Note

Seroconversion of Raccoons Following Two Oral Rabies Vaccination Baiting Strategies

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ABSTRACT Seroprevalence of rabies virus neutralizing antibodies (rVNA) in raccoons (*Procyon lotor*) following oral rabies vaccination (ORV) with RABORAL V-RG® in the United States has annually averaged 30% since 1997, a level that is unlikely to successfully interrupt rabies transmission in raccoon populations. A longitudinal ORV zone is maintained in the eastern United States with raccoon variant rabies established east of the zone but absent to the west. However, questions remain regarding the effect of the bait application strategy towards achieving optimal population immunity. We estimated the number of ORV baits/km^2 of raccoon home range and calculated rVNA seroprevalence following 2 ORV baiting strategies: cluster baiting (≤10 baits dropped at a time) via helicopter and hand distribution of individual baits at regular intervals along roads and trails in suburban Chattanooga, Tennessee, USA, during fall 2013 and 2014. We applied baits at 75 baits/km^2 under both strategies. We established 6 1-km^2 cells in each treatment area, and fitted ≤2 raccoons with global positioning system collars in each cell. We trapped and sampled ≤25 raccoons in each study cell pre- and post-ORV application for rVNA analysis. Overall raccoon home range and core area estimates were 80.7 ha and 17.5 ha, respectively ($n = 36$). Average bait application for home ranges ($n = 32$ home ranges that received bait) was 80.9 baits/km^2 for helicopter baiting and 63.6 baits/km^2 for hand baiting sites. Average bait application for core areas was 104.7 baits/km^2 for helicopter baiting and 69.2 baits/km^2 for hand baiting sites. All home ranges were baited in both treatment areas, whereas 10/18 and 13/14 core areas were baited in the helicopter and hand distribution sites, respectively. Overall, helicopter cluster ORV delivered more baits/km^2 of raccoon home range than hand distribution but was less effective in reaching core areas. Seroprevalence did not change as a function of baiting strategy (helicopter vs. hand baiting). The average overall increase in seroprevalence following ORV application was 8.9%. Evaluation of additional strategies are needed because both methods failed to achieve herd immunity necessary to disrupt rabies transmission in raccoons. © 2017 The Wildlife Society.

KEY WORDS oral rabies vaccination, *Procyon lotor*, rabies, raccoon, suburban, Tennessee.

In the late 1970s, raccoon rabies virus variant (RRV) was found in a raccoon (*Procyon lotor*) that had been translocated to West Virginia, USA and since the mid 1980s, RRV has spread throughout the eastern United States, into regions of Ohio and Tennessee (Rupprecht and Smith 1994, Krebs et al. 2005). Since 1997, the United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services has conducted cooperative oral rabies

vaccination (ORV) programs throughout the eastern United States to prevent the spread of RRV (Slate et al 2005). However, questions remain regarding the effectiveness of current ORV baiting strategies in vaccinating a sufficient proportion of the raccoon population to eliminate RRV transmission.

The only oral rabies vaccine currently licensed for use in wildlife in the United States is RABORAL V-RG (Merial Inc., Athens, GA, USA). Although vaccination thresholds have not been established for eliminating rabies in free-ranging raccoons, seroconversion rates in raccoons following ORV application using RABORAL V-RG were approximately 30% from 1997 to 2007 (Slate et al. 2009), well below

the threshold of 60–90% generally recommended to interrupt rabies virus transmission (Thulke and Eisinger 2008, Rees et al. 2013, Reynolds et al. 2015). In urban and suburban ecosystems, Robbins et al. (1998) suggested vaccination rates of 63% may be sufficient to halt the spread of raccoon rabies via ORV distribution and Rosatte et al. (2009) suggested up to 79% vaccination was required during trap-vaccinate-release programs. Currently it is unknown whether the observed seroconversion rate is due to the vaccine performance in field situations, lack of access by target species to the vaccine-bait, non-target bait competition (but see Olson et al. 2000 for a discussion of ORV consumption by Virginia opossums [Didelphis virginianus], gray foxes [Urocyon conereoargenteus] and feral cats [Felis catus]), overall unattractiveness of the bait itself, or incomplete bait ingestion (i.e., consuming only the outer coating while leaving the vaccine sachet intact).

