Management and Conservation Article

Effects of Natural Barriers and Habitat on the Western Spread of Raccoon Rabies in Alabama

WENDY M. ARJO,[1] *United States Department of Agriculture/Animal and Plant Health Inspection Service/Wildlife Service/National Wildlife Research Center, Olympia Field Station, 9730-B Lathrop Industrial Drive, SW, Olympia, WA 98512, USA*

CHRISTINE E. FISHER, *School of Forestry and Wildlife Sciences, 3301 Forestry and Wildlife Sciences Building, Auburn University, AL 36849, USA*

JAMES ARMSTRONG, *School of Forestry and Wildlife Sciences, 3301 Forestry and Wildlife Science Building, Auburn University, AL 36849, USA*

FRANK BOYD, *United States Department of Agriculture/Animal and Plant Health Inspection Service /Wildlife Services, School of Forestry and Wildlife Sciences, 602 Duncan Drive, Auburn University, Auburn, AL 36849, USA*

DENNIS SLATE, *United States Department of Agriculture/Animal and Plant Health Inspection Service /Wildlife Services, National Rabies Program, 59 Chenell Drive, Suite 2, Concord, NH 03301, USA*

ABSTRACT Although domestic animal transmission of rabies has largely been mitigated, the disease remains a concern in both Europe and North America where wildlife transmission has caused epizootics. Raccoon (*Procyon lotor*) rabies was established in Alabama, USA, in 1975, primarily in the southeastern corner of the state. However, with the exception of isolated events, rabies has not continued to spread westward across the Alabama River. We monitored movements of 100 radiocollared raccoons on 2 sites within hardwood and agriculture habitats in a rabies enzootic area east of the Alabama River, in managed pine habitat area west of the river where rabies sporadically occurs, and in a mixed pine hardwood area outside of the known rabies enzootic area to determine if raccoon movements and habitat use in certain habitat types and the presence of a river may serve as natural barriers preventing the western spread of rabies in Alabama. We also examined raccoon contact rates to determine if they influence disease transmission through static and dynamic interactions. Raccoons in mixed pine–hardwood forest habitats had smaller home ranges and less overlap of ranges compared to the other 3 habitats. However, static interactions between habitats in the use of overlap areas did not differ ($F_{11,129} = 1.63$, $P = 0.09$). Rabies antibody titers were highest in the managed pine habitat (28%) even prior to oral vaccine bait distributions in spring of 2004 and 2005. Biomarker data from radiocollared and additional raccoons captured after the bait distribution west of the Alabama River demonstrated a low efficacy of the vaccine reaching the small southern raccoons. The combination of the river as a partial barrier, the high percentage of pine forested habitat west of the river, and limited spatial movements of raccoons within these forested habitats appears to have reduced the likelihood of rabies establishing west of the river. Understanding different host–habitat–disease systems is important for successful management of diseases. Based on our results, we recommend that the oral vaccine program continue to use the Alabama River as a partial barrier and baiting be concentrated in the fragmented bottomland hardwood forests and around larger bodies of water where raccoon densities are highest. Success of baiting strategies designed to take advantage of northern raccoon dynamics and habitat use may not be applicable to southern populations. (JOURNAL OF WILDLIFE MANAGEMENT 72(8):1725–1735; 2008)

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Rabies is one of the oldest known viral diseases and has become one of the most important viral zoonoses. Rabies management in the United States has grown in complexity over the last several decades as wildlife has replaced domestic animals as the primary reservoir for the disease (United States Department of Agriculture [USDA] 2007). Over $300 million is spent annually on rabies prevention and control including an estimated 18,000 and 40,000 people annually receiving pre- and postexposure prophylaxis, respectively (Real et al. 2005, Centers for Disease Control and Prevention [CDC] 2007). Raccoons (*Procyon lotor*) accounted for approximately 38% of the 6,940 reported wildlife rabies cases in the United States and Puerto Rico in 2006 (Blanton et al. 2007).

An enzootic focus of raccoon rabies has existed in Florida for >50 years (Kappus et al. 1970, McLean 1975). By the 1960s, the disease was well established in southern Georgia. Rabies spread into Alabama >30 years ago with its westward spread along the Florida panhandle (McLean 1975). However, rabies has not continued to spread westward at a rate commensurate with the northward spread up the Atlantic seaboard and the subsequent westward spread through northern states to Ohio (Russell et al. 2005). Translocations were implicated in the northern accelerated spread of raccoon rabies (Nettles et al. 1979, Jenkins et al. 1988).

Raccoons are ecological generalists that are able to exploit temporary and unpredictable resources (Johnson 1970, Gehrt and Fritzell 1997, Chamberlain et al. 2002). Due to the animal's ability to adapt to the constantly changing landscape and increasing urban settings, raccoon populations have increased steadily through the 1990s (Gehrt et al. 2002). Population densities of raccoons are highly variable throughout their range, and in specific urban areas have been reported to reach artificially high densities of ≥300 raccoons/km^2 (Riley et al. 1998). Large populations of raccoons in close proximity to human populations may pose health risks as the potential for zoonotic disease transmission increases (Bigler et al. 1975, Rosatte et al. 2006). In addition, behavioral characteristics such as extensive home range overlap (Riley et al. 1998), polygynous mating systems, or shared daytime resting and denning sites (Kaufmann 1982), may allow for easier transmission of epizootic disease like canine distemper and rabies.

The National Rabies Management Program administered

[1] *E-mail: wendy.m.arjo@aphis.usda.gov*

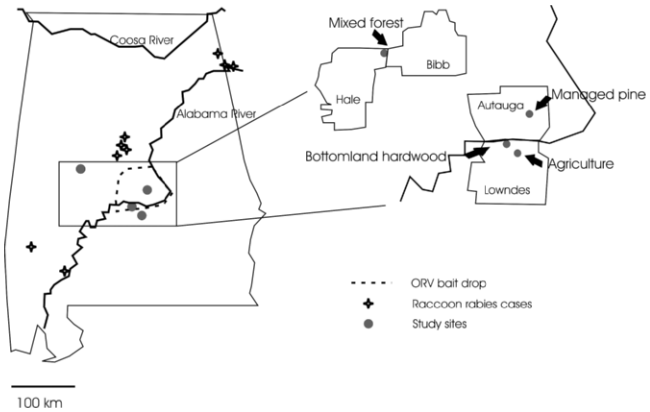

Figure 1. Distribution of Alabama, USA, rabies bait drops in April 2004 and March 2005 and known isolated cases of raccoon rabies across the Alabama and Coosa Rivers. The 4 study areas, bottomland hardwood and agriculture in rabies enzootic area east of the Alabama River, managed pine west of the river, and mixed forest towards the western Alabama–Mississippi border, are denoted and shown in detail by county. ORV = oral rabies vaccination.

