Journal of Wildlife Diseases, 47(3), 2011, pp. 593–602
© Wildlife Disease Association 2011

ORAL VACCINATION AGAINST RACCOON RABIES: LANDSCAPE HETEROGENEITY AND TIMING OF DISTRIBUTION INFLUENCE WILDLIFE CONTACT RATES WITH THE ONRAB VACCINE BAIT

Jean-Philippe Boyer,[1] Pierre Canac-Marquis,[2] Daniel Guérin,[2] Julien Mainguy,[2] and Fanie Pelletier[1,3]
[1] Canada Research Chair in Evolutionary Demography and Conservation, Département de Biologie, Université de Sherbrooke, 2500 Boulevard de l'Université, Sherbrooke, Québec J1K 2R1, Canada
[2] Ministère des Ressources Naturelles et de la Faune, Direction de l'Expertise sur la Faune et ses Habitats, Service de la Biodiversité et des Maladies de la Faune, 880 chemin Sainte-Foy, Québec, Québec G1S 4X4, Canada
[3] Corresponding author (email: fanie.pelletier@usherbrooke.ca)

ABSTRACT: Aerial distribution of oral vaccine baits is one of the available strategies for controlling the spread of infectious wildlife diseases. This technique has commonly been used to control rabies in wild carnivores and, together with other techniques, was used to immunize wild populations of raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) after the detection of the first rabid raccoon in the province of Quebec, Canada, in 2006. Vaccine bait distribution was conducted over large areas where agricultural land is dominant but interspersed with residual forest patches. Our objective was to evaluate the effect of habitat (forest vs. agricultural crops) in space and time on the contact rate between wildlife and the ONRAB® vaccine bait, a recent alternative to the V-RG®. Four transects of eight vaccine baits each were installed parallel to, and at different distances from, the forest's edge (under forest cover, at field-forest edge, and at 50 and 200 m from forest edge in agricultural crops) at three sites composed of various crop types interspersed with forest patches. This experiment was conducted during three periods (late spring, 1–7 June; summer, 27 July–2 August; and fall, 24–30 October) in 2009. Contact rates with vaccine baits were monitored for 7 days in each period to evaluate the potential temporal variations generated within the habitat types. Contact rates with ONRAB vaccine baits were highest under forest cover and in the fall. Of 13 species observed in proximity to the vaccine baits, raccoons were the most frequent (49.5%, $n=55$ visits). Our study underlines the importance of taking into account landscape heterogeneity and timing of distribution when planning the distribution of vaccine baits to control rabies in raccoons.

Key words: Aerial distribution, baits, *Mephitis mephitis*, ONRAB, ORV, *Procyon lotor*, raccoon rabies variant, striped skunk.

INTRODUCTION

Several intervention strategies have been developed to control wildlife diseases (Hudson et al., 2002). Depending on the type of disease targeted, those strategies often include population reduction (PR) of the potential vectors in the infected zone and trap-vaccinate-release (TVR) campaigns around the infected zones to further limit the potential spread of the disease (Hudson et al., 2002). Density reduction and TVR campaigns are, however, generally only applicable to small areas because of both logistic and financial constraints (Baer, 1975; Sterner et al., 2009). Oral vaccination through the distribution of oral vaccine baits has emerged as an alternative control measure (Rosatte et al., 2009a, b) and is now considered a main tool in the control of zoonotic diseases of great concern, such as rabies (Slate et al. 2005).

The distribution of oral vaccine baits was proposed as a likely efficient control strategy in the 1970s after successful captive trials (Baer, 1975) and was first implemented in the wild for the immunization of red foxes (*Vulpes vulpes*) against rabies in Europe (Schneider et al., 1988; Wandeler et al., 1988) and Canada (Johnston et al., 1988; Bachmann et al., 1990). In combination with PR and TVR, it has been successfully used in Ontario, Canada, to eradicate the raccoon (*Procyon lotor*) rabies variant (Rosatte et al., 2009a). For large-scale operations, aerial and hand-distribution of vaccine baits, also known as oral rabies vaccination (ORV), is the often-preferred approach to control rabies (Rosatte et al., 2009a). Despite being efficient for large-scale control operations, this approach is also costly because a large number of vaccine baits must be distributed (generally 75–300 baits/km^2) and often throughout vast areas (Rosatte et al., 2009b; Sattler et al., 2009). The performance of aerial and terrestrial (e.g., hand-baiting) ORV programs can potentially be optimized to minimize cost while maximizing contact and uptake of vaccine baits by the target species. To do so, the density of vaccine distributed should be increased in the habitats preferred by the vector species (Olson and Werner, 1999), instead of adopting a uniform pattern of distribution. During the planning of ORV programs, wildlife managers should consider not only the location of documented rabies cases (Recuenco et al., 2008), but also the likelihood of the targeted species being found in the types of habitats where vaccine baits are to be distributed. Such information should increase the efficiency of control activities by concentrating the highest densities of vaccine baits where the animals to immunize are more likely to be found (Robbins et al., 1998). The efficiency of such an approach, however, may vary greatly depending on the type of landscape where the ORV program is to take place. Coarse habitat heterogeneity (e.g., crops and forests) in the area where the ORV is performed, as well as the time of year, can influence the presence and density of targeted animals and hence the uptake of the vaccine baits.