Operationally in the United States, ORV baits are distributed at a bait density of 75 baits/km^2, or alternatively 150/km^2 under special circumstances such as in response to an outbreak, along sensitive border areas, and in habitats with demonstrated higher raccoon densities (e.g., some suburban areas). Bait application is performed by distributing individual baits at regular intervals along transects via fixed-wing aircraft, helicopter, or by hand along established roads, trails, and other walkways. Research suggests the current baiting strategies are similar with respect to seroconversion rates. Boulanger et al. (2008) reported no difference in antibody response in raccoons among ORV distribution by helicopter, hand distribution, or bait stations (which provide a continuous and clustered source of ORV baits) in a suburban environment. Sattler et al. (2009) evaluated seroconversion among 3 different application rates (75, 150, and 300 baits/km^2) using helicopter and hand-vehicle bait distribution but did not differentiate between methods (~84% of baits were aerially distributed), only application rates. Blackwell et al. (2004) suggested that when distributed at a density of 75 baits/km^2, an average of 3.3 baits/raccoon was consumed, but these results were not confirmed relative to raccoon density and remain largely speculative. Further, Beasley et al. (2015) suggested the use of resource selection data to target specific land cover types did not increase ORV uptake in regions evaluated.

The aforementioned studies provide insight into ORV bait uptake under current baiting strategies in a variety of land cover types and, in some cases, application rates. However, they do not consider uptake under a clustered bait distribution strategy where multiple baits are aerially distributed at a lower distribution frequency than single baits but at the same overall density. Clustered resources may cause some species to alter their space use to include that resource and possibly result in increased resource consumption. For example, Wehtje and Gompper (2011) reported increased spatial overlap among female raccoons in response to experimentally placed clumped food resources. Campbell and Long (2007) reported feral pigs (Sus scrofa) removed baits in a clustered arrangement at a higher rate than expected. In

New Zealand aggregated distribution of compound 1080 (sodium fluoroacetate) was reported to be as effective as broadcast applications in controlling brushtail possum (Trichosurus vulpecula) populations (Nugent et al. 2012). In Ohio, ORV baits distributed in clusters of 8 baits every 13 seconds resulted in higher seroconversion rates, particularly among juvenile raccoons, than a single bait distributed every 2 seconds (U.S. Department of Agriculture [USDA] unpublished data). Comparing seroprevalence and bait availability following aerial cluster baiting versus hand broadcast baiting strategies may provide insight into which strategy may be more effective in achieving the desired population immunity in target wildlife in a suburban environment.

Our objectives were to evaluate rVNA seroprevalence in raccoons pre- and post-ORV distribution via cluster baiting from helicopter and hand distribution of single baits and evaluate ORV bait availability in raccoon home ranges under each baiting strategy. We hypothesized aerial cluster baiting would provide more complete bait coverage and, thus, higher seroconversion rates than hand distribution.

STUDY AREA

We conducted this study in Chattanooga, Hamilton County, Tennessee during summer and fall 2013 and 2014. We established a northern and southern study site. Both sites have a history of annual ORV application with an average seroprevalence of 33.3% following application at 75 baits/km^2 between 2008 and 2012 (USDA National Rabies Management Program [NRMP], unpublished data). Study sites were separated by the Chickamauga River and Chickamauga Lake to reduce potential raccoon movement between study sites (Fig. 1). Each site consisted of a heterogeneous mixture of low to moderate intensity development, interspersed with deciduous and evergreen forest. Chattanooga has a temperate climate with average temperatures ranging from −0.5°C in January to 32.2°C in July. Average annual rainfall is 1,332 mm, which falls throughout the year. In addition to raccoons, local fauna includes opossums, striped skunks (Mephitis mephitis), gray fox, coyote (Canis latrans), beaver (Castor canadensis), muskrat (Ondatra zibethicus), white-tailed deer (Odocoileus virginianus), and various small mammals. The northern study site consisted primarily of deciduous forest (33.4%), large areas of open water (22.4%), and developed open space (9.3%). The southern study site consisted primarily of developed open space (36.1%), low intensity development (18%), and deciduous forest (12.6%; USDA 2011).