by the USDA and Plant Health Inspections Service, Wildlife Services' program (USDA/APHIS/WS) has established oral vaccine bait distribution zones in several strategic areas in the eastern United States (Kostrzewski et al. 2004, Nelson and Slate 2005). The Oral Rabies Vaccination (ORV) program targets rabies vectors (e.g., raccoons, skunks [*Mephitis mephitis*], foxes [*Urocyon cinereoargenteus*]) by attempting to create a biological immunity barrier to halt the spread of the targeted rabies variant. Heterogeneous habitats or host populations can cause changes in the invasive wave front and slow the spread of disease transmission (Murray et al. 1986, Smith et al. 2005). In areas with low host populations or undesirable habitat, disease transmission may falter and stall without events such as long-distance translocations to continue propagation (Smith et al. 2005). Geographical features such as rivers, mountains, and lakes have been integrated into disease prevention and control programs targeting the spread and elimination of red fox (*Vulpes vulpes*) rabies in Europe (Wanderler et al. 1988) and have been suggested to play a role in the variable rate of spread in raccoon rabies up the Atlantic seaboard (Moore and Carpenter 1999; Lucey et al. 2002; Smith et al. 2002, 2005).

Vaccine barriers are permeable (Russell et al. 2005) and understanding how and where breaches occur is important in further refining vaccine programs and managing diseases. We investigated spatial distribution, the potential effect of geographic and habitat barriers, and disease prevalence (rabies and canine distemper) of raccoons in 4 distinct habitats in Alabama. Our objectives were to determine if survival, population densities, and spatial relationships differed within these main habitats in Alabama and their potential influence on disease transmission. In addition, to increase our understanding of rate of disease transmission, we were interested in determining how raccoons use natural barriers or how barriers affect raccoon movements. We used the information obtained from this study, titer results, and bait uptake to recommend to USDA/APHIS/WS ways to increase the efficacy of the ORV program.

STUDY AREA

We conducted our study along a latitudinal gradient in central Alabama (Fig. 1). The central study site spanned the Alabama River in Autauga (west of river with sporadic rabies occurrence) and Lowndes (east of river in rabies enzootic zone) counties. The western study area in Hale and Bibb counties represented an area where raccoon rabies was not known to be present. The humid, subtropical climate in central Alabama had average annual precipitation of 121–170 cm. Mean monthly temperatures ranged from 1.9° C in January to 33.7° C in July.

The first site in the Lowndes County Wildlife Management Area (LWMA) was located in northern part of the county. Covering 4,100 ha, the Lowndes WMA (bottomland hardwood habitat) was primarily composed of mature hardwood forests, consisting of various oaks (*Quercus* spp.), red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), American beech (*Fagus grandifolia*), hickories (*Carya* spp.), and pine (*Pinus* spp.). Food plots within the WMA provided year-round forage for wildlife. Early summer plots typically provided chufa, millet, cowpea, and occasionally corn. Autumn food plots consisted of cereal grains, including oats, wheat, and rye, as well a variety of clovers and other legumes. The core study area in this WMA covered approximately 748 forested hectares and was bordered to the west by the Alabama River. The width of the Alabama River along the LWMA varied from approximately 210 m to 290 m (United States Army Core of Engineers [USACE] 2008*a*) and the flow rate averaged 566 m^3/second (USACE 2008*b*). Land crossing opportunities for raccoons along the Alabama River occurred >25 km (via highway bridges) in either direction from LWMA. The Robert F. Henry lock and dam was approximately 10 km from the Lowndes study site but most likely posed a difficult obstacle for raccoons to cross the river (A. Lovell, Alabama USDA/APHIS/WS, personal communication).

The second study area in Lowndes County, east of the Alabama River, was composed of privately owned agricultural land (agricultural habitat), near the township of St. Clair. This study area was approximately 1,180 ha and was 60% pasture for cattle farming. The remaining land was comprised of fence rows, hardwood forest patches, ponds, streams, and man-made structures, including several chicken houses and storage buildings. Night-time raccoon hunting was allowed on both Lowndes County study sites from 6 September through 28 February, although few animals were harvested (50 raccoons in 2005; McCutcheon 2006).

The third study area was the Autauga Community Hunting Area (AWMA), located in Autauga County, north of the city of Prattville and west of the Alabama River. This area was available to the public for hunting during regulated seasons and was managed by the Division of Wildlife and Freshwater Fisheries, Alabama Department of Conservation and Natural Resources. The entire hunting area, owned by International Paper and leased to the state, encompassed 2,638 ha, approximately 1,600 ha of which were included in the core study area. The Autauga hunting area was dominated by long-leaf (*Pinus palustris*) and loblolly (*P. taeda*) pine forests (≥80%) managed for native restoration and commercial harvest, respectively. Pine stands were intersected with streamside management zones and planted food plots used to attract game species during hunting seasons. In addition to planted food plots of chufa, millet, cowpea, corn, oat, wheat, and rye, management on the AWMA included prescribed burning and herbicide application (managed pine habitat). Raccoon hunting in AWMA occurred from 1 September through 28 February with 7 animals harvested in 2005 (McCutcheon 2006).

The final site was located in Hale and Bibb counties just south of Tuscaloosa, Alabama. Oakmulgee Wildlife Management Area (OWMA) was characterized as a mixed pine–hardwood forest that encompassed approximately 14,960 ha in the Talladega National Forest. The terrain included swamps, valleys, creeks, and a federal camp ground open to the public with a 39-ha lake (Lake Payne). The WMA was an active breeding site for the red-cockaded woodpecker (*Picoides borealis*) and management included year-round prescribed burning in the long-leaf pine habitats. This region was also characterized by slight elevation changes (30–48 m) with hardwoods dominating lowlands and conifers dominating the ridges. Secondary and tertiary creeks were common in the lowlands that often lead to swamplands. Forest composition consisted of approximately 30% hardwoods and 68% pines, mostly long-leaf pine, as well as regenerating pine forests (8%). Hunting of raccoons was permitted from 1 October to 28 February and was popular in this area during our study with 650 raccoons harvested in 2005 (McCutcheon 2006). Raccoon trapping occurred statewide from 15 November through 20 February, and state laws prohibited the translocation of raccoons within the state (Code 220-2-26 of the Alabama Wildlife and Freshwaters Fisheries Regulations).

