision to use a standardized index. Our index was based on cumulative catch of unique raccoons. Our indexing method also had the advantage of using a relatively straightforward protocol to allow for consistent application among wildlife staff across 18 states. We sampled to determine raccoon density indexes (RDIs) when the population should be at its highest density from the addition of the mobile juvenile cohort (Lotze and Anderson 1979), which was also aligned near the time of ORV baiting.

The tradeoffs related to an index based on cumulative catch of individuals are not inconsequential and include a conservative measure of density versus population estimates based on capture and recapture probabilities using mark-recapture methods (Pollock et al. 2002). Given current bait density and distribution options, and the inability to rapidly vary bait densities from fixed wing aircraft over a rapidly changing landscape, an RDI was practical to support baiting decisions.

Our primary objective was to determine the value of RDIs in ORV bait density decisions by comparing bait densities that would be applied based on mark-recaptured estimates. Secondarily, we created 4 density groups ranging from 0.0–5.0 to >25.0 raccoons/km^2 to test their value in bait density decisions. Our final objective was to evaluate relationships between RDI and age, sex, land cover, latitude, and elevation, and to characterize potential bait competitors with raccoons.

STUDY AREA

Density indexing occurred in 18 states in the continental United States from 1997–2011 (Fig. 1). Indexing sites ranged from 2.5–3.5 km^2 (88.1% were within 0.3 km^2 of the target of 3 km^2) and were distributed from northern Maine (47.20216°N, −69.02458°W) to southeastern Michigan (42.54075°N, −83.65504°W) to southwestern Alabama (31.82310°N, −88.18538°W) to west central Florida (27.88542°N, −82.26037°W), with sites predominantly located along the edge of the raccoon rabies distribution (Fig. 1). The topography was flat to mountainous, with mean elevation of indexing sites ranging from 3–1,244 m. The area was encompassed by 4 climatic zones (Karl and Koss 1984), but all sampling occurred in the northeast, Ohio Valley Central, and Southeast zones except for 2 indexing sites on the edge of the Ohio Valley zone. The area has weather characterized by 4 seasons, with winter and snowfall decreasing in intensity along a north to south gradient, except on sites at higher elevations along the Appalachian Ridge and in central Florida where snowfall is extremely rare. Summers are longer and warmer along this same gradient. A full description of the flora and fauna within the area where indexing occurred is presented by Nelson et al. (2014) and Whitaker and Hamilton (1998). Density indexing occurred 253 times on 163 sites (Table 1). We indexed raccoon densities during 3 events on 3 different

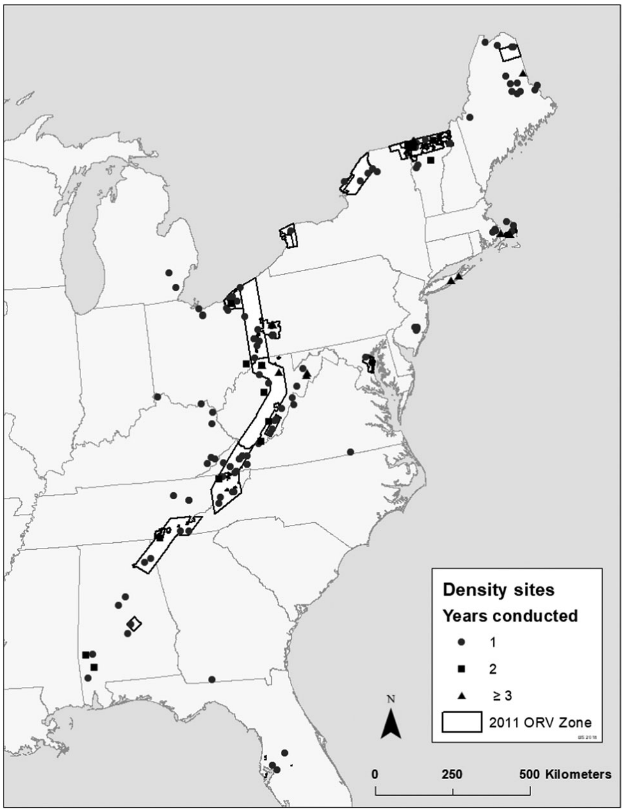

Figure 1. Locations of 253 raccoon density measures on 163 sites relative to oral rabies vaccination (ORV) zones in 18 eastern states, USA, 1997–2011.

sites at 20–30°N (Florida), 100 events on 77 different sites at 30.1–40°N, and 150 events on 83 different sites at >40°N.

Wildlife Services technicians and biologists selected indexing sites to minimize edge effects (i.e., not narrow, linear-shaped areas) based on 3 land cover types: forest, agriculture, and urban-suburban. The Wildlife Services property access policy required formal landowner permission, which had a bearing on securing contiguous 3-km^2 sites for density indexing.

METHODS

Animal Capture, Sampling, and Data Collection

We captured animals using cage traps (Tomahawk model 608, Tomahawk Live Trap, Hazelhurst, WI, USA) and checked traps every 24 hours. We euthanized and tested suspect rabid animals (Lembo et al. 2006, Rupprecht et al. 2014) and shipped rabies positives to the CDC in Atlanta, Georgia, USA, or the New York State Department of Health (NYSDOH) Rabies Laboratory in Slingerlands, New York, USA, for confirmation and rabies virus variant typing. We sedated captured raccoons with no suggestive signs of rabies using an intramuscular injection of 5:1 ketamine:xylazine (Kreeger 1999), marked them with unique numbered ear tags, collected blood for rabies virus neutralizing antibody (rVNA) determination at CDC (Smith et al. 1973, 1996) or NYSDOH (Trimarchi et al. 1996), and extracted a first premolar for age and biomarker analysis (Johnston et al. 1987, Algeo et al. 2013). We recorded date and global positioning system (GPS) coordinates for target and non-target captures. We also recorded sex, female reproductive status, and general condition for each raccoon. Upon recovery from sedation, we released marked raccoons at their capture site. We processed non-target striped skunks (*Mephitis mephitis*) and gray foxes under the same protocol, although marking was inconsistent. We released other non-target captures unmarked at their site of capture such that recaptured non-targets could not be identified. We evaluated the ratio of raccoons to potential bait competitors. We collected blood serum from raccoons (and skunks) during indexing to bolster sera samples collected during ORV program monitoring, independent of density indexing. We handled all captured animals according to Sikes and the Animal Care and Use

Table 1. Raccoon density indexes ($n = 253$) by number of sites ($n = 163$) for 18 eastern states, USA, 1997–2011.