METHODS

Capture and Handling
We live captured raccoons up to 12 weeks prior to and 5–6 weeks following ORV bait application using cage traps (Tomahawk Live Trap, Hazelhurst, WI, USA) baited with marshmallows and fruit extract. We immobilized each captured raccoon via intramuscular injection of 5:1 ketamine:
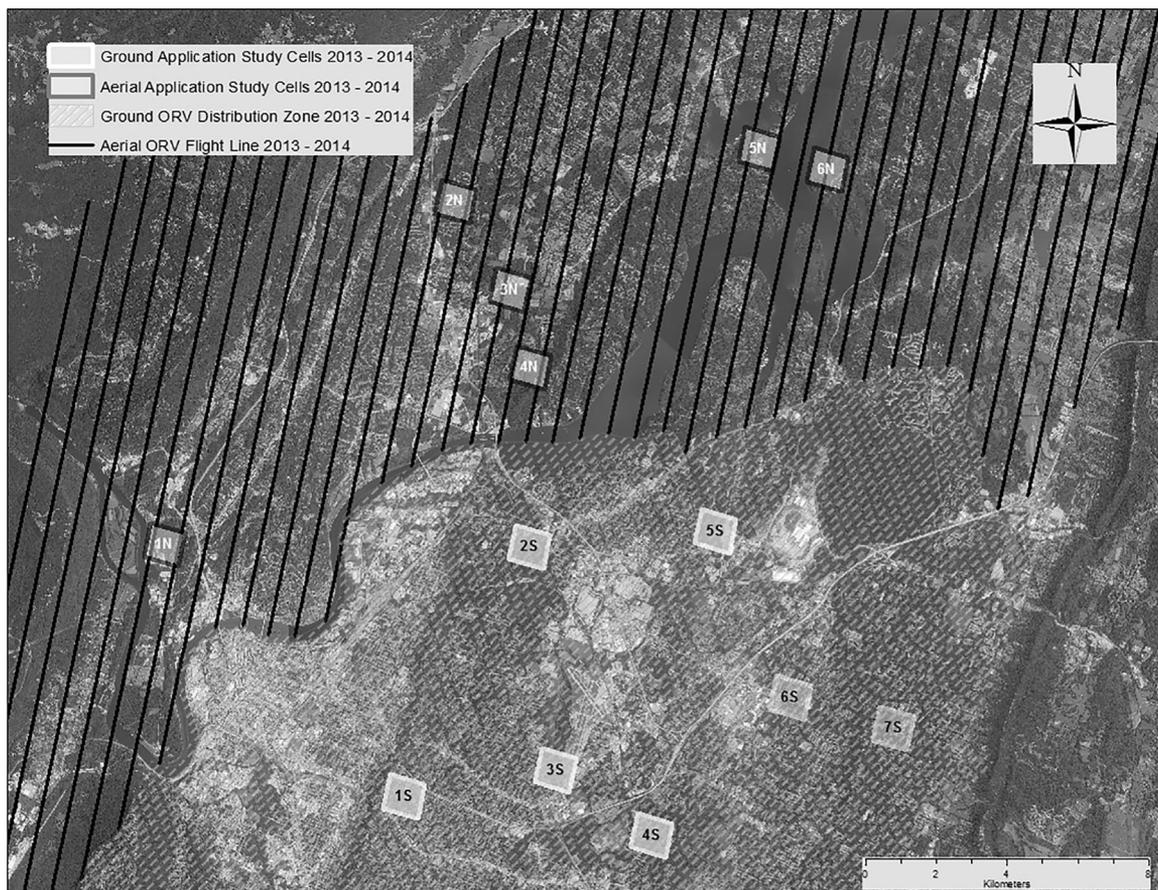
Figure 1. Flight lines and locations of oral rabies vaccination (ORV) aerial and hand broadcast study cells, Chattanooga, Tennessee, USA, 2013–2014.

xylazine (Kreeger and Arnemo 2007), applied uniquely labeled metal ear tags, and collected up to 3.0 ml of whole blood from each raccoon via venipuncture of the jugular vein. We centrifuged blood samples, transferred serum to cryovials, and froze them. Upon initial capture, we fitted ≤ 2 raccoons (1 M, 1 F) in each cell with a radio-collar equipped with a global positioning system (GPS; Telonics, model TGW-4200-2, Mesa, AZ, USA and Telemetry Solutions, model Quantum 4000E, Concord, CA, USA). We programmed the collars to record a GPS location every 30–60 minutes for approximately 3 months, starting approximately 4 weeks prior to planned ORV bait application. We deployed store-on-board collars requiring collar retrieval for data collection in 2013 and collars with remote download capability in 2014. All capture and handling of animals was approved by the National Wildlife Research Center's Institutional Animal Care and Use Committee under research protocol QA-2178.