METHODS

Raccoon Demography

We captured raccoons in 0.8 × 0.25 × 0.30 m single-entry Tomahawk box traps (Tomahawk Live Trap Company, Tomahawk, WI) baited with sardines, anise oil, and marshmallows from January 2004 through October 2005. We deployed traps in late morning or early afternoon in locations that contained sign (e.g., tracks, scat) or in areas frequented by raccoons throughout the study sites to maximize trap success. We distributed traps throughout each habitat to ensure coverage of the area. We immobilized raccoons with ketamine hydrochloride and xylazine (5:1 ratio), injected with a handheld syringe intramuscularly. We did not vaccinate animals against rabies nor did we administer antibiotics. We weighed, sexed, ear-tagged (Monel no. 3; National Band and Tag Company, Newport, KT), and microchipped (AVID®; MicroChip ID, Folsom, LA) animals for individual identification. We determined initial age classification, adults (≥12 months) or juvenile (<12 months) using tooth wear (Grau et al. 1970) and reproductive characteristics (Sanderson 1961). We extracted a lower premolar with dental elevators and submitted it to Matson's Laboratory LLC (Milltown, MT) for cementum age analysis and tetracycline biomarker determination. We drew approximately 5 mL of blood from each individual to test for prevalence of rabies virus neutralizing antibodies and canine distemper. Lab analyses were conducted by the Atlanta CDC (National Center for Zoonotic, Vector-Borne, and Enteric Diseases, Atlanta, GA) and Cornell University, respectively.

We radiocollared adult (≥1 yr) raccoons with either a mortality-sensor very high frequency (VHF) transmitter (Advanced Telemetry Systems, Inc., Isanti, MN and Telemetry Solutions, Walnut Creek, CA) or a 200-g Global Positioning System (GPS)-Posrec™ transmitter (Telemetry Solutions). We fitted collars with GPS transmitters only on raccoons that weighed ≥3.5 kg; size and weight of the radiocollar typically resulted in a poor fit on smaller animals. The GPS transmitters recorded 4 locations from 1900 hours to 0100 hours, 7 days a week, and a VHF beacon was scheduled to transmit 2 days a week, during 0600–1500 hours. An internal drop-off mechanism was initiated with the transmitter activation, which we preprogrammed to cause the release of the collar from an animal's neck at 180 days of activity or low battery power. We attempted to radiocollar and maintain ≥10 adults within each habitat with an even distribution of GPS collars across habitats. We monitored raccoons until recovery and released them at the point of capture. A capture and handling protocol was approved by the Institutional Animal Care and Use Committees at Auburn University, Alabama, and USDA/APHIS/WS/National Wildlife Research Center, Fort Collins, Colorado (no. QA-1105).

We located radiocollared animals ≥3 times/week using a handheld 3-element directional Yagi. We monitored animals throughout a 24-hour period with ≥2 hours between consecutive locations. We triangulated locations of collared raccoons using the LOCATE (Pacer, Truro, Nova Scotia) software package with ≥2 bearings taken <10 minutes apart. To minimize error, we maintained bearing angles between 20° and 160° (Gese et al. 1988). Sequential locations, obtained at least twice a week, were run on a 12-hour basis, with a location on each raccoon recorded every 2 hours. In addition, we made monthly attempts during the daytime to track animals to their resting and denning sites. In the event that we could not locate a radiocollared raccoon, we conducted extensive searches for the individual by driving throughout the study areas and surrounding areas on established roads. We conducted 3 telemetry flights to locate animals that had been missing for >1 month (Mech 1983). We assessed telemetry bearing error with a double-blind beacon study (White and Garrott 1990) using test transmitters in the Lowndes WMA, OWMA, and AWMA. Precision of bearings was 7.3° and 6.8° at Lowndes

WMA and AWMA, respectively. Bearing error was slightly lower in the OWMA at 5.8°.

Population densities not only influence rate of transmission, but also rate and perhaps distance of dispersal (Kauhala et al. 2006). In areas where density is low and contacts few, rabies may not be able to perpetuate. To estimate populations, we conducted density trapping sessions October–November in the bottomland hardwood forest, agriculture, and mixed pine–hardwood forest habitats in 2004 and 2005 and the managed pine habitat in 2005. We were unable to trap the managed pine habitat in 2004 due to study constraints. We conducted density studies for 10 nights, using a 50-trap grid in a 3-km^2 area using ORV program protocols (D. Slate, USDA/APHIS/WS, unpublished data), with the goal of capturing all unique (not previously captured) raccoons in the grid area. This approach provides a conservative point in time estimate. We conducted a smaller scale density study on the agriculture site using a 50-trap grid (1.5 km^2) for 5 nights in 2004 due to study constraints.

We monitored radiocollared raccoons to determine difference in survival for animals within and outside of the rabies enzootic area. We determined possible cause of mortality by examining the carcass for external and internal injuries, puncture wounds, and hemorrhaging. Physical evidence at the site of mortality such as tracks, scat, or hair also assisted in determining possible cause of death. For analyses, we divided study sites according to recorded presence of rabies: east of the Alabama River (rabies known to be present), west of the Alabama River (sporadic and isolated cases, some rabies may be present), and OWMA (no reported rabies cases). We estimated annual and seasonal survival based on number of radio-days an animal survived, using MICROMORT (Heisey and Fuller 1985). We defined survival as the probability of a radiocollared animal surviving from the beginning through the end of a specified time period. We defined biological seasons following Chamberlain and Leopold (2002): breeding (1 Feb–31 May), young rearing (1 Jun–30 Sep), and dispersal (1 Oct–31 Jan). We produced a minimum estimate of survival by assuming all missing animals had died (Heisey and Fuller 1985). Additionally, we used the bias-corrected estimate of survival in analyses, as estimations of interval survival rates are known to become more biased with smaller samples, longer interval lengths, and lower daily survival rates (Heisey and Fuller 1985). We tested for differences in survival among study sites and between sexes and seasons using a z-test (Nelson and Mech 1986) and we considered survival rate differences significant at $P \leq 0.05$.