In 2006, a first case of the raccoon rabies variant was confirmed in southern Quebec, Canada (Canac-Marquis et al., 2007), in an area characterized by a fragmented agricultural landscape, producing mainly corn (*Zea mays*) and soybeans (*Glycine max*), and interspersed with forest patches. Since the discovery of raccoon rabies in this area, the Ministère des Ressources Naturelles et de la Faune (MRNF) du Québec, Canada, and its collaborators have increased surveillance efforts and conducted large-scale ground operations (PR and TVR) and an aerial ORV program (Canac-Marquis et al., 2007) in an attempt to control the epizootic (see Rosatte et al., 2001, for a similar approach). Initially, the RABORAL V-RG® vaccine bait (Merial Ltd., Athens, Georgia, USA) was used in aerial ORV, with the objective of immunizing both raccoon and striped skunk (*Mephitis mephitis*) populations. Since 2008, the newly available ONRAB® bait (Artemis Technologies, Guelph, Ontario, Canada), in collaboration with the Ontario Ministry of Natural Resources (Peterborough, Ontario, Canada), was adopted for the control of raccoon rabies in Quebec, Canada. Rosatte et al. (2009b) have shown that antibody prevalences obtained with the ONRAB baits are much higher for both raccoons and skunks than they are when V-RG is used. However, given that the ONRAB bait is new, no information has been made available on the species that are attracted to this bait in the wild nor at what rate the baits are consumed after distribution. Previous field studies on the V-RG and other types of vaccine baits, have shown that the rate of disappearance of baits can sometimes be as high as 90% a week after their distribution (Hadidian et al., 1989; Hable et al., 1992; Hanlon et al., 1998; Olson and Werner, 1999; Blackwell et al., 2004). Our goals were to evaluate whether ONRAB baits are consumed at a similar rate under natural conditions and to investigate whether targeted species (raccoons and skunks) and nontargeted species were attracted to this alternative to the V-RG bait.

Past aerial ORV campaigns in southern Quebec, Canada, used uniform patterns of aerial distribution (i.e., vaccine baits were distributed at an average density of 75–150 baits/km^2, except over water bodies, roads, and residential areas) with no consideration for the type of habitat encountered (Guérin et al., 2008). As of 2009, aerial distribution of ONRAB baits in mid-August targeted mainly forests and forest edges (approximately 30-m buffer zone in agricultural landscapes adjacent to forested areas), thus avoiding the central portions of large fields. Given that aerial ORV are now largely focused on forested landscapes that are fragmented by agricultural land use in Quebec, Canada, our specific objective was to evaluate the effects of bait location (forest, edge of forest, or agricultural field) and time of year when the distribution occurred on the contact rates by wildlife with ONRAB baits. It has been shown that raccoons and skunks frequently travel along the edges between crops and forested areas (Dijak and Thompson, 2000) and that the population density in those areas can be high (Barding and Nelson, 2008). Thus, we hypothesized that vaccine baits dropped near forest edges would be more likely to be discovered rapidly by raccoons and skunks than those that were deeper in forested areas or in the central parts of crop fields. It is also possible that natural food resources will be less available in autumn, a period when raccoons and skunks are accumulating fat reserves for winter (Gehrt, 2003; Rosatte and Larivière, 2003), leading to our prediction that animals may also be more likely to consume vaccine baits during that period.

MATERIALS AND METHODS

Study area

The study area was located at the Dairy and Swine Research and Development Centre in Lennoxville, Quebec, Canada (71°49′W, 45°22′N; Fig. 1A). This site consists of >50 ha of woodland and >300 ha of crop land and is bordered to the northwest by the Saint-Francois River (Fig. 1B). The main crops are corn, grain, and livestock pasture. Both raccoons and skunks are known to inhabit this area according to occasional sightings by employees of the Centre.

