Evolving Analyses of the Shoshone River Skunk Rabies Epizootic in Wyoming

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ABSTRACT: A rabies epizootic occurred in striped skunks from 1988-1993 in a previously rabies-free area of northwestern Wyoming. USDA APHIS Wildlife Services (WS) cooperated with state and local officials by providing a rabies monitoring and depopulation program starting in 1990. Wyoming WS asked for assistance in 1991 from the National Wildlife Research Center (NWRC) to analyze the epizootic's movements. The goal was to address the public's concerns about their health and safety and that of their domestic animals and livestock. All rabid skunks were diagnosed by the Wyoming State Veterinary Laboratory (WSVL) using standardized fluorescent antibody testing of brain tissues. The "Index Case" was collected on August 15, 1988 near Cowley. The epizootic moved radially out from this location and was limited by skunk habitat that was itself constrained by physiographic barriers. Rabies spread up and down Polecat and Sage Creeks before entering the rest of the lower Shoshone River Basin (SRB). It then moved both downstream to the Bighorn Lake and upstream toward Yellowstone National Park. However, when this epizootic ended in 1993, it had reached only the lower SRB downstream from Buffalo Bill's Reservoir and Canyon. This area has been rabies-free ever since. Over the years various analytical techniques have been utilized by the authors to better understand and describe this epizootic. These have included: traditional county surveillance data (1988); GPS, digitized, and geocoded locations (1991); and GIS databases with and rudimentary landscape epidemiology (1992). Following the epizootic, we used more detailed GIS databases as they were developed for land cover (i.e., habitat), hydrology, and human populations from 1999 - 2006. Subsequent rabies analyses have included: movement of the monthly mean locations (2007); spatial ellipsoid movements indicating "wave fronts" or "crests" (2008); and multivariate movement maps (MMM) (2009). MMM were used to illustrate the rabies front(s) with the instantaneous and spatially described density of cases and directional flow of spreading disease. The advantages and drawbacks of each analysis tool are discussed. The evolution of these different analytical tools and their uses should assist epidemiologists in analyzing and understanding future rabies epizootics.

KEY WORDS: disease, epizootic, geographic dispersal, landscape epidemiology, *Mephitis mephitis*, multivariate movement maps, novel analyses, rabies, Shoshone River, striped skunks, surveillance, Wyoming

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INTRODUCTION

Rabies is one of the oldest known mammalian diseases, with descriptions in canines recorded by Democritus and Aristotle circa 500 BC and 400 BC, respectively, and in humans by Hippocrates circa 400 BC (Baer 1994). It is a viral encephalomyolitic disease that is usually transmitted by the bite from an infected animal, and it has a nearly ubiquitous worldwide distribution occurring on all continents except Antarctica and Australia (Hattwick and Gregg 1975). Rabies may have occurred in the New World before European colonization and possibly as long ago as the Bering Land Bridge (~50,000 years ago) (Rupprecht et al. 1995). In the United States, it was reported in California about 1700, and it became a national reportable disease in 1938. Initially rabies was diagnosed mainly in domesticated mammals, and rabies has one of the oldest surveillance databases. However, the epidemiology of rabies changed in the 1960s when the major reservoirs of the disease changed from domesticated dogs and cats to wildlife (McLean 1970). Wildlife rabies has been described primarily in skunks, foxes (*Vulpes fulva*) and (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), and bats (e.g., Vespertilionidae) (Smith 1988). Spillover to domestic and other mammals from these principal wildlife reservoirs has been described as a common phenomenon (Niezgoda et al. 2002), particularly during regional epizootics (Gremillion-Smith and Woolf 1988).