Rabies Prevalence and Distribution

We compiled information obtained from the Alabama Department of Public Health (ADPH) on reported raccoon rabies cases (brain stem analyses) from 1975 through 2005 by county and entered it into a Geographic Information System using ARCVIEW (v3.3). Surveillance conducted by ADPH and WS from 2002 to 2003 confirmed raccoon rabies cases in wildlife and domestic animals in Clarke and Autauga counties, indicating that raccoon rabies may be spreading west across the Alabama River (Kostrzewski et al. 2004).

Baits containing oral rabies vaccine were distributed as a contingency action to create a vaccination buffer in response to recently confirmed raccoon rabies cases west of the Alabama River. This management action was taken in an attempt to produce an integrated barrier to reduce the risk of raccoon rabies spreading to the west of the Alabama River. We distributed fishmeal polymer (FMP) baits containing 1.5 ml of Raboral V-RG® rabies vaccine and 150 mg tetracycline as biomarker (MERIAL Limited, Athens, GA) in parts of Lowndes, Montgomery, Bibb, Chilton, Coosa, Elmore, and Autauga counties (3,504.4 km^2) from 5 to 8 April 2004 (Kostrzewski et al. 2004) in an effort to establish a rabies-immune buffer (Fig. 1). The standard baiting density of 75 baits/km^2 was increased to 150 baits/km^2 in the center of the ORV bait zone, encompassing a 16-km radius around the most recent 2004 confirmed raccoon rabies case (Kostrzewski et al. 2004). We conducted an additional bait distribution from 3 to 5 March 2005 to continue to maintain a rabies-immune area west of the Alabama River (Nelson and Slate 2005). We distributed FMP baits from a fixed-wing aircraft (237,520 baits) and by hand (vehicle access with some hand-baiting along the river and railroad tracks; 17,280 baits) in a 3,521.4 km^2 area in parts of Autauga, Bibb, Chilton, Coosa, Dallas, Elmore, Lowndes, and Montgomery counties.

We collected blood samples from captured raccoons and sent serum samples to CDC for analyses. We compared rabies titers between habitats using an analysis of variance (ANOVA; SAS® Version 8.0, SAS Institute Inc., Cary, NC). As a measure of rabies and canine distemper disease prevalence, we used the ratio of positive antibody ($>$0.05 IU/mL) to the number of raccoons tested (Riley et al. 1998).

Spatial Relationships and Movements

We examined interactions of neighboring raccoons to understand the risk of contacts and the rate of disease transmission. We estimated home ranges and core areas for animals with $\geq$30 locations, with the adaptive kernel method using 95% and 50% isopleths respectively, in the program CALHOME (Kie et al. 1996). We eliminated location data with errors $\leq$0.1 km^2 from the home range analyses. We calculated a smoothing parameter (h_{cv}) in CALHOME by least square cross-validation and manually altered it, following Kie et al. (1996) and Worton (1995), to reduce bias in the adaptive kernel density estimation of home ranges. We examined overlap between neighboring raccoons using static interaction indices constructed based on seasonal home ranges and core areas estimated by the adaptive kernel method (Kernohan et al. 2001). Static interactions examine the spatial relationship of neighboring animals during a given time period. We delineated area of overlap using ARCVIEW and calculated static overlap indices following Kernohan et al. (2001). We sorted interactions into sex-specific dyads (M-M, F-F, M-F) and pooled seasonal overlap percentages across 2004 and 2005.

Prior to analysis, we applied an arcsine transformation to the proportional data of the indices and combined the coefficients according to season. We used a 3-way ANOVA with least square means (SAS) to test for differences in home range and core area overlap indices blocked by years within dyads, across seasons and sites.

We further refined our static interaction indices for neighboring raccoons using point locations within overlap areas. We calculated home range overlap indices following Gehrt and Fritzell (1998) methodology for quantifying association patterns:

$$\frac{n_1 + n_2}{N_1 + N_2} \times 100$$

where n_1 and n_2 are the number of locations within the overlap zone of the adjacent raccoons, and N_1 and N_2 refer to the total number of locations recorded for each raccoon. We tested mean home range overlap indices with an ANOVA (SAS) to test for differences between seasons and across sites. We did not consider difference between dyads because transmission of rabies is not sex dependent.

Dynamic interactions differ from static interactions in that the temporal nature of the relationship between neighboring animals is considered (Kernohan et al. 2001) and therefore, simultaneous locations of neighboring animals are used. Raccoons may exhibit static interactions but temporally avoid one another thus reducing possibility of disease transmission. We calculated dynamic interactions between raccoons if animals exhibited static interactions (e.g., home range overlap). We computed observed distance for raccoons between locations obtained within 30 minutes and expected distances from a randomized boot-strapped sample of all possible pair locations using Ranges 6 (Anatrack Ltd., Wareham, United Kingdom). For all interactions pooled by season for each habitat, we compared the difference between expected and observed distances using a Jacobs Index (Jacobs 1974) and compared indices among habitats using a sign test (Zar 1996, Gorman et al. 2006). Positive interactions (attraction) were suggested when observed distance were less than expected distances and may suggest an increased chance of disease transmission.

RESULTS

Raccoon Demography

We captured 217 raccoons on the 4 study sites: 127 in 2004 and 90 in 2005. We captured 121 raccoons (62 M, 59 F) in the rabies enzootic area east of the river and the study site just west of the river. Of these captures, we fit 26 raccoons with radiocollars in LWMA, 16 at the agriculture site, and 19 at AWMA. We captured 77 raccoons (45 M, 32 F) in OWMA. Of these, we radiocollared 25 males and 14 females.

Density estimates based on trapping were highly variable among study areas and within study areas between years (Table 1). We know these estimates are conservative because given the size of the area and sampling period, we did not capture several radiocollared raccoons during density indexing. We combined information obtained from the density estimate with known alive radiocollared animals in the area to estimate minimal number of animals known alive. Animals not captured during the density estimate, but known alive, tended to be females in 2004 (100%) and males in 2005 ($n = 15$, 65%). Density estimates for the pine–hardwood mixed forest (OWMA) may be biased due to trapping near Lake Payne where raccoons are likely concentrated compared to the surrounding pine forests.