Simulation of ONRAB bait distribution along transects

To evaluate the effect of habitat type on contact rates by wildlife with vaccine baits, we installed transects at three sites within our study area. At each site, four linear transects consisting of eight ONRAB placebos (containing water instead of vaccine and placed 15 m apart) were installed parallel to one another 1) at 50 m from the forest-crop edge toward the forest interior; 2) at the forest-crop edge (0 m); 3) at 50 m from the forest-crop edge, in the field; and 4) at 200 m from the forest-crop edge, in the field, for a total of 96 vaccine baits (Fig. 1B, C). Vaccine baits were kept frozen until the day they were distributed. The attractant on the ONRAB bait is composed of partially hydrogenated vegetable shortening (34%), MicrobondH wax (International Wax Ltd., Agincourt, Ontario, Canada; 30%), stearine (12.5%), icing-sugar (20%), vegetable oil (1%), artificial marshmallow flavor, (1%) artificial sweet flavor (1%), and fat-soluble food dye (0.5%; khaki green) to camouflage the baits (Rosatte et al., 2009b). Transects were checked on days 1, 3, 5, and 7 after bait distribution in June (late spring), July/August (summer), and October (fall), to determine at which rate the vaccine baits were consumed or disturbed. At each visit, presence or absence of the baits was recorded, and, if present, the condition of the remaining baits left were noted as 1) bait coating eaten, but vaccine envelope not punctured; 2) vaccine envelope punctured; or 3) no apparent contact with the bait. We defined contact rate as the proportion of baits that disappeared or were touched by wildlife (i.e., Condition 2). When vaccine bait was not found at its initial position, we attempted to locate it within a 3-m radius before categorizing it as *absent*. Generally, we were unable to identify the species responsible for bait disturbance according to the marks on the baits. This experiment was performed for each of the weeks starting 1 June, 27 July, and 24 October 2009.

Identification of species observed in close proximity to vaccine baits

To identify which animal species were more likely to visit the vaccine baits, we set up camera traps in 12 locations in 2009 and 2010. At each location, three to five placebo ONRAB baits were placed in front of motion-triggered infrared camera traps (RapidFire RC55 or RC60, Reconyx, Holmen, Wisconsin, USA). When possible, we used a setup with one camera trap located in the forest and another in a crop field. Unlike in transects, the ONRAB baits were replaced when missing or disturbed. The infrared detection mechanism the cameras used was ideal because animals were not disturbed or frightened by a flash when the camera was triggered. Because it was difficult to confirm whether the animal

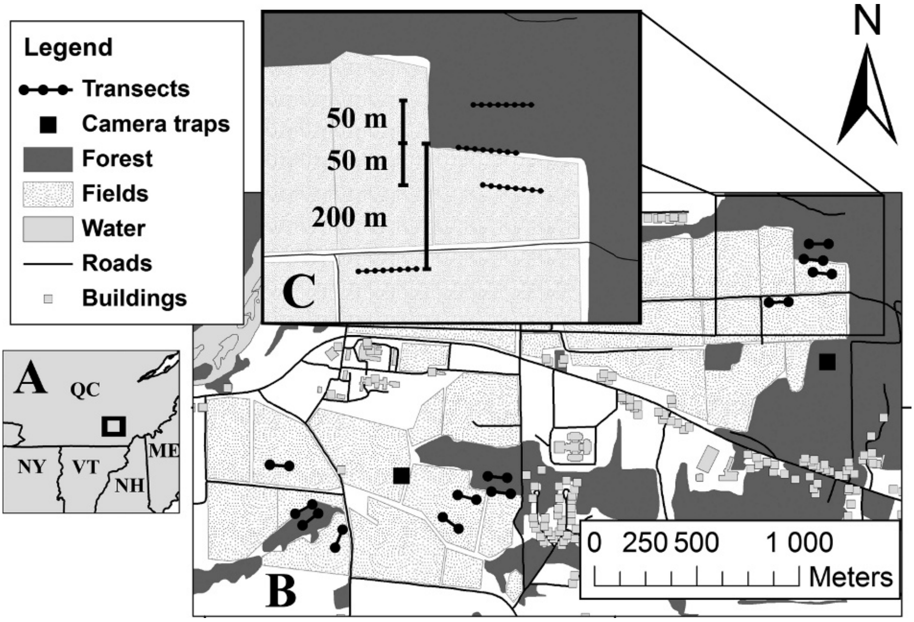

FIGURE 1. Study areas for field experiments of oral vaccine for raccoon (*Procyon lotor*) rabies in southern Quebec, Canada. (A) Location of the study site. (B) Location of transects in the Dairy and Swine Research and Development Centre in Lennoxville, Canada. The locations of camera traps used to identify the species visiting the vaccine baits are also shown. (C) Large-scale image of a part of the study area to show position of baits on each transect. QC = Quebec; NY = New York, USA; VT = Vermont, USA; NH = New Hampshire, USA; ME = Maine, USA.

triggering the cameras consumed or interacted with the vaccine bait, we recorded bait visitation rather than consumption of the baits. In 2009, four camera traps were set up, including two in Lennoxville, Canada (the study area where the transect experiment was conducted) and two at Mont-Orford National Park, about 32 km east of Lennoxville (71°14′W, 45°22′N) in Quebec, Canada. This second site is characterized by a well-visited campground and forested areas (Lefebvre, 1998) and has been used in a long-term study of raccoon ecology since April 2009. Thus, the habitats found at Mont-Orford National Park were different from the ones observed at the first study area, potentially allowing different species to approach the baits. In 2010, we placed camera traps in different regions in spring and summer. Three camera traps were again placed at Mont-Orford National Park from 5 May to 4 June. We also set up five camera traps at locations in southern Quebec, Canada, in both fields and forest patches (Montérégie region; 73°19′W, 45°14′N). These cameras were set up from 23 August to 27 August just after the 2010 ORV program was conducted.