Bait Application

We applied baits aerially and by hand distribution at a rate of 75 baits/km² during annual operational ORV. We baited the northern study site with coated sachet baits by helicopter and hand-baited the southern site with fishmeal polymer baits while on foot or from vehicles. In each study site, we established 6 1-km² cells for raccoon serologic sampling and radio-collaring (Fig. 1). We moved 1 hand-baited study cell

approximately 1.5 km southeast between 2013 and 2014 because of heavy construction.

We conducted aerial application by helicopter flying along transects spaced 750 m apart (Fig. 1) and depositing 1 bait approximately every 18 m, until we encountered study cells. When flying over study cells, we suspended the normal distribution method and applied baits in clusters of 10, with 178 m between clusters. In addition, we baited a 750-m (1 flight transect) buffer zone surrounding each 1-km² study cell to ensure each cell was adequately baited. We distributed baits by hand approximately every 25 m into raccoon habitat while driving along roads or walking established walking paths. During aerial broadcast over the individual study cells, we predetermined the location of each bait cluster and entered coordinates into the aircraft's GPS. During hand distribution, we recorded in a handheld GPS the location from which we threw the bait from the vehicle. Because we conducted bait application during a large-scale operational ORV distribution program, we recorded the location of bait clusters only when applying bait over the individual study cells, with a 750-m buffer surrounding each cell to account for potential raccoon movements outside the study cell borders.

We entered bait locations into ArcGIS (version 10.1; ESRI, Redlands, CA, USA). To account for bait separation during aerial application of bait clusters, we generated a 25-m buffer around each cluster location in ArcGIS. We based the

25-m distance on the mean distance from the bait drop location (recorded by the bait applicator in the helicopter) to the actual bait locations on the ground during a mock bait application performed under operational conditions (i.e., flight speed and altitude) prior to field operations. Buffer zones that intersected the perimeter of a home range or core area had 5 baits (50%) assigned as inside the home range or core area.

Data Analysis

We shipped frozen serum samples to the Centers for Disease Control and Prevention (Atlanta, GA) for rabies virus neutralizing antibody (rVNA) analysis via rapid fluorescent focus inhibition test (RFFIT; Smith et al. 1996). We considered raccoons with RVNA titers ≥ 0.05 IU/mL seropositive. We calculated seroprevalence for each cell by dividing the number of seropositive animals by the total captured in that cell. We determined overall seroprevalence by calculating the mean seroprevalence for cells in each study area, pre- and post-vaccination. We used a generalized linear mixed model (function LMER in package LME4, program R; Bates et al. 2015) to compare the difference between seropositive proportions pre- and post-ORV application, with study cells as random effects nested within each treatment area and bait strategy and year as fixed effects (Zuur et al. 2009). To account for unequal sample size, we weighted the cell values based on the number of animals sampled in each cell. We ranked models using Akaike's Information Criterion corrected for small sample sizes (AIC$_c$; Burnham and Anderson 2002) and considered models within 2 ΔAIC$_c$ from the top model as competitive.

We evaluated GPS relocations of each collared raccoon for accuracy by visual inspection and dilution of precision of each relocation (Berentsen et al., 2014), and removed all inaccurate relocations from further analysis. We used the adehabitat statistical package in program R (R Foundation for Statistical Computing, Vienna, Austria) to calculate utilization distributions (UDs) for each collared raccoon and determine the home range size at the 50% (core) and 95% (overall) contours and to estimate the number of baits that were dropped within the core and overall home ranges. We used the biased random bridge movement-based kernel density estimator (MKDE; Benhamou 2011) to calculate the UDs and extract the areas of the core and overall home range contours. Using the MKDE for our data allowed us to use all accurate GPS relocations because the MKDE accounts for serial correlation of consecutive relocations, periods of inactivity, and locational error associated with GPS relocations (Cornélis et al. 2011). We log-transformed mean core and overall home range sizes and mean baits/km^2 of home range and core area and compared means using the GLM procedure in SAS (SAS Institute, Cary, NC, USA). We considered results statistically significant when $P < 0.05$.