Table 1. Fall raccoon population density estimates based on a 3-km^2, 50-trap grid area in 4 habitats in central Alabama, USA, 2004–2005. We obtained additional estimates reported as minimal animals known alive (MAKA) from combining trapping information with collared animals not captured during the density estimate but known to be in the alive in the area. Data are presented as unique raccoons per square kilometer at the Oakmulgee Wildlife Management Area (OWMA), agricultural site, Lowndes Wildlife Management Area (LWMA), and Autauga Wildlife Management Area (AWMA).

	2004		2005	
Habitat	Estimate	MAKA	Estimate	MAKA
Pine–hardwood forest (OWMA)	5.0	5.3	7.0	9.0
Agriculture	8.0[a]	9.3	5.3	5.6
Bottomland hardwood (LWMA)	10.0	10.7	3.0	5.7
Managed pine forest (AWMA)			3.0	5.3

[a] Densities in this study area in 2004 were based on a 1.5-km^2 area.

During the study 22 raccoons (10 M, 12 F) died. An additional 35 animals had unknown fates. Although we were able to locate carcasses in <2 days, we were unable to determine cause of death for several of the animals due to the fast degradation of carcasses from the southern climate and scavenger activity. We assumed unknown fate animals dead, although we found transmitter failure to be a problem for $\geq$8 animals when we ultimately recaptured them. Our estimates are therefore likely to be lower than expected across habitats. Annual survival rates were similar between study areas for males in 2004 and 2005 and females in 2004. Female raccoon survival rate west of the river (rabies sporadically occurs) was lower than both the eastern females (rabies enzootic zone; $z = -3.47$, $P < 0.001$) and the OWMA females (no known rabies cases; $z = 1.63$, $P = 0.05$) in 2005. Distribution of the FMP baits west of the river may have increased raccoon survival in the area compared to east of the river. Although the study area east of the river included the ORV bait area, bait uptake by radiocollared animals was low and did not appear to increase survival. Survival rates between study sites were similar during the 2004 rearing season (Table 2) except between males in the west and east during the 2004 dispersal season ($z = -1.66$, $P = 0.05$). Survival rates between males in the OWMA and west of the river differed in the 2005 breeding ($z = -1.75$, $P = 0.04$) and rearing ($z = 1.68$, $P = 0.04$) seasons. We also observed differences in the breeding 2005 season between western and eastern female raccoons ($z = -1.79$, $P = 0.04$) and the 2005 rearing season between OWMA and western females ($z = 1.68$, $P = 0.04$).

Table 2. Seasonal survival rates of male and female raccoons in 3 areas in central Alabama, USA, 2004–2005. The areas are defined by recorded presence of raccoon rabies: east (rabies enzootic zone), west (sporadic occurrence of rabies), Oakmulgee Wildlife Management Area (OWMA; no known rabies cases).

	F					M				
			95% CI					95% CI		
Interval	*n*	Estimate	Lower	Upper	Variance	*n*	Estimate	Lower	Upper	Variance
Rearing 2004										
OWMA	12	0.821	0.638	1.0	0.012	3	0.574	0.263	1.0	0.082
East	23	0.909	0.802	1.0	0.004	15	0.866	0.716	1.0	0.007
West	10	0.687	0.469	1.0	0.021	6	0.832	0.607	1.0	0.021
Dispersal 2004										
OWMA	15	0.643	0.435	0.991	0.019	15	0.864	0.665	1.0	0.014
East	12	0.932	0.818	1.0	0.004	8	0.653	0.464	0.950	0.015
West	6	0.581	0.315	1.0	0.044	6	0.757	0.481	1.0	0.037
Breeding 2005										
OWMA	9	0.444	0.242	0.909	0.025	9	0.722	0.485	1.0	0.025
East	19	0.539	0.365	0.833	0.013	12	0.831	0.656	1.0	0.011
West	6	0.823	0.589	1.0	0.022	5	0.417	0.193	1.0	0.042
Rearing 2005										
OWMA	11	0.809	0.618	1.0	0.013	9	0.728	0.525	1.0	0.017
East	17	0.634	0.453	0.916	0.013	12	0.581	0.379	0.937	0.019
West	6	0.457	0.241	0.983	0.030	4	0.242	0.075	1.0	0.067

Rabies Prevalence and Distribution

Single isolated raccoon rabies cases in Alabama were reported in 1954, 1957, and 1961, although it is unknown whether these cases represented the raccoon variant of the disease. By 1975, raccoon rabies was established in the state, concentrated in the southeast corner near Georgia and Florida, with a zenith in cases reported in 1985 (Fig. 2). Although isolated raccoon rabies cases occur sporadically west of the Alabama River, the disease never appeared to become established (Fig. 3). Fifteen isolated cases of raccoon rabies variant occurred west of the Alabama River with 67% of the reported cases occurring in raccoons. Domestic horses, skunks, and gray fox comprised the other reported cases. Reported cases for raccoons occurred mostly during the dispersal season (50%; 1 Oct–31 Jan).

Rabies antibody titers were reported from the CDC as exact numbers or titers <0.05 IU/mL (no reaction exposure) for 188 samples of 166 animals. If animals were tested twice, we used the greater titer to determine prevalence in the habitats. We observed a difference in rabies titers between the habitat types ($F_{3,162} = 3.35$, $P = 0.02$). Most of the animals ($n = 43$ of 46) in mixed pine–hardwood forest outside the rabies enzootic area showed no exposure to rabies (7% prevalence). Those that tested positive had low titers (0.08, 0.09, and 0.1). Prevalence at the managed pine site (AWMA) west of the river was higher (28%, $n = 7$ of 28) than the agriculture (19%, $n = 6$ of 31) and bottomland hardwood (LWMA, 13%, $n = 8$ of 61) areas east of the river. In the managed pine habitat, prior to the April 2004 bait drop, 25% ($n = 4$ of 12) of raccoons were positive, all within the breeding season. We captured 22 raccoons more than once and calculated titers. Only seven had positive titers. In the sites east of the river, titers usually remained the same or decreased on the second sampling.