		Number of indexes/site											
State	**Years**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Total sites**	**Total indexes**
AL	2003–2011	8	3	0	0	0	0	0	0	0	0	11	14
FL	2003	3	0	0	0	0	0	0	0	0	0	3	3
GA	2011	1	0	0	0	0	0	0	0	0	0	1	1
KY	2002–2009	7	0	0	0	0	0	0	0	0	0	7	7
MA	2001–2011	6	0	0	1	0	1	0	0	0	0	8	16
MD	2003	1	0	0	0	0	0	0	0	0	0	1	1
ME	2002–2011	13	0	1	0	0	0	0	0	0	0	14	16
MI	2005–2006	2	0	0	0	0	0	0	0	0	0	2	2
NC	2007–2010	5	0	0	0	0	0	0	0	0	0	5	5
NH	2002–2011	2	0	0	0	0	0	0	0	0	0	2	2
NJ	2011	4	0	0	0	0	0	0	0	0	0	4	4
NY	1998–2010	6	0	0	0	2	0	0	0	0	0	8	16
OH	1999–2011	12	2	0	0	0	0	0	0	0	0	14	16
PA	2005–2008	8	0	0	2	0	0	0	0	0	0	10	16
TN	2002–2011	7	1	0	0	0	0	0	0	0	0	8	9
VA	2002–2011	20	0	0	0	0	0	0	0	0	0	20	20
VT	1997–2011	8	4	7	2	0	0	0	0	0	2	23	65
WV	2001–2010	15	4	0	1	1	0	0	1	0	0	22	40
Total		128	14	8	6	3	1	0	1	0	2	163	253

Committee of the American Society of Mammalogists (2016). In cases where euthanasia became necessary, we followed the guidelines of the American Veterinary Medical Association (2020). In addition, we adhered to all relevant United States Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS), Wildlife Services Program Directives (USDA 2018).

We did not evaluate the potential for sedation, blood sampling, and premolar extraction effects on recapture probabilities. Anesthesia (Gehrt et al. 2001) and premolar extraction during 10-day sampling intervals did not have an effect on recapture probabilities over longer-term sampling intervals (Beasley and Rhodes 2007).

Density Indexing

We conducted density indexing from the beginning of June to early November, when juveniles were generally available to be captured and populations approached their highest densities. All Wildlife Services personnel were trained in the density protocol, which required setting and checking 50 cage traps once every 24 hours at dispersed locations for 10 consecutive nights on sites approximating 3 km^2 (10-day protocol). We modified the 10-day protocol for lower and higher numbers of raccoon captures. If we captured ≤2 unique raccoons at the end of day 4, we pulled traps on day 5. If we captured >2 unique raccoons at the end of day 4, we continued trapping to day 9. If we captured ≤75 unique raccoons at the end of day 9, we pulled traps on day 10. If we captured >75 unique raccoons at the end of day 9 and there was a ≥5% increase from day 8 to day 9, we continued trapping until day 15. Of the 253 indexing events, 233 fell into the 10-day trapping protocol, 13 in the 5-day protocol, and 7 in the 15-day protocol. We baited traps with Hard Core® Raccoon Lure No. 1 (Wildlife Research Center, Ramsey, MN, USA) and marshmallows. We moved traps that did not catch raccoons after 2–3 nights ≥50 m to ensure better coverage of the indexing site. We used this approach in lieu of a formal trapping grid with 50 fixed locations because this method would have been impractical largely because of available staff hours.

We evaluated trap distribution for a subset of 87 indexing sites based on complete GPS trap location data. We analyzed trap locations by site using the average nearest neighbor tool (ArcGIS Pro 2.1.0, Esri, Redlands, CA, USA; Ebdon 1985, Mitchell 2005). We calculated the nearest neighbor distance using the Euclidean distance method and the site-specific area. To determine the effect of trap clustering, we compared the distribution of density groups among sites with no trap clustering to those with low (nearest neighbor ratio >0.75) to moderate (nearest neighbor ratio 0.25–0.75) clustering with a 3 × 3 contingency analysis. We omitted sites with RDIs >25.0 raccoons/km^2 because of inadequate sample size ($n = 6$).

We did not evaluate the effect of releasing marked raccoons back into the population rather than removing them for the 2% reduction in trap availability/night due to each recaptured raccoon. Rather, we monitored recaptures for potential use in mark-recapture models as context estimates for RDIs.

We calculated RDI as the number of unique raccoons divided by the area of the site (km^2). We grouped RDIs from lowest to highest densities (raccoons/km^2) to facilitate ORV baiting decisions and referred to them as A (0.0–5.0 raccoons/km^2), B (5.1–15.0 raccoons/km^2), C (15.1–25.0 raccoons/km^2), and D (>25.0 raccoons/km^2). We used analysis of variance (ANOVA) and least square multiple comparison to determine if the density of raccoons in each group was significantly different.

We calculated mean daily capture rates in 5-day increments to evaluate reduction in unique raccoon captures to establish appropriate RDI sampling intervals and support density groupings. We also calculated the mean daily capture rates for a subset of 35 density indexing events from the 233 that met the 10-day protocol. Of these, 29 and 6 were arbitrarily extended to 15 and 20 days, respectively, to determine the upper asymptote for unique raccoon captures. These 35 events did not meet the threshold for sampling beyond 10 days so we excluded captures beyond 10 days from all analysis except when reporting raccoon capture rates. We performed 2-way ANOVAs for captures by day increments and RDI groups in Program R (version 3.4.3, www.r-project.org, accessed 25 Jun 2018). We used least square multiple comparisons to analyze pairwise differences in average capture rates for day increments.

Mark-Recapture Estimates

We applied 26 10-day events to 2 closed mark-recapture methods to calculate population estimates for comparison to RDIs (Schnabel 1938, Huggins 1989). We assumed that there were no births, deaths, immigration, or emigration during the 10-day trapping period. We selected sites for mark-recapture analysis that had ≥3 density indexing events at the same site (not necessarily in successive years) and ≥25% recaptures. We converted population estimates to density by dividing by area of the site.

We estimated population size using the Schnabel method in EXCEL (Microsoft Office, Redmond, WA, USA; Schnabel 1938, C. J. Krebs, University of British Columbia, unpublished report) and then with the Huggins model in Program MARK (White and Burnham 1999) to allow for a capture effect (Huggins 1989). For the Huggins method, we limited our selection to the following predefined models because of the simplicity of the 10-day events: M_o (capture probabilities are constant), M_b (capture probabilities vary by behavioral responses such as trap happy and trap shy individuals), and M_t (capture probabilities vary with time; Otis et al. 1978). We used second-order Akaike's Information Criterion (AIC_c) to rank models. We used the estimates from the top model (model with the lowest AIC_c value) unless multiple models were within 2 AIC_c of the best model, then we model averaged the abundance estimates across all models (Burnham and Anderson 2004). We evaluated mark-recapture estimates in relation to RDI using simple linear regression in Program R.

Land Cover Associations and Raccoon Population Structure

We retrospectively determined specific land cover composition for all density indexing sites using GAP/LANDFIRE National Terrestrial Ecosystems 2011 version 2.0 (formerly

GAP NLCD; U.S. Geological Survey 2011). This dataset was the most detailed land cover map of the United States at the time. We reclassified the 259 land use values in our regions into 15 land cover types that from here forward are referred to as National Rabies Management Program (NRMP) land cover classes: barren and miscellaneous, cultivated cropland, deciduous forest, evergreen forest, mixed forest, grasslands, herbaceous wetlands, high developed, low developed, medium developed, developed open space, open water, pasture or hay, shrub or scrub, and woody wetlands.

In ArcMap 10 (Esri), we clipped GAP/LANDFIRE grids to the indexing site. We quantified land cover for 160 sites (we omitted 3 sites from Florida considered outliers). We also quantified land cover for a 5-km buffer surrounding each indexing site. For each of the 15 land cover types, we compared the 2 groups (indexing sites and buffer sites) to determine if the indexing site reflected land cover composition in the general sampling area. We used the Wilcoxon rank-sum test with PROC NPAR1WAY in SAS 8 (SAS Institute, Cary, NC, USA) for these 2-way comparisons.