Statistical analyses

We used a generalized linear mixed model (GLMM) with a binomial error structure to determine the factors explaining the variation in vaccine-bait contact rates, defined as the proportion of vaccine baits per transect that were removed or showed signs of disturbance (e.g., bite marks). Mixed-effects models allowed us to model random effects and thus control for potential nonindependence in the data structure (Pinheiro and Bates, 2000). The fixed independent variables we considered to potentially explain the variation in contact rates were transect distance from the forest edge (*distance*, categoric: forest interior, forest-crop edge, 50 m or 200 m in the agricultural field), time of year (*season*, categoric: late spring, June; summer, August; and fall, October), number of days since bait distribution (*day*, continuous from day 1 to day 7), and number of days squared. Additionally, *site* was considered as a random term to account for the possible temporal autocorrelation of contact rates within each of the three sites. To test whether the random term *site* influenced contact rates, we calculated an approximated χ^2 statistic equal to twice the

TABLE 1. Estimates from a generalized linear model with a quasibinomial error structure on the effect of season, number of days since bait distribution, and habitat type (forest interior, −50 m; forest-crop edge, 0 m; agricultural field 50 m from forest; and agricultural field 200 m from forest) on contact rates of wildlife with ONRAB baits in Quebec, Canada.

	Estimate	SE	*t*-value	*P*-value
Intercept	−2.240	0.384	−5.836	<0.001
Season				
Summer (August)[a]	—	—	—	—
Late spring (June)	0.622	0.285	2.184	0.031
Autumn (October)	1.245	0.303	4.109	<0.001
Days since distribution	0.225	0.051	4.367	<0.001
Distance				
Forest-crop edge[a]	—	—	—	—
Forest interior	0.800	0.318	2.519	0.013
Field 50 m	−0.352	0.336	−1.047	0.297
Field 200 m	−0.482	0.340	−1.418	0.159

[a] Used as reference value.

absolute difference in log likelihoods for the model with and without the random term, and then divided the associated *P*-value by two (Steele and Hogg, 2003). The results of this likelihood-ratio test suggested that the variance explained by this random factor was not significant ($\chi^2=0$, $P=0.99$), so it was removed from further statistical analyses, and we present the results obtained with a generalized linear model instead. The following two-way interactions were also included in the full model: day-by-distance, season-by-day, and distance-by-season. Given that our data were overdispersed because the residual variance of the full model was larger than the number of the degrees of freedom (ratio of 2.83), we modeled contact rates using a quasibinomial error distribution. For model selection, we started with a full model containing all variables and interactions of interest and sequentially removed the least-significant terms one at a time, following a backward model selection process, until only those significant at $\alpha=0.05$ remained.

Finally, we used a Pearson χ^2 test to determine whether some animal species were more likely than others to approach the vaccine baits placed in front of the camera traps, according to habitat type. Because there were very few visitations by skunks (see "Results"), we pooled ORV-targeted species (raccoon, striped skunk, red fox) together and nontarget species in a second group. All statistical analyses were performed using the R package version 2.7.0 (R Development Core Team, 2008).

RESULTS

After 7 days, 45.4±5.8% (mean±SE throughout) of the 288 vaccine baits monitored showed evidence of contact by wildlife. Of 44 baits that were still present after 1 wk and had been disturbed, 41 (93%) had been punctured, suggesting that animals visiting the baits typically chewed them. Although the contact rates with ONRAB baits obtained in *forest-interior* transects were significantly higher than those observed in the *forest-edge* and *field* transects (Table 1 and Fig. 2A), the contact rates among the three other transects did not vary significantly from one another. Animals also tended to encounter vaccine baits more frequently in fall and late spring than they did during summer, with fall having the highest contact rates (Fig. 2B). The number of vaccine baits removed or disturbed increased with the number of days since distribution (Fig. 2). We also tested for a quadratic effect of the variable *day*, but it was not statistically significant (−0.05±0.03, $P=0.099$). None of the interactions considered were significant (all *P*-values >0.20).