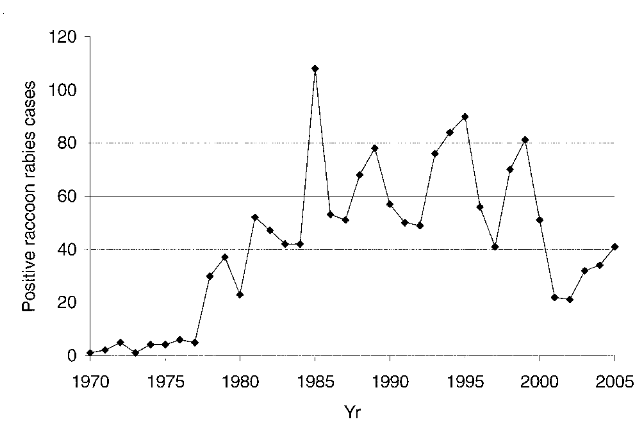

Figure 2. Positive raccoon rabies cases confirmed in Alabama, USA, and reported to the Alabama Department of Public Health from 1970 through 2005.

West of the river the titers increased in 1 of 3 raccoons tested on the second sampling period. Of the 24 samples from the managed pine habitat, 5 showed positive titers after the bait drops; however, only 2 of these animals were known to have consumed the vaccine from biomarker evidence. In addition, one animal with biomarker evidence showed no rabies titers.

Two animals (C7305 and C1404) at the managed pine habitat had titers above the full neutralization of the virus (≥0.56 UI/mL; K. Nelson, USDA/APHIS/WS, personal communication; C. Rupprecht, CDC, unpublished data). Bait uptake as determined from biomarking appeared to be low in that only 12% of radiocollared animals tested after the bait drops ($n = 24$) showed evidence of tetracycline biomarkers. Testing of additional animals (not radio-collared) in the bait zone demonstrated a continual low uptake and marking of the FMP baits (11/133 = 8%; A. Lovell, personal communication). Canine distemper anti-

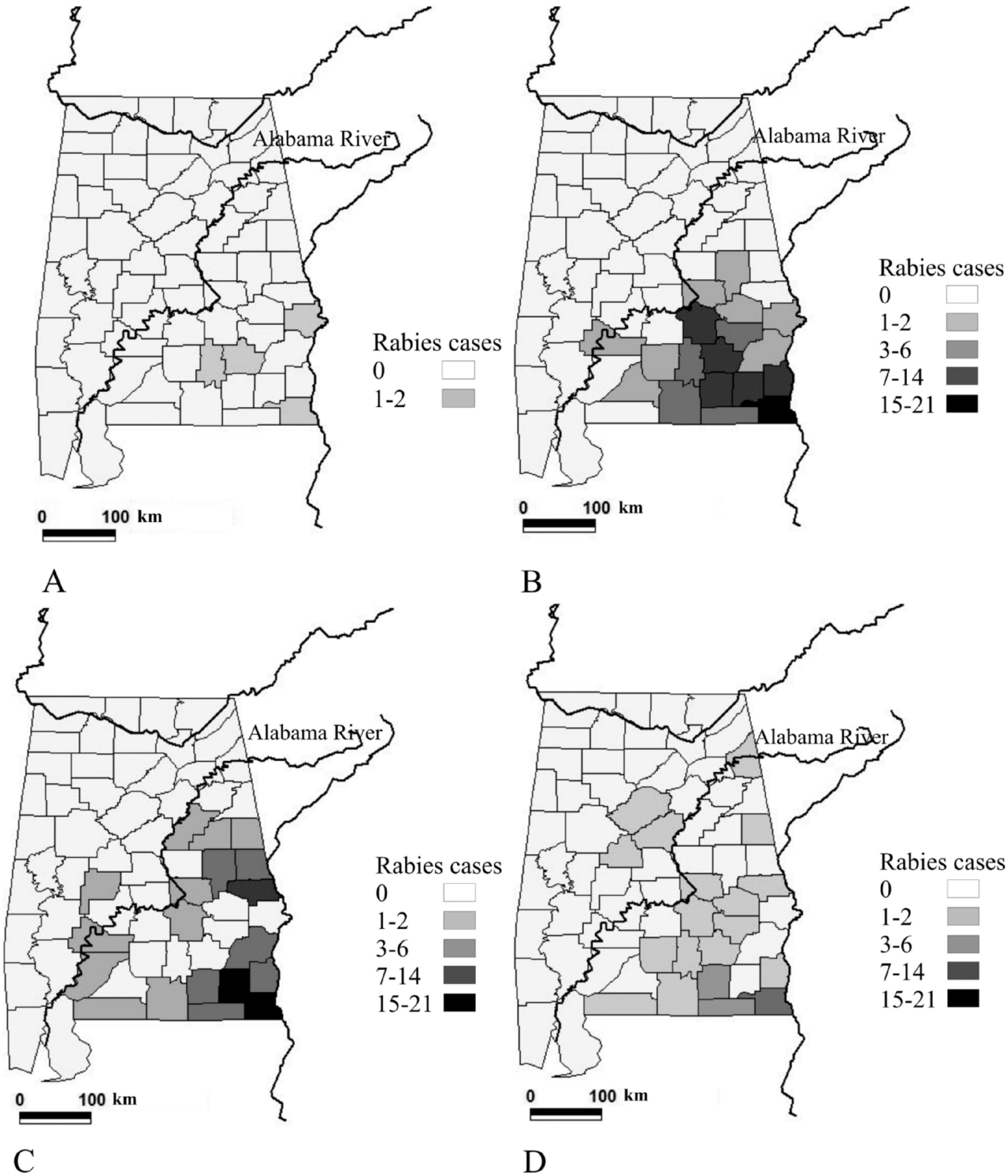

Figure 3. County distribution of raccoon rabies cases in Alabama, USA, reported to the Alabama Department of Public Health in (A) 1975, (B) 1985, (C) 1995, and (D) 2005.

body results from the 2004 samples (n = 113) showed a higher prevalence for distemper in the habitats east of the river (bottomland hardwood = 25%, n = 10 of 40, and agriculture = 40%, n = 7 of 18) than those habitats west of the river (managed pine = 20%, n = 4 of 14, and mixed pine–hardwood forest = 14%, n = 6 of 42).