Rabid striped skunks (*Mephitis mephitis*) have been reported in North America since the early 1800s (Charlton et al. 1991) and in the western United States during the 19th century when they were sometimes referred to as "phobey cats" by cowboys (Baer 1994). Striped skunks were initially the major reservoir in North American wildlife from 1960 to 1989, and since 1989 they have continued to be the major reservoir on the Great Plains (Charlton et al. 1991), while fox have become the major reservoir in other areas of the U.S. (Winkler 1975). In 1986, Smith (1989) presented 6 distinct ecotypes of rabies virus hosts endemic to North America. They suggested that the endemic skunk rabies area of North America had two separate origins, with a northern strain occurring in the north central and eastern states including probably Wyoming, and a southern strain located in the south central states (CDC 1985), but these strains (i.e., variants) are not geographically static. For instance, in Kansas rabid skunk DNA and RNA isolates from brain tissues were

analyzed, and they were not only useful in separating the Kansas southern variant from the South Dakota northern variant, but the data also suggested the southern rabies variant is advancing northward (Barton et al. 2010). This may be of special interest in Wyoming where these genomes may soon overlap and increase the chance for the emergence of viral recombinants, which are often characterized by higher pathogenicity and greater potential for vaccine resistance (Barton et al. 2010). Skunk rabies is becoming even more complex with two new variants, one in California (Sterner et al. 2008) and the other in Arizona.

RABIES HISTORY IN NORTHWESTERN WYOMING

In Wyoming, wildlife rabies has been reported in the scientific literature at least since 1938, and it has mostly involved striped skunks (61%) and bats (*Chiroptera* spp. – 26%) (Thorne and McLean 1982). Thorne and McLean studied 29 skunk rabies cases from 1975 - 1979, and 27 were from the northeastern corner of the state (i.e., Campbell and Crook Counties). Recent epizootics have occurred around Sheridan and Cheyenne, all generally east of the Rocky Mountains/Bighorn Mountains on the Great Plains. However, the area of northwestern Wyoming including the Shoshone River Basin (SRB) has been historically considered to be "rabies-free" for skunks (CDC 1985, Reid-Sanden et al. 1990, Charlton et al. 1991, Ramey et al. 2003).

The rabid skunk that was the Index Case of the epizootic discussed in this manuscript was observed on August 15, 1988 east of Deaver in Bighorn County (Figure 1). The rabies epizootic radiated out from this location near the confluence of Polecat and Sage Creeks (Ramey et al. 2009). During the epizootic, rabies was identified mainly in skunks. All potentially rabid animals were submitted to the Wyoming State Veterinary Laboratory (WSVL), at the University of Wyoming, Laramie, for testing.

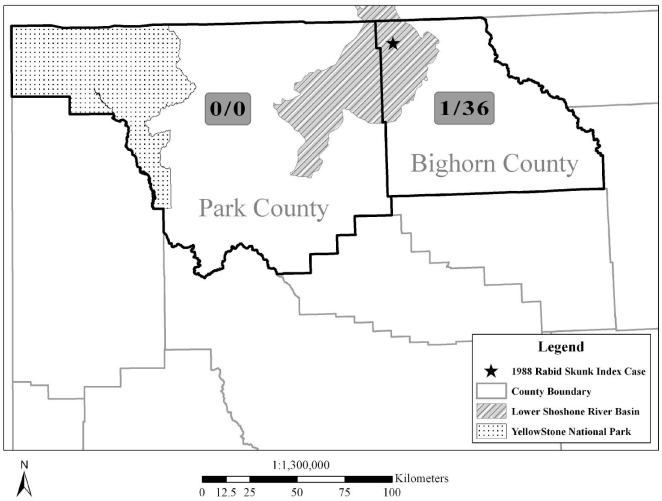

Figure 1. The location of the lower Shoshone River Basin in Bighorn and Park Counties of northwestern Wyoming depicting the Centers for Disease Control's county surveillance data for rabid skunks from 1988/1989. Annual rabid skunk totals from 1988 are listed over 1989 data (1988/1989).

The public and private groups associated with the initial response to the SRB rabies epizootic in 1988 to 1989 included local veterinarians, Bighorn County Predator Board (BCPB), and Wyoming Department of Agriculture (WDA), as well as the state and county Public Health Departments. The public was primarily concerned with human and domestic animals' health and safety, and they wanted quick and effective rabies control. They had observed or heard with alarm about the increasing number of human-skunk contacts in the valley that later turned out to be rabid. These occurred near human dwellings and out-buildings, trailers, dams, bridge riprap, and canals. Unbeknownst to the public, such increases in contact during an outbreak had been reported about rabid skunks in the scientific literature by Ferguson and Heidt (1980) and others. These scientists had postulated that the increased human-skunk contacts were due to the infection altering the rabid skunks' behavior.