We further reclassified the 15 land cover types into 5 groupings: forest evergreen (evergreen forest), forest deciduous (deciduous forest), developed (high developed, low developed, medium developed, developed open space), agriculture (cultivated cropland, pasture or hay), and other (barren and miscellaneous, grasslands, herbaceous wetlands, open water). We classified mixed forest and woody wetlands into evergreen or deciduous forest depending on the dominant cover type. We classified shrub or scrub into forest evergreen, forest deciduous, developed, or agriculture depending on the dominant landscape (e.g., we classified a cluster of shrubs in a hay field as agriculture and shrub or scrub in a city park as developed).

We examined the relationship between RDIs and land cover type, latitude, and elevation at indexing sites. We used a lognormal mixed model implemented in Program R (R Core Team 2017) using package lme4 (Bates et al. 2015). To account for nested levels of heterogeneity, we used year and month as random effects to account for temporal variability, and the variables state and event nested in locale to address spatial variability. The locale effect accounted for event locations in close proximity of one another and event effect accounted for the trapping locations within a locale that were used for multiple years. We considered land cover covariates, latitude, and elevation as fixed effects. We examined non-linear relationships for elevation using basis functions (Hastie 2017) implemented in R using package splines2 (Wang and Yan 2018). We examined the relative support for individual covariates using cumulative covariate weights (w_i) and considered values >0.5 to be supported (Burnham and Anderson 2002). We followed the recommendations of Zuur et al. (2009) for mixed model selection. We examined random effects first using the fully parameterized fixed effects; we fit models using the restricted maximum likelihood (REML; Zuur et al. 2009). We compared random effects using AIC_c (Burnham and Anderson 2002). Using the most-supported random effects (i.e., random effects with cumulative $w_i > 0.5$), we compared all combinations of fixed effects using AIC_c (Burnham and Anderson 2002) using maximum likelihood estimation. We estimated results of the model with the covariates with cumulative $w_i > 0.5$ with REML estimation (Zuur et al. 2009).

We defined juveniles as <1 year, yearlings as 1 year, adults as ≥2–4 years, and older adults as ≥5 years based on cementum annuli from readable premolar sections. We evaluated age classes by density group. We used chi-square tests conducted in Program R to analyze age by sex (based on expected evenness) ratios. We grouped the predicted RDIs from the most-supported lognormal mixed model to evaluate age and sex distributions within the 4 density groups. We also analyzed survivorship (Pollock 1982, Huggins 1989) on 4 sites for which limited data were available (Table S1, available online in Supporting Information).

RESULTS

We set 50 traps on average at 125.1 (95% CI = 113.4–136.8) locations/site on the 87 sites. Fifty (57.5%) of the 87 sites had random or dispersed trap distributions. Thirty-seven (42.5%) of the 87 sites had clustered trap distributions (distance between traps: $\bar{x} = 56.7$ m, range = 19.3–328.8 m). Of the clustered sites, 62.2% were moderately clustered (nearest neighbor ratio = 0.26–0.75, $n = 23$, distance between traps: $\bar{x} = 49.4$ m, range = 2.2–349.4 m) and 37.8% had low clustering (nearest neighbor ratio >0.75, $n = 14$, distance between traps: $\bar{x} = 68.7$ m, range = 5.8–294.9 m). There was no effect ($\chi^2_4 = 0.56$, $P = 0.967$) of trap clustering based on the frequency of events in density groups A, B, and C.

Raccoon Capture Rates

Individual raccoons (8,415) accounted for 68.0% of captures ($n = 12{,}367$, excluding 2,669 raccoon recaptures). Mean capture rates for 10-day indexing events ($n = 233$) were lower ($F_{3,\,2{,}322} = 64$, $P < 0.001$) in days 6–10 than days 1–5 for all density groups except group A based on least square multiple comparisons (Table 2). Mean capture rates based on 15 consecutive days ($n = 7$) were lower ($F_{2,\,102} = 43.5$, $P < 0.001$) for days 11–15 than days 6–10, which was lower than days 1–5 by multiple comparison (Table 2). The indexing events in group A that followed the 5-day protocol ($n = 13$) averaged 0.3 raccoon captures/day (Table 2). As support for the 5-day protocol, RDIs ($n = 57$) from the 10-day protocol that fell within group A showed a decline ($F_{1,\,568} = 45.7$, $P < 0.001$) in mean capture rate from days 1–5 to 6–10 and mean RDI did not shift to a higher density group as a result of trapping days 6–10 (Table 2).

A subset of 29 from the 10-day protocol events were extended to 15 days (Table 3). Irrespective of density grouping, significant ($F_{2,\,423} = 49$, $P < 0.001$) decline occurred in mean capture rates from days 1–5 to 6–10 to 11–15. Mean capture rates within density group A remained low and similar at 0.7–0.8 raccoons/day from days 1–5 through days 11–15 by multiple comparison, again supporting the 5-day protocol. In density groups B, C, and D, mean capture rates were significantly higher ($F_{6,\,423} = 14$, $P < 0.001$) for days 1–5 than days 6–10 and 11–15, which were similar (Table 3).

Table 2. Mean daily capture rates (unique raccoons/day) for 5-, 10-, and 15-day trapping protocols by raccoon density group (raccoons/km^2) for 253 indexing events conducted in 18 eastern states, USA, 1997–2011.

	5-day protocol	**10-day protocol**				**15-day protocol**
	($n = 13$)	**($n = 233$)**				**($n = 7$)**
	Density group	**Density group**				**Density group**
	A (0.0–5.0)	**A (0.0–5.0)**	**B (5.1–15.0)**	**C (15.1–25.0)**	**D (>25.0)**	**D (>25.0)**
Days	**($n = 13$)**	**($n = 57$)**	**($n = 129$)**	**($n = 31$)**	**($n = 16$)**	**($n = 7$)**
1–5	0.3	1.2	3.6	7.7	13.3	14.1
6–10		0.6	1.8	3.5	7.7	8.5
11–15						4.7

The extended 5 days resulted in a shift of mean RDI to a higher density group only in 1/29 events. For the 6 10-day events extended to 20 days, we pooled the capture rates for both density groups (B and C) because group C included a single event (Table 3). Of these pooled events, there was a similar pattern of reduced mean capture rate ($F_{3,116} = 37.1$, $P < 0.001$) from days 1–5 to 6–10 to 11–15. Extension to 20-day trapping effort did not result in a mean RDI shift to a higher density group.

Density Index and Mark-Recapture Estimates

The 253 RDIs were distributed within the following density groups: A (27.7%, $n = 70$), B (51.0%, $n = 129$), C (12.2%, $n = 31$), and D (9.1%, $n = 23$; Table 2). Mean RDI from lowest to highest density group was: 2.5 (95% CI = 2.1–2.9), 9.1 (95% CI = 8.6–9.6), 19.1 (95% CI = 18.1–20.1), and 37.8 (95% CI = 33.2–42.4) raccoons/km^2, respectively. The highest RDI was 56.9 raccoons/km^2 with 5 RDIs >50 raccoons/km^2. Mean raccoon density significantly differed for the 4 groups ($F_{3,249} = 524$, $P < 0.001$) by multiple comparison test.