Spatial Relationships and Movements

We recorded 7,297 locations for 97 raccoons from 17 February 2004 to 15 December 2005 that met our filtering criteria. We estimated 510 seasonal overlap indices for 71 raccoons (37 M, 34 F). Home range overlap differed among season, sites, and dyad ($F_{36,473} = 2.9$, $P < 0.001$); however,

Table 3. Estimated home range and core area overlap between male–female (M-F), male–male (M-M), and female–female (F-F) raccoon dyads in central Alabama, USA, 2004–2005. Four habitats are represented by the sites: agriculture, bottomland hardwood (Lowndes Wildlife Management Area), managed pine (Autauga Wildlife Management Area), and mixed pine–hardwood forest (Oakmulgee Wildlife Management Area).

		Home range		Core area	
Site	*n*	Overlap (%)	SE	Overlap (%)	SE
M-F					
Agriculture	39	34	6	17	5
Bottomland hardwood	51	23	5	8	3
Managed pine	19	44	10	9	6
Mixed pine–hardwood	61	24	4	8	3
M-M					
Agriculture	26	19	6	7	2
Bottomland hardwood	50	25	4	13	4
Managed pine	48	14	4	5	2
Mixed pine–hardwood	66	9	3	8	3
F-F					
Agriculture	42	15	5	5	3
Bottomland hardwood	30	21	6	5	3
Managed pine	10	48	12	12	8
Mixed pine–hardwood	68	19	3	5	2

core area overlap did not differ ($F_{36,473} = 1.3$, $P = 0.12$). Year did not affect static home-range interactions ($F_{1,473} = 0.84$, $P = 0.36$) or core area interactions ($F_{1,473} = 1.24$, $P = 0.27$). The main effects of season ($F_{2,473} = 5.61$, $P = 0.004$), site ($F_{3,473} = 5.91$, $P < 0.001$), and dyad ($F_{2,473} = 4.395$, $P = 0.008$) contributed to the model. Interactions of biological season and site ($F_{6,473} = 4.39$, $P < 0.001$) and site and dyad ($F_{6,473} = 2.74$, $P = 0.01$) also influenced the model. Home range overlap in the mixed pine–hardwood habitat was less than both at the agricultural ($P = 0.005$) and bottomland hardwood habitats ($P < 0.001$; Table 3). Home ranges for animals in the bottomland hardwood habitat exhibited less overlap when compared to managed pine ($P = 0.008$). Seasonal overlap only varied between the rearing and breeding season ($P < 0.001$) when changes in female behavior likely contributed to the reduced overlap during kit rearing time.

We found that overlap at all sites was always greater between male and female dyads than either female–female dyads ($P = 0.01$) or male–male dyads ($P = 0.006$). Adult male home ranges in the mixed pine–hardwood site during the breeding season usually overlapped $\geq$2 adult female home ranges and overlap persisted into the rearing season. Male home ranges also overlapped $\geq$2 females in both the agricultural and managed pine sites, but only 1–2 females at bottomland hardwood. Little overlap occurred during the rearing season on the latter 3 habitat areas. On a finer scale, we found no difference between habitats or season in the use of the overlap area ($F_{11,129} = 1.63$, $P = 0.09$) based on the point overlap indices.

Most (58%) of the dynamic interactions between raccoons at the agricultural habitat were positive where observed distances were less than expected distances (sign test, $C = 12.5$, $P < 0.001$). Raccoons in the mixed pine–hardwood ($C = 11.0$, $P = 0.009$) and the bottomland hardwood ($C = 8.0$, $P = 0.01$) also showed positive associations. Observed distance between raccoons in the managed pine did not differ than expected under the null hypothesis of no attraction or avoidance ($C = 4.0$, $P = 0.17$).

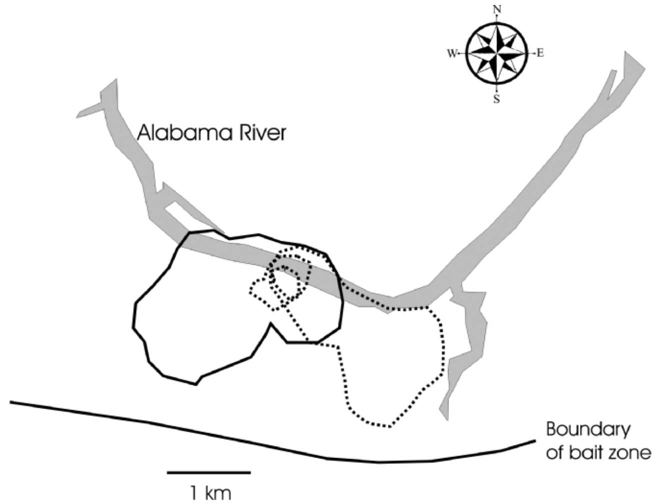

Figure 4. Breeding season home ranges of raccoons with positive rabies antibodies (dashed lines) and an unaffected raccoon (solid lines) in the rabies enzootic zone along the Alabama River, Lowndes County, Alabama, USA, 2005.

We recorded long-distance movements for 2 male raccoons and one female at the LWMA east of the river. One adult male captured east of the river made 2 long-distance movements ($\geq$5.4 km) in the course of 4 days in April 2005. Another subadult male (1 yr old) captured along the river also made 2 long-distance movements across the Alabama River, in July 2005 (1.9 km and 4.6 km). Although one adult female moved 3.5 km in a 5-month period in 2005, her movement was confined to her estimated home range. None of these animals exhibited positive rabies antibody titers at the time of capture; however, other raccoon home ranges adjacent to the Alabama River were positive for rabies antibodies (Fig. 4).

DISCUSSION

This study was designed to better understand raccoon ecology and movement patterns along a portion of the Alabama River to determine its role as a natural, physical barrier to east–west raccoon movements, and therefore, its potential effect on reducing the risk of raccoon rabies spreading. We found that survival rates and raccoon densities were not different between the rabies enzootic area east if the river and study areas west of the river. In addition, spatial movements and home range overlap were restricted in the pine forest habitats reducing possible animal contact and disease transmission. We demonstrated that the Alabama River did not impede raccoon movements, although river crossings were not frequent and were confined to the low-water summer months for radiocollared animals.