Based on the photos taken by the camera traps, raccoons encountered the

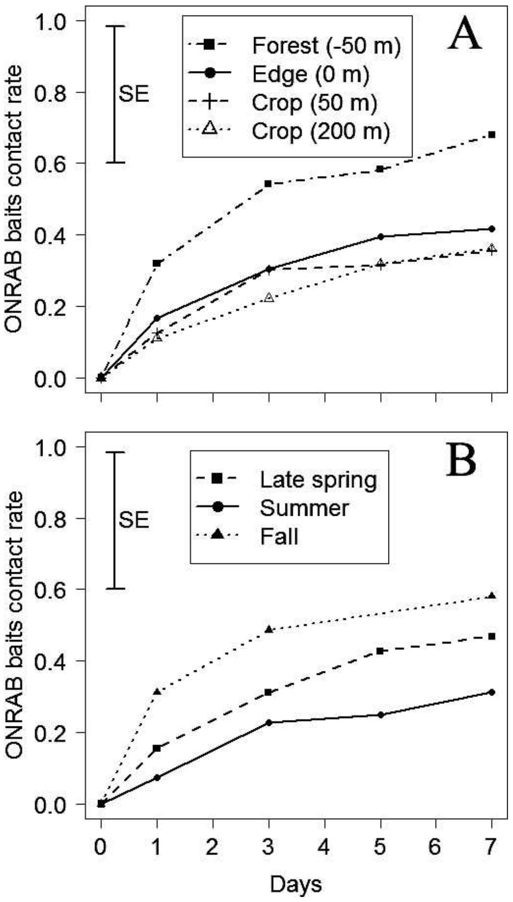

FIGURE 2. Average contact rates of ONRAB oral rabies vaccine baits by wildlife in Quebec, Canada, as a function of the number of days since distribution by (A) habitat (forest, edge, or crop) and (B) season (late spring, 1–7 June; summer, 27 July–2 August; and fall, 24–30 October 2009). The average standard error is represented by the vertical line labeled SE.

vaccine baits most frequently (49.5%). Skunks (4.5%) and red foxes (1.8%), two other potential rabies vectors, visited the baits at a much lower frequency. Nontarget animals that triggered the cameras included other mammals (38.7%), such as white-tailed deer (*Odocoileus virginianus*) and red squirrels (*Tamiasciurus hudsonicus*), birds such as the American Crow (*Corvus brachyrhynchos*) and unidentified species of small rodents (1.8%). There were no detectable differences in the species visiting the vaccine baits among habitat types.

DISCUSSION

Our results suggest that contact rates with the ONRAB bait were highest in forested habitats and in late October, and weakest outside of forests and in July/August. Raccoon, the main targeted vector, was the most commonly observed species near the vaccine baits, suggesting that the ONRAB bait can be considered as an appropriate vaccine delivery vehicle for the control of raccoon rabies. Our results also suggest that in landscapes largely composed of agricultural fields interspersed with forest patches, delaying the distribution of vaccine baits until October to control the raccoon rabies variant could maximize the immunization of juvenile, as well as adult, raccoons before they gather in overwintering locations. Generally, by autumn, the young of the year are old enough to move around and must start accumulating fat reserves for winter, probably making them more likely to eat the baits as well, potentially leading to the greater contact rates observed in that season.

Increasing the density of vaccine baits distributed over forest patches while reducing it in crops in the agricultural zone found in southern Quebec, Canada, appears to be a valid strategy for optimizing raccoon immunization. Aerial distribution of vaccine baits could also be timed to coincide with periods of low food availability in crops because raccoons will likely be concentrated in wooded regions to feed. Based on the available literature, raccoons preferentially select forest cover, particularly where a water source is available (Beasley and Rhodes, 2010); tend to avoid the middle of crops, often opting instead to travel along crop edges (Barding and Nelson, 2008); and use agricultural habitats mainly when crops are mature (Beasley et al., 2007). These previous findings, together with those from our study, highlight the importance of considering landscape heterogeneity and season simultaneously when planning an aerial vaccine bait distribution. A factor that might also limit the efficiency of the vaccine baits distributed in summer is the occurrence of agricultural activities that can negatively affect the ORV campaigns. For example, one of the fields used in our study underwent pesticide spraying at the beginning of our June observation period, and transects located there were left untouched for the 7-day observation period. This suggests that aerial distribution of vaccine baits should avoid areas where pesticide spraying has recently occurred or is planned within the vaccine's viability period. Excluding those transects from the analysis did not, however, change our results (analyses not shown).

Weather could also affect bait coating degradation and, consequently, contact rates. Although there was some rainfall during our study (average rainfall: 1–7 June, 0.3 mm/day; 27 July–2 August, 8.4 mm/day; and 24–30 October, 4.8 mm/day, data obtained from Sherbrooke weather station, 13 km north of our study site; Environment Canada, 2010), it did not seem to affect the observed contact rates. Contact rates were maximal in October, even though it rained on the first day of the experiment (32 mm). Further direct investigation of the effect of weather on the vaccine bait coating is needed to properly evaluate the environmental conditions under which its efficacy is reduced. A plastic matrix containing the vaccine that has lost its coating may no longer be attractive to wildlife and may compromise bait uptake.