All RDIs were more conservative than mark-recapture model estimates except for the Huggins estimate for the West Virginia Wetzel site in 2006. One RDI equaled the lower 95% confidence limit and 1 fell within the 95% confidence interval of the Schnabel estimates; 2 RDIs equaled (including West Virginia Wetzel site in 2006) the lower 95% confidence limit and 9 were within the 95% confidence interval for the Huggins estimates (Table 4). Forty-six and 58% of Schnabel and Huggins estimates, respectively, occurred within the same density groups as the RDIs. Twenty of 26 RDIs suggested bait densities that aligned with both of the mark-recapture methods, and 24 of 26 RDIs aligned with bait densities suggested by one of the mark-recapture estimates. Bait densities of 75 baits/km^2 suggested by 2 RDIs were not aligned with the 150 baits/km^2 suggested by either of the mark-recapture estimates. There was a simple linear relationship between RDIs and estimates from both mark-recapture models (Fig. 2), with a stronger fit for Schnabel ($r^2 = 0.93$, $F_{1,24} = 338.4$, $P < 0.001$) than the Huggins method ($r^2 = 0.53$, $F_{1,24} = 27.8$, $P < 0.001$).

Raccoon Population Structure

We determined specific age for 5,643 of 8,415 unique raccoons. In a composite sex and specific age profile, the juvenile cohort represented 22% (age <1, $n = 1{,}227$) of 5,643 raccoons and their sex ratio was even ($\chi^2_1 = 3.2$, $P = 0.072$). There was a significant disparity toward males among ages 1 ($\chi^2_1 = 25.7$, $P < 0.001$) and 2–4 ($\chi^2_1 = 21.0$, $P < 0.001$). Over 88% of raccoons were ≤4 years of age. Females were better represented than males ($\chi^2_1 = 14.4$, $P < 0.001$) from ages 5–14, although only 12% of the sample was ≥5 years of age, with few raccoons ≥8 years of age; the oldest individual was a 14-year-old female.

There was a positive relationship between the percent of yearlings and RDI (Fig. 3). From ages 0–4, males exceeded females in all density groups except for juveniles in group C and adults in group D (Table 5). From ages 5–14, there were more females than males in all density groups. Density group D had the highest number of females at the oldest ages.

Sex ratios were highly variable among sites where RDI ranged from near zero to slightly >5.0 raccoons/km^2. Sex ratios varied less at RDIs ≥6.0, favoring males up to RDIs of 15.0 raccoons/km^2. Sex ratios approximated 1:1 among the

Table 3. Mean daily capture rates (unique raccoons/day) by raccoon density group (raccoons/km^2) for 29 of 233 density indexing events that we extended from the 10-day trapping protocol to 15 days and 6 of 233 that we extended from the 10-day trapping protocol to 20 days. We conducted indexing events in 18 eastern states, USA, from 1997 to 2011.

	10 days extended to 15 days ($n = 29$)[a]				**10 days extended to 20 days ($n = 6$)[a]**		
	Density group				**Density group**		
	A (0.0–5.0)	**B (5.1–15.0)**	**C (15.1–25.0)**	**D (>25.0)**	**B (5.1–15.0)**	**C (15.1–25.0)**	**Pooled**
Days	**($n = 5$)**	**($n = 17$)**	**($n = 4$)**	**($n = 3$)**	**($n = 5$)**	**($n = 1$)**	**($n = 6$)**
1–5	0.7	2.8	6.4	10.9	4.2	5.8	4.5
6–10	0.8	1.8	3.8	5.7	1.8	4.6	2.3
11–15	0.7	1.2	3.5	4.0	1.0	0.2	0.9
16–20					0.6	0.6	0.6

[a] These density indexing events are a subset of the 233 from the 10-day protocol that were arbitrarily extended to 15 and 20 days to determine the upper asymptote for unique raccoon captures. These did not meet the threshold for sampling beyond 10 days.

Table 4. Comparison of raccoon density indexes (RDI; raccoons/km^2) to Schnabel and Huggins mark-recapture population density estimates (raccoons/km^2; for $\geq$3 RDI events at the same site and $\geq$25% recaptures) from 6 sites in 4 eastern states, USA, 2001–2011. Bait densities (baits/km^2) that would be used based on the RDI, Schnabel, and Huggins estimates are indicated.

			Schnabel			Huggins			Bait density (baits/km^2)		
Indexing event[a]	RDI	Group[b]	Estimate	95% CI	Group[b]	Estimate	95% CI	Group[b]	RDI	Schnabel	Huggins
MAY06	6.3	B	10.8	7.8–17.3	B	14.5	0.0–143.7[c]	B	75	75	75
MAY07	9.0	B	15.7	12.0–22.4	C	9.1	8.7–11.4	B	75	75	75
MAY08	13.3	B	21.7	17.4–29.0	C	25.3	0.0–60.8[c]	D	75	75	150
MAY09	6.3	B	11.2	8.2–17.3	B	7.3	6.5–12.6	B	75	75	75
MAY11	15.0	B	31.6	25.3–42.2	D	31.8	22.9–50.7	D	75	150	150
NYS05	7.1	B	12.0	9.1–17.5	B	14.2	9.9–25.4	B	75	75	75
NYS06	7.9	B	9.7	7.9–12.5	B	10.7	6.7–14.7	B	75	75	75
NYS07	9.4	B	13.6	11.0–17.6	B	10.4	9.4–15.1	B	75	75	75
NYS08	5.6	B	9.5	7.1–14.2	B	16.4	6.3–166.3	C	75	75	75
NYS09	5.0	A	9.1	6.5–15.4	B	9.8	6.5–20.1	B	75[d]	75	75
NYH05	25.9	D	45.5	38.7–55.3	D	28.2	26.6–33.4	D	150	150	150
NYH06	23.1	C	42.5	35.6–52.9	D	24.6	23.8–28.0	C	75	150	75
NYH07	25.5	D	45.1	38.3–55.0	D	44.1	28.4–59.8	D	150	150	150
NYH08	16.2	C	26.8	22.0–34.3	D	17.0	16.4–20.0	C	75	150	75
VTD01	10.7	B	23.9	18.0–35.9	C	23.8	7.2–40.5	C	75	75	75
VTD02	9.3	B	16.4	12.9–22.4	C	14.0	7.5–20.5	B	75	75	75
VTD09	8.6	B	11.3	9.3–14.4	B	10.3	7.6–12.9	B	75	75	75
VTF01	13.6	B	29.7	23.5–40.6	D	29.2	21.3–46.4	D	75	150	150
VTF02	10.7	B	16.3	13.1–21.8	C	11.4	10.8–14.8	B	75	75	75
VTF07	7.9	B	9.2	7.1–12.9	B	20.7	0.0–147.2[c]	C	75	75	75
VTF08	10.0	B	13.0	10.4–17.6	B	33.7	0.0–256.4[c]	D	75	75	150
WVW01	14.8	B	21.3	17.6–26.9	C	22.2	18.2–31.0	C	75	75	75
WVW03	8.6	B	18.6	14.3–26.6	C	20.0	13.7–36.0	C	75	75	75
WVW05	4.8	A	7.1	5.2–11.5	B	7.7	5.6–14.8	B	75[d]	75	75
WVW06	5.2	B	9.1	6.4–15.3	B	5.2	5.2–6.1	B	75	75	75
WVW07	11.7	B	22.4	17.4–31.5	C	13.6	12.1–20.2	B	75	75	75

[a] Indexing event names reflect the state, shortened indexing site name, and year conducted.
[b] RDIs, Schnabel, and Huggins population density estimates were grouped as follows: A = (0.0–5.0 raccoons/km^2), B = (5.1–15.0 raccoons/km^2), C = (15.1–25.0 raccoons/km^2), and D = (>25 raccoons/km^2).
[c] Model averaging resulted in a negative lower confidence limit, which we truncated to zero because a negative population estimate is not plausible.
[d] Bait density of 37 baits/km^2 is not a current option but may be a viable option for low densities pending further testing.

highest RDIs. Results from 4 sites indicated survivorship estimates for juveniles and adults were generally similar (Table S1).