The temporal dynamics and intensity of rabies epizootic among wildlife is influenced by physiological and biological factors that relate habitat quality and the resulting carrying capacity for a species (Childs et al. 2000). In the south, a higher density of raccoons can be found in deciduous than pine forest habitats (Leberg and Kennedy 1988). Denser populations tend to sustain the disease and thus may be more impacted by contact (Riley et al. 1998). In fox rabies control, decreased populations stopped the spread of rabies because carrying capacity dropped below a threshold to maintain the disease (Wanderler et al. 1988). However, others argue that dispersal distances are negatively correlated with population density, which may allow for a faster rate of spread of rabies where population densities are lower (Holmala and Kauhala 2006). Raccoon densities in all 4 habitats of our study ranged from 5.3 raccoons/km^2 to 10.7 raccoons/km^2 and appear to range on the lower end of densities reported in other rural settings (Riley et al. 1998). Rabies spread from the mid-Atlantic states into northeast Canada at a rate of 35–47 km/year (CDC 2000, Childs et al. 2000), demonstrating the rate at which the disease can spread unimpeded. The virus spread through high density raccoon populations that had not experienced rabies for decades (Rupprecht and Smith 1994), resulting in an epizootic outbreak substantially greater in magnitude than the previous southern epizootic (Real et al. 2005). Unlike the higher densities observed in the mid-Atlantic region, raccoon population densities in our Alabama study areas may not have been contiguously high enough to perpetuate the disease.

Temporal, spatial, and gender-specific differences in behavior, movements, habitat use, and territory overlap are all factors that affect contact rates (Holmala and Kauhala 2006) and the spread of disease. Contact rates and home range size, in turn, can be influenced by spatial distribution of food resources (Hoffman and Gottschang 1977, Seidensticker et al. 1988) because raccoon activity is often concentrated where water and food resources are abundant (Johnson 1970). In fragmented forested habitats, raccoons are usually concentrated in forest patches and movements are concentrated along streams (Beasley et al. 2007). Raccoons in the agriculture habitat showed positive dynamic interactions and had the greatest core area overlap as home ranges were concentrated in the hardwood forest patches (Fisher 2007). Several of our radiocollared animals east of the river were concentrated along the river in overlapping home ranges, and we observed several animals swimming in the river.

Modeling of the mid-Atlantic epizootic suggested that forested habitat slows rabies transmission where changes in forest composition from coniferous to deciduous forest had substantial effect on contact rates (Real et al. 2005, Smith et al. 2005). Not only were home ranges smaller in mixed pine–hardwood forested habitat in OWMA (Fisher 2007), but ranges tended to overlap less compared to managed pine (AWMA) and agriculture habitats. The managed pine habitat west of the river was a fragmented forest where raccoons concentrated in the hardwood forest with large home ranges (Fisher 2007). Home range overlap was the greatest in this habitat, yet raccoons showed no association (low contact rate) with one another compared to the other habitats.

When there is no exclusive use of space from clumped food resources, the opportunity for increased contact rates and disease transmission occurs (Seidensticker et al. 1988, Prange et al. 2004). Breeding and gestation periods offer increased intraspecific contact, and diseases such as canine distemper are found to be more prevalent during these periods (Chamberlain et al. 1999). Contact rates can be influenced by social systems where increased sociality can lead to increased contact rates and disease transmission. Raccoons tend to be promiscuous or polygynous, with males spending time with several females. We found that male–female dyads always had greater overlap, yet core area overlap was relatively low in all habitats ($<7\%$). Unlike raccoons in other southern locations (Kaufmann 1982), raccoons in central Alabama were not found in communal dens suggesting an abundance of resources (e.g., den sites). Furthermore, we found that male home ranges did not overlap multiple females in the bottomland hardwood habitat east of the river, thus potentially further reducing risk of transmission.

Diseases such as canine distemper and rabies tend to be cyclic in wildlife populations (Roscoe 1993), and rabies outbreaks appear to have seasonal occurrences in winter and spring (McLean 1970), where survival of disease depends upon transmission by infected animals during a short period. Rabies cases in Alabama peaked in 1985 and have continually fluctuated on approximately a 5-year cycle since that time. However, rabies cases remain prevalent in the southeastern portion of the state with only occasional reports west of the Alabama River and south of the Coosa River. The managed pine habitat west of the Alabama River had higher rabies prevalence than the other 3 habitats. Additionally, no clear picture was evident from seasonal prevalence of antibody between habitats east of the river. Animals tested prior to April 2004 in the managed pine habitat (first bait drop) had natural antibody from exposure to rabies in the wild ($n = 4$ of 12). A few animals following the bait drops showed increased rabies titers indicating either an increase in the exposure to rabies or successful booster in immunization from the vaccine. Distemper may also be regulating raccoon populations east of the river in the agriculture and bottomland hardwood forests where 5 recovered raccoons had elevated rabies and distemper titers.

In Europe, the Alps temporally slowed the spread of fox rabies and fast-running rivers and lakes often functioned as natural barriers (Wanderler et al. 1988). Reinforcement of natural and artificial barriers, like the Adirondack Mountains and Cape Cod Canal in the northeastern United States, with oral vaccine deliveries can be an integral component in managing the spread of rabies (Robbins et al. 1998). In areas with few environmental impediments to the spread of rabies, such as Ohio, other drastic remedial interventions are necessary (Russell et al. 2005). A slower spread of rabies transmission associated with river crossings was predicted through modeling (Real et al. 2005) and may be one reason that rabies only occurs infrequently and has not become established west of the Alabama River. Supported by an intensive oral rabies vaccine bait drop program, westward spread of raccoon rabies in Alabama has been significantly reduced but not eliminated.

MANAGEMENT IMPLICATIONS

Rabies was prevalent, even prior to the 2004 ORV program, just west of the Alabama River; however, it appears that biological and ecological factors may affect the establishment of rabies in this area. Reinforcement of natural barriers, such as the Alabama River, with oral vaccine deliveries west of the river should continue to be an integral component in managing the spread of rabies. Long-distance movements especially across a river can result in the spread of rabies and negate the effects of the oral vaccine used in conjunction with natural barriers. Thus baiting during the breeding season, when resident home ranges have the greatest overlap, and prior to long-distance movements, may increase baiting efficacy. Furthermore, a successful vaccination program relies on not only acceptance of a bait, but also successful delivery of the vaccine. Other bait types, such as the Merial coated sachets which have been shown to be more effective for juvenile raccoons (B. Schmit, USDA/APHIS/WS, unpublished data), should be considered when baiting for the smaller southern raccoons in Alabama. Additionally, baiting commensurate with raccoon densities should be ensured in those areas of fragmented and deciduous forests on both sides of the Alabama River, as well as large water sources in pine forests where raccoon populations are likely to concentrate.

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