The overall contact rate with vaccine baits after 7 days in this study was lower than what has been found in similar studies in the United States with the V-RG or alternative baits (Hadidian et al., 1989; Hable et al., 1992; Hanlon et al., 1998; Blackwell et al., 2004). This discrepancy may be explained by differences among study areas in density of raccoons and potentially other species attracted to the bait, as well as the time when these studies were conducted. For instance, Blackwell et al. (2004) estimated a mean density of 24.5 raccoons/km^2 in their study area, whereas the density near our study site has been estimated at 13 raccoons/km^2 (Montérégie, Québec, Canada; Jolicoeur et al., 2009). Differences in animal density can, therefore, partly account for the higher rate of disappearance of the V-RG baits in previous studies. More studies on the effect of landscape characteristics on contact rates of vaccine baits will be valuable to improve the efficiency of aerial distribution.

Vaccine baits distributed in crops are more likely to be seen by birds, such as corvids, a group of species known to disturb vaccine baits (Bachmann et al., 1990). They are also more susceptible to being disturbed or destroyed by agricultural machinery or rendered unattractive by pesticide spraying. Contrary to our predictions, however, the contact rates were the same for transects at the field-forest edge and those further (50 and 200 m) in the fields. This result was unexpected because raccoons have been shown to follow linear habitat features, such as fences, roads, and forest edges, and to only rarely cross crop lands (Barding and Nelson, 2008). However, as we were unable to identify the species responsible for disturbing the vaccine baits along the transects, it is possible that different species were responsible for disturbing the baits on transects in different habitat types (forest or crop), despite raccoons being identified most frequently in proximity to vaccine baits by the camera traps.

Another finding of the camera trap experiment was the scarce number of bait visitations by striped skunks when compared with raccoons. This difference could be explained in part by a lower density of striped skunks in the areas studied (1–2/km^2) compared with raccoons (Jolicoeur et al., 2009). In the Mont-Orford National Park study area, however, we noticed the complete absence of striped skunks in the pictures taken despite confirmation of their presence through the capture of individuals with live-traps. In fact, at least five individual striped skunks had been captured in the Mont-Orford National Park site in close proximity to the camera traps. This result could suggest that, under natural conditions, the ONRAB bait may not be attractive, or not as easily located by skunks. A potential explanation might relate to the sweet-smelling coating of the ONRAB baits used in this study, whereas fish and chicken scents were preferred by striped skunks in captivity during scent-preference trials (Jojola et al., 2007). Additionally, striped skunks are mainly insectivorous and carnivorous (Rosatte and Larivière, 2003), which may further limit their interest for the ONRAB baits. Further investigation is warranted to determine whether this vaccine bait requires additional improvement to attract striped skunks in a similar manner to raccoons.

In summary, our results suggest that to better target raccoons, aerial and hand-distribution of ONRAB vaccine baits should mainly focus on forested habitats in regions fragmented by extensive agricultural exploitation, although other habitats should be considered based on field experience (e.g., river and stream shores, abandoned farms). Because striped skunks have been shown to use habitat edges (Larivière and Messier, 2000), it would be valuable to continue to distribute baits along field edges adjacent to forested patches to better attain skunks. Furthermore, vaccine baits could be distributed later in the fall instead of during August because food availability in crops is likely lower at that time, thus concentrating the target species spatially and temporally near or in forested regions. As a result, a greater proportion of the raccoon population, and part of the skunk population, would be exposed to the baits, while reducing the costs by lowering the number of baits distributed in the center of large agricultural fields. Although the refinements suggested here to optimize control activities are specific to both region and habitat, they can be applied elsewhere if similar field work is conducted to determine the species present and where the baits are more likely to be encountered by the target species. Our results, combined with those on antibody prevalences obtained by Rosatte et al. (2009b), indicate that vaccination of raccoons with ONRAB baits is an appropriate tool to control raccoon rabies and the costs of an ORV campaign can be significantly reduced when habitat-specific distribution, rather than uniform baiting, is adopted.

ACKNOWLEDGMENTS

We are grateful for the funding contribution of the MRNF to this research. F.P. is funded via the NSERC discovery grant, the Canadian Foundation for Innovation, and the Canada Research Chair in Evolutionary Demography and Conservation. We would also like to thank Rémi Poulin and his colleagues at the Dairy and Swine Research and Development Centre in Lennoxville, Canada, for letting us use their property and Artemis Technologies for the ONRAB placebos. We are particularly grateful to Jennifer Chambers who provided comments on an earlier version of this manuscript.