Species Composition and Potential Bait Competitors

Raccoons accounted for the highest and increasing percent of total captures on a south to north latitudinal gradient, ranging from 213 (43.5%, $n = 490$) at 20–30°N to 5,542 (74.3%, $n = 7{,}460$) at >40°N (Table 6). The opossum (*Didelphis virginiana*) was the most common non-target at 17.7% ($n = 2{,}194$). Opossums accounted for 76% ($n = 211$) of non-targets ($n = 277$) at 20–30° N. The opossum declined as a percentage of total captures along a south to north gradient, whereas the striped skunk increased ($\chi^2_1 = 509$, $P < 0.001$) at latitudes >40°N, with an abrupt and highly significant ($\chi^2_1 = 434$, $P < 0.001$) shift to the striped skunk as the most common non-target >44°N. We did not include recaptured raccoons ($n = 2{,}669$) in this analysis, but they would have ranked third behind opossums at 20–30°N ($n = 122$) and 30.1–40°N ($n = 863$) and second ahead of the opossum at >40°N ($n = 1{,}684$). Opossums and skunks were numerically the primary potential bait competitors (Table 6).

At 20–30°N latitude, the ratio of unique raccoons:potential bait competitors was 0.8, whereas raccoon and opossum captures were equal. At 30.1–40°N, raccoons:potential bait competitors was 2.0, with 2.1 raccoons:opossum. At >40°N, raccoons:potential bait competitors was 3.9 and raccoons to opossum captures increased to 7.5 raccoons:opossum. At >44°N as a subset of >40°N ($n = 88$ density indexing events, $n = 2{,}588$ animals, only 5 opossums were captured), raccoons:potential bait competitors was 3.2, and we captured 358 unique raccoons/opossum.

We captured more unique raccoons than non-targets in 77% ($n = 194$) of density indexing events. Events where non-targets exceeded raccoon captures were 43.0% of group A, 20.2% of group B, 6.5% of group C, and 4.3% of group D.

Land Cover Associations

Differences ($P < 0.05$) occurred between density indexing sites and the 5-km buffers for 7 of 15 land cover types (Table 7). The effect was small for all land cover types but approached a moderate effect ($r \geq 0.3$; Field and Miles 2010) at $r = 0.25$ for grasslands and open water. Both represented only 1.8–4.6% of index or buffer areas.

The random effects of state and event nested within locale had high importance on RDI (cumulative w_i for both = 1.00), whereas year and month were relatively uninformative (cumulative w_i of 0.25 and 0.26, respectively). There were 4 fixed effects that met or exceeded the 0.5 cutoff for variable importance (Burnham and Anderson 2002). These were evergreen cover (cumulative $w_i = 0.88$),

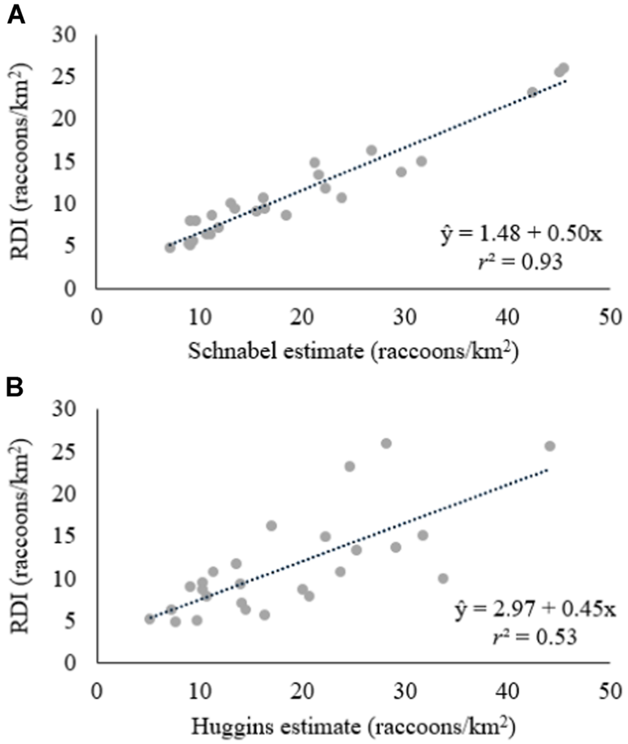

Figure 2. Linear relationship between raccoon density indexes (RDIs; raccoons/km^2) and Schnabel (A) and Huggins (B) mark-recapture model population density estimates (raccoons/km^2) that we calculated for 26 of the 253 RDIs conducted in 18 eastern states, USA, 1997–2011.

elevation (cumulative $w_i = 0.84$), deciduous cover (cumulative $w_i = 0.59$), and developed area (cumulative $w_i = 0.50$). The negative trend was strongest for increasing percent evergreen cover ($\beta = -1.32$, 95% CI $= -2.06$–-0.58; Fig. 4). For example, the effect of a change in evergreen cover from 20% to 30% related to a decrease in RDI of 1.5 raccoons/km^2. Raccoon density index decreased as deciduous cover increased ($\beta = -0.43$, 95% CI $= -1.02$–0.16), but the effect was less than for evergreen cover. By comparison, the effect for a change in deciduous cover from 20% to 30% related to a decrease in RDI of 0.6 raccoons/km^2. Raccoon density index increased as developed area increased ($\beta = 0.30$, 95% CI $= -0.46$–1.06). The effect for a change in developed area from 20% to 30% related to an increase in RDI of 0.4 raccoons/km^2. We observed the highest RDIs in elevations <500 m (Fig. 4). The effect of an increase in elevation from 200 m to 600 m related to a decrease in RDI of 3.7 raccoons/km^2. The estimated effect of parameters shown as examples are not constant rates of change because of nonlinear relationships among covariates. Percent agriculture and latitude were not supported as relatively important covariates (cumulative w_i of 0.41 and 0.25, respectively). The positive relationship with percent developed and the negative relationship for percent evergreen forest were more pronounced with RDIs within density groups (Fig. 5).

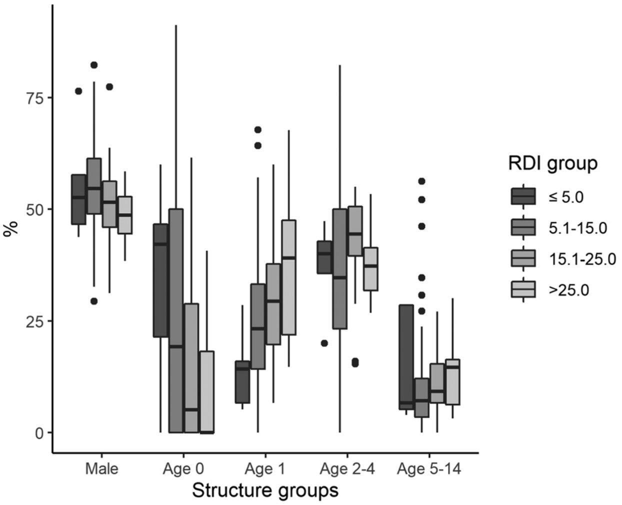

Figure 3. Boxplots of percentages of males by raccoon density index (RDI) group and percentages of age classes by RDI group for 253 raccoon density measures conducted in 18 eastern states, USA, 1997–2011.