RESULTS

We collected sera from 535 raccoons prior to vaccination during 2013–2014, 80 of which were seropositive. Following ORV application, we sampled 579 raccoons, 139 of which were seropositive. The overall average increase in seroprevalence following ORV application was 8.9% ($\pm 11\%$ [SE]; Table 1). Seroprevalence did not change as a function of baiting strategy or year (Table 2). Year showed a weak negative effect ($\beta = -0.05 \pm 0.04$ [SE]).

We fitted 43 raccoons with GPS collars (18 store-on-board in 2013, 25 remote-download in 2014). We did not recover 3 store-on-board collars and recovered 1 with insufficient data following mortality. One remote-download collar malfunctioned and we lost contact with 2 additional collars for unknown reasons a few weeks after deployment. We retrieved sufficient data to calculate home range estimates from 36 collars: 14 (10 M, 4 F) in 2013 and 22 (11 M, 11 F) in 2014.

Mean overall home range was 80.7 ± 1.07 ha (range $=$ 15.2–323.2 ha, 95% CI $=$ 59.1–102.4) and mean core area was 17.5 ± 2.4 ha (range $=$ 3.1–56.0 ha, 95% CI $=$ 12.6–22.4). Mean overall home range was 109.5 ± 14.6 ha (range $=$ 34.6–323.2 ha, 95% CI $=$ 79.1–140.0) for males and 40.3 ± 7.5 ha (range $=$ 15.2–131.1 ha, 95% CI $=$ 24.3–56.4) for females. Mean core area estimate was 24.4 ± 2.4 ha (range $=$ 5.0–56.0 ha, 95% CI $=$ 17.7–31.2) for males and 7.8 ± 1.3 ha (range $=$ 3.1–23.1 ha, 95% CI $=$ 4.9–10.7) for females. Males had larger overall home range estimates ($F = 28.16$, $P < 0.001$) and core areas ($F = 30.66$, $P < 0.001$) than females. There was no difference in overall home range ($F = 0.02$, $P = 0.88$) or core area estimates ($F = 0.33$, $P = 0.57$) by year. Overall home range size ($F = 3.31$, $P = 0.08$) and core areas ($F = 1.46$, $P = 0.23$) did not differ between the aerial broadcast and hand baiting zones.

Four raccoons moved outside the cells or buffer areas in which we recorded bait application. We calculated baits/km^2 of home range and core area for 32 raccoon home ranges: 18 by aerial application and 14 by hand distribution. Of 18 home ranges baited by helicopter, 10/18 core areas received baits, whereas 13/14 core areas baited by hand distribution received baits. Average application was 80.9 ± 8.6 (range $=$ 49.9–196.7, 95% CI $=$ 62.7–99.1) and 63.6 ± 5.7 (range $=$ 25.6–97.2, 95% CI $=$ 51.2–76.0) baits/km^2 of home range for aerial and hand baiting sites, respectively. Average application for core areas that received baits was 104.7 ± 28.7 (range $=$ 15.0–341.5, 95% CI $=$ 39.7–169.7) and 69.2 ± 12.5 (range $=$ 8.6–138.9, 95% CI $=$ 41.9–96.4) baits/km^2 of core area for aerial ($n = 10$) and hand baiting sites ($n = 13$), respectively. Baits/km^2 did not differ between aerial and hand distribution for overall home ranges ($F = 3.12$, $P = 0.08$) or core areas ($F = 1.12$, $P = 0.30$).

DISCUSSION

Seroprevalence between helicopter and hand baiting suggests that both are similar in delivering ORV baits to raccoons. Although not statistically significant, aerial cluster broadcast delivered more baits/km^2 of raccoon home range than hand distribution but was less efficient in reaching core areas. However, core areas represent a relatively small proportion of a raccoon's home range and the 178-m interval between bait clusters along flight transects may have resulted in some core areas being missed.

Table 1. Total captures and number of seropositive raccoons pre- and post-oral rabies vaccination (ORV) application, Chattanooga, Tennessee, USA, 2013–2014.