LITERATURE CITED

Bachmann, P., R. Bramwell, S. J. Fraser, D. A. Gilmore, D. H. Johnston, K. F. Lawson, C. D. MacInnes, F. O. Matejka, H. E. Miles, M. A. Pedde, and D. R. Voigt. 1990. Wild carnivore acceptance of baits for delivery of liquid rabies vaccine. Journal of Wildlife Diseases 26: 486–501.

Baer, G. M. 1975. Wildlife vaccination *In* The natural history of rabies, G. M. Baer (ed.). Academic Press, New York, New York. pp. 261–266.

Barding, E. E., and T. A. Nelson. 2008. Raccoons use habitat edges in northern Illinois. American Midland Naturalist 159: 394–402.

Beasley, J. C., and O. E. Rhodes. 2010. Influence of patch- and landscape-level attributes on the movement behavior of raccoons in agriculturally fragmented landscapes. Canadian Journal of Zoology 88: 161–169.

———, T. L. DeVault, M. I. Retamosa, and O. E. Rhodes Jr. 2007. A hierarchical analysis of habitat selection by raccoons in northern Indiana. Journal of Wildlife Management 71: 1125–1133.

Blackwell, B. F., T. W. Seamans, R. J. White, Z. J. Patton, R. M. Bush, and J. D. Cepek. 2004. Exposure time of oral rabies vaccine baits relative to baiting density and raccoon population density. Journal of Wildlife Diseases 40: 222–229.

Canac-Marquis, P., R. Rioux, A. Dicaire, D. Rajotte, C. Sirois, M. Huot, D. Guérin, M. Gagnier, and J. Picard. 2007. Le contrôle de la rage du raton laveur en Montérégie en 2006: Rapport des opérations de terrain. Ministère des Ressources naturelles et de la Faune, Direction du développement de la faune, Direction de la protection de la faune, Direction de l'aménagement de la faune en Montérégie, Département de Santé publique de la Montérégie. 140 pp. [In French.]

Dijak, W. D., and F. R. Thompson. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. Journal of Wildlife Management 64: 209–216.

Environment Canada. 2010. National Climate Data and Information Archive. [Online] http://climate.weatheroffice.gc.ca/. Accessed March 2011.

Gehrt, S. D. 2003. Raccoon *Procyon lotor* and allies. *In* Wild mammals of North America: Biology, management and conservation, G. A. Feldhamer, B. C. Thompson and J. A. Chapman (eds.). Johns Hopkins University Press, Baltimore, Maryland. pp. 611–635.

Guérin, D., H. Jolicoeur, P. Canac-Marquis, F. Landry, and M. Gagnier. 2008. Le contrôle de la rage du raton laveur en Montérégie en 2007: Rapport des interventions terrestre et aérienne. Ministère des Ressources Naturelles et de la Faune, Direction générale de l'Expertise sur la Faune et de ses Habitats. 148 pp. [In French.]

Hable, C. P., A. N. Hamir, D. E. Snyder, R. Joyner, J. French, V. Nettles, C. Hanlon, and C. E. Rupprecht. 1992. Prerequisites for oral immunization of free-ranging raccoons (*Procyon lotor*) with a recombinant rabies virus vaccine: Study site ecology and bait system development. Journal of Wildlife Diseases 28: 64–79.

Hadidian, J., S. R. Jenkins, D. H. Johnston, P. J. Savarie, V. F. Nettles, D. Manski, and G. M. Baer. 1989. Acceptance of simulated oral rabies vaccine baits by urban raccoons. Journal of Wildlife Diseases 25: 1–9.

Hanlon, C. A., M. Niezgoda, A. N. Hamir, C. Schumacher, H. Koprowski, and C. E. Rupprecht. 1998. First North American field release of a vaccinia-rabies glycoprotein recombinant virus. Journal of Wildlife Diseases 34: 228–239.

Hudson, P. J., A. Rizzoli, B. T. Grenfell, H. Heesterbeek, and A. P. Dobson. 2002. The ecology of wildlife diseases. Oxford University Press, New York, New York. 197 pp.

Jojola, S. M., S. J. Robinson, and K. C. Vercauteren. 2007. Oral rabies vaccine (ORV) bait uptake by captive striped skunks. Journal of Wildlife Diseases 43: 97–106.

Jolicoeur, H., G. Daigle, V. Jomphe, and N. Vandal. 2009. Évaluation des densités de ratons laveurs et de moufettes rayées dans le cadre des interventions de lutte contre la rage du raton laveur en Montérégie en 2006 et 2007. Ministère des Ressources Naturelles et de la Faune, Direction de l'Expertise sur la Faune et Université Laval, Service de Consultation Statistique. 75 pp. [In French.]