DISCUSSION

Our density index approach provided the sensitivity required to aid in rabies management decisions. That RDIs were lower when compared to our density estimates from Schnabel and Huggins models, except for the West Virginia Wetzel site in 2006, was not unexpected given that unique captures represented a minimum number of raccoons/area during a 10-day sampling interval. The disparity between RDIs and Huggins estimates generally increased at higher raccoon abundance. In a comparison study exploring calibration of RDIs, Beasley et al. (2012) reported that on average RDIs used by Wildlife Services were 48% lower than mark-recapture estimates in fragmented agricultural areas in north-central Indiana, USA. However, from a rabies management perspective, 20 of our 26 density groups aligned with bait densities suggested by both mark-recapture estimates.

Capture rates were generally lower, often significantly, following the first 5 days of sampling and continued to decline or level off for extended 15-day and 20-day events. Decline in unique individuals captured over short sampling intervals is not as pronounced for raccoons as may be expected in small-mammal populations, where estimates from regression removal models may be appropriate (Slade and Blair 2000). The 5-day protocol evolved from 10-day trapping efforts that produced few captures during days 1–5 and no or few captures from days 6–10; none of these RDIs would have shifted above density group A, saving staff time for density indexing without an effect on RDI. In areas supporting higher raccoon numbers, there were sufficient captures beyond 10 days to meet the 15-day protocol, although capture rates also declined on days 10–15 (Table 2).

Our protocol forced trap movement every 2–3 days if a unique raccoon was not captured to better ensure trap coverage in the indexing area. Although this resulted in 50 traps distributed on average at 125.1 locations/site on the 87 sites, nearest neighbor analysis indicated trap clustering on 37 of 87 sites. Clustering was deemed low to moderate and had no major effect on RDI. The low to moderate trap clustering defined by nearest neighbor analysis often reflected avoidance of open pastures and hay fields in favor of wooded

Table 5. Sex ratios (shown as males/female) by age cohort and density groups for 5,643 unique raccoons of known specific age from cementum annuli determination that we captured during 253 raccoon density indexing (RDI) events conducted in 18 eastern states, USA, 1997–2011.

		Age 0 juveniles		Age 1 yearlings		Age 2–4 adults		Age 5–14 older adults	
Density group (raccoons/km^2)	***n* RDI events**	**Ratio**	***n***	**Ratio**	***n***	**Ratio**	***n***	**Ratio**	***n***
A (0.0–5.0)	70	1.1	49	1.6	87	1.8	153	0.9	37
B (5.1–15.0)	129	1.1	735	1.4	648	1.4	930	0.9	221
C (15.1–25.0)	31	1.0	258	1.2	314	1.1	438	0.9	113
D (>25.0)	23	1.1	185	1.1	505	1.0	699	0.6	271
Total	253	1.1	1,227	1.3	1,554	1.2	2,220	0.7	642

areas, followed by trapping along road access. Future trapping protocols should be designed to prevent clustering.

Juveniles represented 22% of our specific age sample. Other studies (Hoffmann and Gottschang 1977, Leberg and Kennedy 1988, Prange et al. 2003) have reported the juvenile cohort accounting for 35–50% of populations. Males were more common than females from ages 1–4. Sex ratios favoring males due to catchability bias have been suggested (Schneider et al. 1971, Gehrt and Fritzell 1996) and may reflect, in part, the lower adult female representation we observed from ages 1–4 because adult females travel with juveniles in family groups. Our age ratios are suggestive of high juvenile mortality for density groups A and B. Raccoon numbers fell off markedly past the age of 4, which is not uncommon among raccoon age structure for largely rural-derived samples (Rosatte 2000, Prange et al. 2003). Recent field trials showed an asymptotic population immune response after 2 consecutive years of ORV baiting (Gilbert et al. 2018), highlighting the value of understanding sex and age structure and dynamics to further support decisions regarding when baiting may cease in an area to achieve raccoon rabies elimination. Our survivorship rates based on 4 sites were lower than expected (Supplemental Discussion, available online in Supporting Information).

In general, the proportion of non-targets to unique raccoons may be inflated because of inconsistent marking. Nevertheless, the opossum accounted for an increasing proportion of captures along a north to south latitudinal gradient, ranging from 10% (>40°N) to 43.1% (<30°N), with 28.1% at mid-latitudes, underscoring its potential as a bait competitor. Factoring the effect of non-targets, and opossums in particular, remains a critical issue in formulating more effective baiting strategies, with perhaps less concern in rural areas northeast of the Appalachian Mountains. Moreover, potential bait competitor effects may increase in importance as ORV moves east at middle and southern latitudes to lower elevations that likely support robust raccoon and opossum populations (McKeever 1959, Olson and Werner 1999, Olson et al. 2000). Given the relative importance of opossums as a potential bait competitor, future bait competition studies should evaluate all 3 vaccine baits currently used (RABORAL V-RG fishmeal polymer and coated sachet baits [Boehringer Ingelheim Animal Health USA, Duluth, GA, USA], and ONRAB Ultralite bait [Artemis Technologies, Guelph, Ontario,

Table 6. Summary of unique raccoon and non-target captures by latitude, not including 2,669 recaptured raccoons, for 253 density indexing events conducted in 18 eastern states, USA, from 1997–2011; number of indexing events in parentheses.

			Captures by latitude									
	Total captures ($n = 253$)		20–30°N ($n = 3$)		30.1–40°N ($n = 100$)		>40°N ($n = 150$)		≤44°N ($n = 165$)		>44°N ($n = 88$)	
Species	***n***	**%**	***n***	**%**	***n***	**%**	***n***	**%**	***n***	**%**	***n***	**%**
Raccoon	8,415	68.0	213	43.5	2,660	60.2	5,542	74.3	6,627	67.8	1,788	69.1
Virginia opossum	2,194	17.7	211	43.1	1,244	28.2	739	9.9	2,189	22.4	5	0.2
Striped skunk	536	4.3	0		42	1.0	494	6.6	124	1.3	412	15.9
Woodchuck (*Marmota monax*)	382	3.1	0		225	5.1	157	2.1	356	3.6	26	1.0
Squirrels (*Sciurus* spp. and *Tamiasciurus* sp.)	179	1.4	0		21	0.5	158	2.1	100	1.0	79	3.1
Domestic cat	138	1.1	3	0.6	45	1.0	90	1.2	75	0.8	63	2.4
Cottontail (*Sylvilagus floridanus*)	136	1.1	2	0.4	80	1.8	54	0.7	116	1.2	20	0.8
Turtles (sub-order Cryptodira)	76	0.6	5	1.0	57	1.3	14	0.2	73	0.7	3	0.1
Snowshoe hare (*Lepus americanus*)	69	0.6	0		0		69	0.9	0		69	2.7
Foxes	61	0.5	49	10.0	6	0.1	6	0.1	61	0.6	0	
Fisher (*Martes pennanti*)	45	0.4	0		0		45	0.6	1	0.0	44	1.7
Muskrat (*Ondatra zibethicus*)	18	0.1	0		1	0.0	17	0.2	1	0.0	17	0.7
Pine marten (*Martes americana*)	16	0.1	0		0		16	0.2	0		16	0.6
Armadillo (*Dasypus novemcinctus*)	16	0.1	7	1.4	9	0.2	0		16	0.2	0	
Miscellaneous	86	0.7	0		27	0.6	59	0.8	40	0.4	46	1.8
Non-target total	3,952	32.0	277	56.5	1,757	39.8	1,918	25.7	3,152	32.2	800	30.9
Potential bait competitors total[a]	3,024	24.5	263	53.7	1,356	30.7	1,405	18.8	2,471	25.3	553	21.4
Grand total	12,367		490		4,417		7,460		9,779		2,588	

[a] Potential bait competitors included black bears (*Ursus americanus*), domestic cats, domestic dogs, fishers, foxes, pine martens, minks (*Mustela vison*), opossums, rats (*Sigmodon* spp., *Rattus* spp., and *Neotoma* spp.), eastern spotted skunks (*Spilogale putorius*), striped skunks, and weasels (*Mustela* spp.).