	Pre-ORV captures	No. seropositive (%; SE)[a]	Post-ORV captures	No. seropositive (%, SE)[a]
2013				
Helicopter	132	18 (13.0; 2.4)	152	38 (25.7; 3.1)
Hand baiting	118	21 (17.4; 4.4)	129	38 (28.5; 6.3)
Total	250	39 (15.2; 2.5)	281	76 (27.1; 3.4)
2014				
Helicopter	159	25 (17.0; 3.7)	168	36 (21.9; 3.6)
Hand baiting	126	16 (13.8; 3.3)	130	27 (20.6; 3.0)
Total	285	41 (15.4; 2.4)	298	63 (21.3; 2.3)
Combined				
Helicopter	291	43 (15.0; 2.2)	320	74 (23.8; 2.3)
Hand Baiting	244	37 (15.6; 2.7)	259	65 (24.5; 3.5)
Total	535	80 (15.3; 1.7)	579	139 (24.2; 2.1)

[a] Seroprevalence (%) is calculated by calculating the mean of the seroprevalence for each study cell and not the overall total positive/total captured.

In the southern study site, 2 raccoon home ranges were only approximately 50% baited because of a shift in raccoon movements relative to the study cell, likely resulting an underestimate of bait density for those 2 home ranges. In the northern site in 2014, data from remote-download GPS collars showed that 2 raccoons had moved out of the study cells in which they were captured. An unintended consequence was that these cells did not receive cluster baits during 2014, although they were baited operationally at 75 baits/km². Raccoons sampled in these cells during 2014 were included in serologic analysis. Seroprevalence increased by 8.9% overall following baiting, for an average post-ORV seroprevalence of 24.2%. This is still well below the recommended threshold for population immunity but essentially consistent with historical annual mean seroconversion following oral rabies vaccination using RABORAL V-RG (Slate et al. 2014, 2009).

Hand baiting typically relies on roads or trails to access raccoon habitat to apply baits, which can be a limiting factor in reaching some home ranges. As a result, aerial broadcast of baits is likely to be more effective in reaching a higher proportion of raccoon home ranges than hand application in many areas, simply because of limited access to interior habitats by personnel during hand baiting. Bait application by helicopter using cluster baiting or individual baits may overcome this lack of access. In theory targeting core areas may be an effective strategy, but detailed knowledge of individual raccoon use of the landscape is typically unknown prior to initiating ORV operations. Although 50% of core areas were not reached during aerial application, it is likely related to flight-line spacing or to the lower frequency of cluster baiting. Reducing the flight-line spacing from 750 m to 500 m or lower could result in more consistent distribution of ORV baits to raccoons in some targeted suburban environments. *Post hoc* simulations of aerially applying baits with 500 m between transects but the same overall application rate (75/km²) suggest 15/18 and 13/18 core areas would be reached at clusters of 6 (178 m between clusters) and 10 (266 m between clusters) baits, respectively. In this study we deposited clusters of 10 baits at 178-m intervals along the flight line, rather than the operational standard of 1 bait every 18 m, which may have contributed to relatively fewer baits applied aerially to core areas.

MANAGEMENT IMPLICATIONS

The applied nature and results of this research directly affected current ORV baiting strategies targeting raccoons by increasing the use of helicopters in areas where it was potentially more efficient, and at least as effective, as hand baiting. Helicopter cluster bait application and hand baiting by vehicle using Raboral V-RG have similar results in terms of seroconversion rates in raccoon populations and the degree to which the target species has access to bait based on estimated home range. In addition, depositing individual baits at regularly spaced intervals, rather than clusters, may increase the ability to target raccoon core areas and provide a more even distribution of ORV baits in suburban raccoon habitat. Evaluation of additional strategies are needed because both methods failed to achieve herd immunity necessary to disrupt rabies transmission in raccoons.

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Table 2. Model results for factors affecting the difference in seroprevalence in raccoons between pre- and post-oral rabies vaccination application, Chattanooga, Tennessee, USA, 2013–2014. Results are from a linear mixed-effects model. All models include a random effect of cell nested in the bait strategy (helicopter or hand baiting). We ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c). Smaller AIC_c values have more support, and the model weight (w_i) shows the relative model support.

Model	K[a]	AIC_c	ΔAIC_c	w_i	LL[b]
Intercept only	3	−32.12	0.00	0.50	19.66
Yr	4	−31.50	0.62	0.37	20.80
Bait strategy	4	−29.26	2.86	0.12	19.68
Yr × bait strategy	6	−24.81	7.30	0.01	20.88

[a] Number of parameters in the model.
[b] Log likelihood for the model.

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