Johnston, D. H., D. R. Voight, C. D. MacInnes, P. Bachmann, K. F. Lawson, and C. E. Rupprecht. 1988. An aerial baiting system for the distribution of attenuated or recombinant rabies vaccines for foxes, raccoons and skunks. Reviews of Infectious Diseases 10 (suppl): S660–S664.

Larivière, S., and F. Messier. 2000. Habitat selection and use of edges by striped skunks in the Canadian prairies. Canadian Journal of Zoology 78: 366–372.

Lefebvre, F. 1998. Étude de la dynamique de population du raton laveur (*Procyon lotor*) dans le parc du Mont-Orford dans le but d'éviter l'entrée de la rage. MSc Thesis, Université de Sherbrooke, Sherbrooke, Canada. 52 pp.

Olson, C. A., and P. A. Werner. 1999. Oral rabies vaccine contact by raccoons and nontarget species in a field trial in Florida. Journal of Wildlife Diseases 35: 687–695.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-plus. Springer-Verlag, New York, New York. 528 pp.

R Development Core Team. 2008. R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2630 pp.

Recuenco, S., M. Eidson, B. Cherry, and G. Johnson. 2008. Risk-based cost modelling of oral rabies vaccine interventions for raccoon rabies. Zoonoses and Public Health 56: 16–23.

Robbins, A. H., M. D. Borden, B. S. Windermiller, M. Niezgoda, L. C. Marcus, S. M. O'Brien, S. M. Kreindel, M. W. McGuill, A. DeMaria, Jr., C. E. Rupprecht, and S. Rowell. 1998. Prevention of the spread of rabies to wildlife by oral vaccination of raccoons in Massachusetts. Journal of the American Veterinary Medical Association 213: 1407–1412.

Rosatte, R., and S. Lariviere. 2003. Skunks (Genera *Mephitis*, *Spilogale* and *Conepatus*). *In* Wild mammals of North America, biology, management and conservation, G. A. Feldhamer, B. C. Thompson and J. A. Chapman (eds.). Johns Hopkins University Press, Baltimore, Maryland. pp. 692–707.

———, D. Donovan, M. Allan, L. Bruce, T. Buchanan, K. Sobey, B. Stevenson, M. Gibson, T. MacDonald, M. Whalen, J. C. Davies, F. Muldoon, and A. Wandeler. 2009a. The control of raccoon rabies in Ontario, Canada: Proactive and reactive tactics, 1994–2007. Journal of Wildlife Diseases 45: 772–784.

———, ———, ———, L. A. Howes, A. Silver, K.

Bennett, C. MacInnes, C. Davies, A. Wandeler, and B. Radford. 2001. Emergency response to raccoon rabies introduction into Ontario. Journal of Wildlife Diseases 37: 265–279.

———, ———, J. C. Davies, M. Allan, P. Bachmann, B. Stevenson, K. Sobey, L. Brown, A. Silver, K. Bennett, T. Buchanan, L. Bruce, M. Gibson, A. Beresford, A. Beath, C. Fehlner-Gardiner, and K. Lawson. 2009b. Aerial distribution of ONRAB baits as a tactic to control rabies in raccoons and striped skunks in Ontario, Canada. Journal of Wildlife Diseases 45: 363–374.

Sattler, A. C., R. A. Krogwold, T. E. Wittum, C. E. Rupprecht, T. P. Algeo, D. Slate, K. A. Smith, R. L. Hale, G. A. Nohrenberg, C. D. Lovell, M. Niezgoda, A. J. Montoney, and R. D. Slemons. 2009. Influence of oral rabies vaccine bait density on rabies seroprevalence in wild raccoons. Vaccine 27: 7187–7193.

Schneider, L. G., J. H. Cox, W. W. Muller, and K. P. Hohnsbeen. 1988. Current oral rabies vaccination in Europe: An interim balance. Reviews of Infectious Diseases 10 (suppl): S654–S659.

Slate, D., C. E. Rupprecht, J. A. Rooney, D. Donovan, D. H. Lein, and R. B. Chipman. 2005. Status of oral rabies vaccination in wild carnivores in the United States. Virus Research 111: 68–76.

Steele, B. M., and J. T. Hogg. 2003. Measuring individual quality in conservation and behavior *In* Animal behavior and wildlife conservation, M. Festa-Bianchet and M. Apollonio (eds.). Island Press, Washington, D.C., pp. 243–269.

Sterner, R. T., M. I. Meltzer, S. A. Shwiff, and D. Slate. 2009. Tactics and economics of wildlife oral rabies vaccination, Canada and the United States. Emerging Infectious Diseases 15: 1176–1184.

Wandeler, A. I., S. Capt, A. Kappeler, and R. Hauser. 1988. Oral immunization of wildlife against rabies: Concept and first field experiments. Reviews of Infectious Diseases 10 (suppl): S649–S653.

Submitted for publication 19 November 2010.
Accepted 24 March 2011.