Table 7. Results from the Wilcoxon 2-sample test comparing National Rabies Management Program land cover composition (derived from GAP and LANDFIRE data) between the raccoon density indexing site and its buffer area for the 160 unique sites in 18 eastern states, USA, 1997–2011.

Land cover	W_s[a]	*P*	*Z*	*R*[b]	*n* sites	*n* buffer area	Median site area (km^2)	Median buffer area (km^2)	% of site ($\bar{x}$)	% of buffer ($\bar{x}$)
Cultivated cropland	11,257.5	0.220	0.77	0.05	104	105	0.4	10.1	13.2	9.3
Pasture or hay	15,227.5	0.211	−0.80	−0.05	125	125	0.6	17.7	19.8	16.5
Deciduous forest	20,237	0.002	2.91	0.18	136	135	0.7	32.4	24.4	29.3
Evergreen forest	2,208	0.363	0.35	0.04	47	46	0.5	15.5	15.4	14.6
Mixed forest	19,188	0.011	−2.29	−0.14	144	144	0.7	29.6	24.6	27.8
High developed	1,526.5	0.446	−0.13	−0.02	39	39	0.1	2.3	3.5	2.1
Medium developed	6,091	0.097	1.30	0.11	77	75	0.1	3.4	4.5	3.4
Low developed	13,078.5	0.034	0.07	0.00	111	110	0.2	8.4	6.6	7.9
Open space	20,899	0.013	−2.23	−0.13	150	150	0.2	9.1	8.2	8.5
Woody wetlands	13,914.5	0.031	−1.87	−0.12	122	122	0.2	5.7	6.1	5.8
Shrub or scrub	4,055	0.065	−1.52	−0.13	66	66	0.1	2.1	2.9	2.1
Herbaceous wetlands	18,891	0.228	−0.74	−0.04	139	139	0.2	4.9	5.7	5.0
Grasslands	7,406	0.001	3.13	0.25	81	80	0.1	2.6	1.8	3.2
Open water	610	0.008	2.42	0.25	84	9	0.0	0.2	2.6	4.7
Barren and miscellaneous	954	0.154	1.02	0.13	31	29	0.0	0.6	0.4	0.8

[a] Wilcoxon statistic.

[b] Effect size estimate for the Wilcoxon rank sum test.

Canada]) in the United States, including evaluation of sero-prevalence pre- and post-ORV for fixed bait density and distribution patterns in relation to areas with varying opossum:raccoon ratios to establish a baseline for potential baiting modifications.

In a north-central Indiana study using placebo fishmeal polymer baits (1 of 2 bait options to deliver RABORAL V-RG vaccine) containing Rhodamine B biomarker, Smyser et al. (2010) reported opossums to be more efficient *per capita* consumers of ORV baits with their

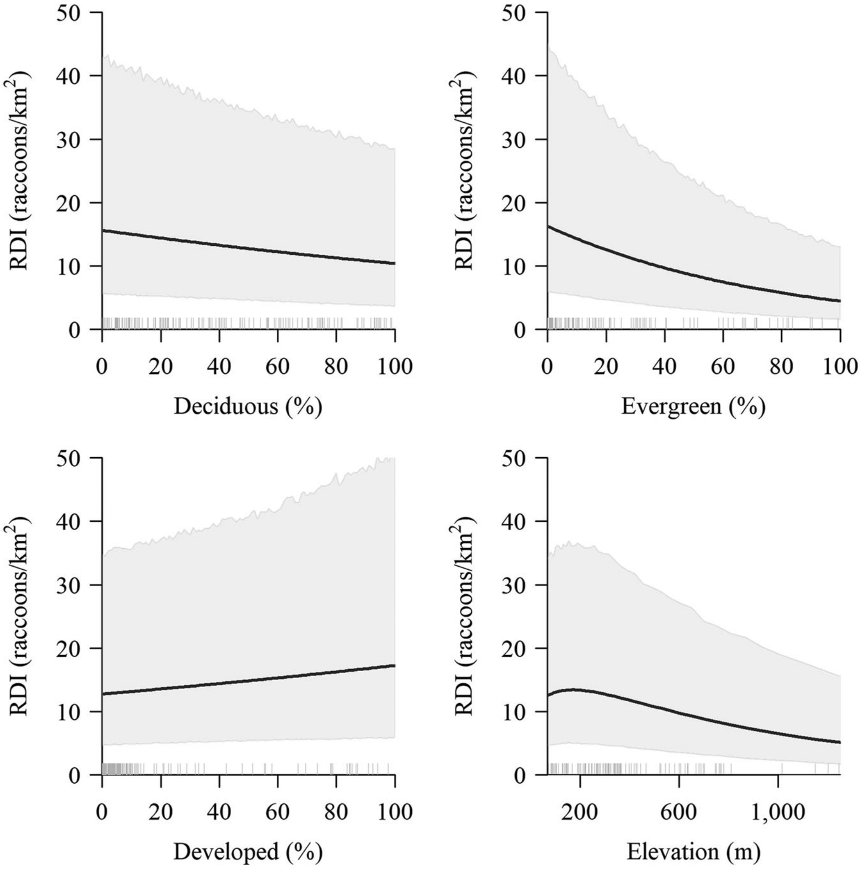

Figure 4. Land cover and elevation relationships with raccoon density indexes (RDI; raccoons/km^2) based on 253 raccoon density measures conducted in 18 eastern states, USA, 1997–2011. Predicted relationships between RDI and each plotted covariate are shown using the mean of all other covariates. Shaded regions are 95% confidence intervals. The distribution of these covariates in the dataset are shown graphically as rugs (vertical tick marks along the x-axis).

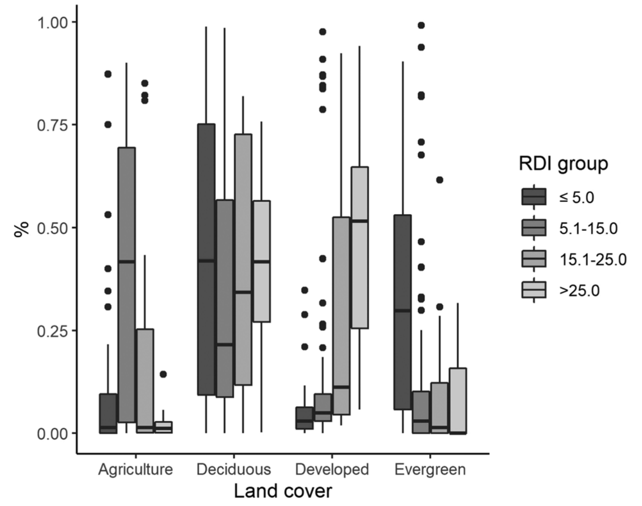

Figure 5. Boxplots of land cover distributions by raccoon density index (RDI) group for 253 raccoon density measures conducted in 18 eastern states, USA, 1997–2011.

abundance among multiple factors that influenced patterns of bait acceptance between raccoons and opossums. Results from Smyser et al. (2010) point toward targeting specific habitat patches to reduce competition with opossums or alternatively concentrating baits where raccoons are more likely to encounter them (Beasley and Rhodes 2010, Boyer et al. 2011, Beasley et al. 2015). Raccoons demonstrated an affinity for forests or forest patches in a highly fragmented agricultural landscape in Indiana, with seasonal activity shifts to corn-dominated croplands (Beasley and Rhodes 2008, Beasley and Rhodes 2010). Campaigns to eliminate raccoon rabies from the St. Lawrence River valley in Quebec is perhaps the best example of an ORV success in targeting raccoon preferred habitats in a fragmented agricultural landscape (Boyer et al. 2011). Given that ORV in the United States has been largely conducted in forested areas, targeting has been to date mostly confined to urban-suburban areas or edges of these land cover types where ground and helicopter baiting are practical alternatives to fixed-wing bait distribution.

Non-target striped skunks represent another potential bait competitor; however, they are commonly infected with rabies virus spillover from the raccoon (Wallace et al. 2014) that may help maintain this rabies variant in the wild (Guerra et al. 2003). Consequently, bait uptake by skunks is viewed as an opportunistic byproduct of ORV targeting raccoons. Unfortunately, current vaccine baits have not achieved levels of rVNA in skunk populations in the field (Fehlner-Gardiner et al. 2012, Mainguy et al. 2013, Slate et al. 2014) thought necessary for control.

Coniferous forest was commonly associated with RDIs in density group A. As ecological generalists, raccoon home ranges may contain a variety of land cover types, including conifers (Chamberlain et al. 2003). Mature hardwoods have been recognized as important in these pine-dominated (*Pinus* spp.) landscapes for hard mast and den sites for raccoons (Kirby et al. 2016). Short controlled burning schedules common in southeastern pine stands substantially reduced use by raccoons, particularly on annual (Jones et al. 2004) or 2–3-year burn cycles (Chamberlain et al. 2003). As ORV moves east onto the coastal plains in the southeastern United States, a comprehensive understanding of raccoon density in managed and unmanaged pine forests at more refined scales (Chamberlain et al. 2002, 2003) may be required to optimize ORV baiting strategies (Algeo et al. 2017).

Areas dominated by a mixture of deciduous forest and development (low and developed open space based on NRMP classifications), with interspersed agriculture were more characteristic of densities in groups B and C. The negative effect of deciduous cover on RDI in our analysis may be inflated given the well-documented importance of deciduous trees to raccoons (Stuewer 1943, Kirby et al. 2016). Raccoon densities based on large-scale mark-recapture studies ($n = 154{,}416$ raccoon captures) in southern Ontario from 1994–2007 (Rosatte et al. 2010) had similar land covers to density group B (5.1–15.0 raccoons/km^2; $n = 129$), with mean densities in Ontario rural areas averaging 10.3 raccoons/km^2 and urban cells averaging slightly higher at 12.1 raccoons/km^2. Developed areas (predominantly low and developed open space) interspersed with deciduous land cover generally supported the highest RDIs in group D. Urban-suburban settings frequently support high, often exceptional raccoon numbers in comparison to many rural environments (Schinner and Cauley 1974, Riley et al. 1998, Prange et al. 2003). Such areas have proven to be challenging for ORV effectiveness perhaps in part because of anthropogenic foods (Prange et al. 2003) that are more attractive to raccoons than ORV baits. Four sites (2 each from WV and VA) from the top 10 with respect to percent of developed areas (85–98%) had RDIs that ranged from 4.0 to 8.8 raccoons/km^2 with 3 within density group A, suggesting caution when extrapolating across urban-suburban settings with respect to sustained exceptional densities.

Habitat at higher elevations generally supported RDIs of $\leq$5 raccoons/km^2. These sites were largely forest-dominated on acidic, nutrient-poor soils, often interspersed with exposed, rocky substrate (U.S. Geological Survey 2016). However, oaks (*Quercus* spp.) and other hard mast producing species were often present in West Virginia, Virginia, and North Carolina, with eastern hemlock (*Tsuga canadensis*) and other hardwoods. Northern hardwoods, hemlock, and spruce-fir (*Picea* spp. and *Abies balsamea*) were common on forested northern sites (U.S. Geological Survey 2016). We recommend additional indexing in high-elevation forests in the eastern United States to validate the pattern of low RDIs we observed based on only 4 events >1,000 m in elevation. At low elevations on sites where pine, pine-oak, managed pine plantations, or pine barrens occurred from coastal Massachusetts to the south generally supported low RDIs. Low-elevation sites dominated by spruce-fir and northern hardwoods in the north also generally supported low RDIs.

A measure of raccoon density is fundamental for making ORV baiting decisions against which population immune responses can be evaluated to determine if rabies management goals were achieved. Previous studies have discussed concerns regarding rVNA population levels from ORV with RABORAL V-RG® to meet rabies management goals in the context of raccoon and bait densities (Blackwell et al. 2004, Ramey et al. 2008, Pedersen et al. 2019). A strong immune response in recent field trials with an experimental oral vaccine bait ONRAB at 75 baits/km^2 in predominantly mixed forests in West Virginia (Slate et al. 2014) and northern New York, Vermont, and New Hampshire (Gilbert et al. 2018) indicated the importance of vaccine bait type rather than insufficient bait densities relative to RDIs at these locations. Raccoon density indexes from West Virginia were predominantly from density group B, whereas RDIs from New York, Vermont, and New Hampshire were within groups A ($n = 16$), B ($n = 46$), and C ($n = 3$), all within the currently recommended 75 baits/km^2. Additional ONRAB field trial results are needed to further evaluate the effect of vaccine bait type and other pertinent variables in relation to RDI, bait density, and the immune response deemed necessary for raccoon rabies elimination. Greater insight into habitat characteristics and potential bait competitor effects as a complement to RDI should be sought to enhance future baiting decisions and strategies. Modeling to determine if land cover type may be an effective surrogate for RDI for ORV baiting plans is a direction to be contemplated in the future.

MANAGEMENT IMPLICATIONS

The 4 density groups were an appropriate scale to aid in ORV baiting decisions based on modeling results, RDI alignment with bait densities suggested by mark-recapture, and in light of current limitations to execute refined bait density adjustments in real time by fixed-wing aircraft over rapidly changing landscapes. Potential bait competition may be addressed by targeting obvious habitat fragments preferred by raccoons to maximize their bait uptake and minimize non-target bait consumption (e.g., targeting forest patches and edges in landscapes dominated by agricultural crops may be effective when crops are not attractive). Increasing bait densities to mitigate potential bait competitors remains an option when target and non-target population information is available and raccoon habitat targeting is not practical. Evergreen forests that supported low RDIs place emphasis on the need for adaptive baiting strategies. For example, sizeable islands of pines used infrequently by raccoons may be baited at lower bait densities, only along edges, along bisecting drainage travel corridors at more concentrated bait densities, or bypassed completely. Such baiting strategies could conserve resources (baits represent the single greatest cost associated with ORV at $1.25–1.50/bait) for application at other priority areas.

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