The Bighorn County Predator Board provided a trapper in 1989 "anticipating" the possible occurrence of more rabies cases following the index case. Starting in February 1989, more rabid skunks were recorded and found throughout the remainder of the year. In 1990, USDA's Wyoming Wildlife Services (WS) was asked to provide a trapping program to monitor the epizootic's locations and to assist in its control (i.e., depopulation) (Davis 1991). WS shared their trapping results and more detailed rabid skunk locations with the valley's concerned citizens (W. Rightmire, WS State Director, pers. commun., 1991).

Although rabies was local news, rabies hysteria as described by Van Der Veer (1971) did not follow, probably because of the extensive flow of information to the public. Newspapers and radio accounts focused on various types of rabid skunk interactions with other species including humans (Davis 1991). Examples included the following: one skunk attacked a fisherman; another chased a rancher's son; and a third attacked a dog (local veterinarian report to WSVL, June 17, 1993). In addition, 5 rabid bats were found out of 41 tested (1989-1994) (WSVL 1989-1993), and 1 rabid dog. Rabies also was the cause of death of a horse in the Cody area (Cloudwalker 1991, O'Toole et al. 1993). The majority of the lower SRB citizens supported the trapper(s) activities of surveillance and depopulation. As a headline in the Powell Tribune (newspaper) from May 2, 1991 stated, "Trapper kills skunks to help control spread of rabies" (Davis 1991).

In 1991, the National Wildlife Research Center (NWRC) of USDA APHIS WS was asked by Wyoming WS to analyze the spreading rabies epizootic so as to assist in answering the public's health and safety concerns (W. Rightmire, WS State Director, pers. commun., 1991). WS and the NWRC believed by studying the epizootic's movements in the "lower" SRB (Figure 1) from 1988 - 1991 and beyond, WS should be better able to answer some of the public's concerns. This paper provides a synopsis of the evolving analytical methods and maps that were employed. Some were novel at the time they were used, and they illustrated this epizootic's movements and increased our understanding of the Shoshone River skunk rabies epizootic from its beginning in 1988 to its end in 1993.

STUDY AREA

The Shoshone River Basin (SRB), a smaller portion of the Big Horn Basin, lies west of the Bighorn Mountains and just east of Yellowstone National Park. The SRB occurs in Bighorn and Park Counties in the northwestern corner of Wyoming (Ramey et al. 2007). Some of the SRB's headwaters originate near the east entrance of Yellowstone National Park at an elevation of ~2,750 m. The Shoshone River flows eastward ~180 km between arid benches down to the Bighorn Canyon and Lake at an elevation of ~1,200 m. River terracing caused by erosion above the current flood plain led to the formation of gravel benches (Ritter 1975).

The specific epizootic study area has been described in Ramey et al. (2009). It was restricted by the availability of skunk habitat and natural barriers to the "lower SRB" from Buffalo Bill's Reservoir at an elevation of 1,750 m downstream ~90 km to the Bighorn Canyon and Lake (Figure 2). The Shoshone River descends very slowly (i.e., average rate of descent is 6.1 m/km) travelling near several towns including Cody, Powell, Byron, Cowley, Deaver, and Lovell. The study area was restricted to the valley floor, an area of ~843 km^2 of skunk habitat that was composed of a narrow band of riparian habitat along the river (~109 km^2) surrounded by irrigated crops (~734 km^2). These areas formed the primary landscape epidemiological feature of the valley floor, which was a narrow floodplain. Extending up river ~40 km from the mouth of the Shoshone River was a narrow band of 66 km^2 of forest-dominated riparian woodlands including a smaller area of juniper (*Juniperus* g.). Next, a shrub-dominated riparian area (43 km^2) occurred upstream for ~46 km ending just of east of Buffalo Bill Reservoir. The last 4 km of the river's habitat was the steep and arid Shoshone Canyon.

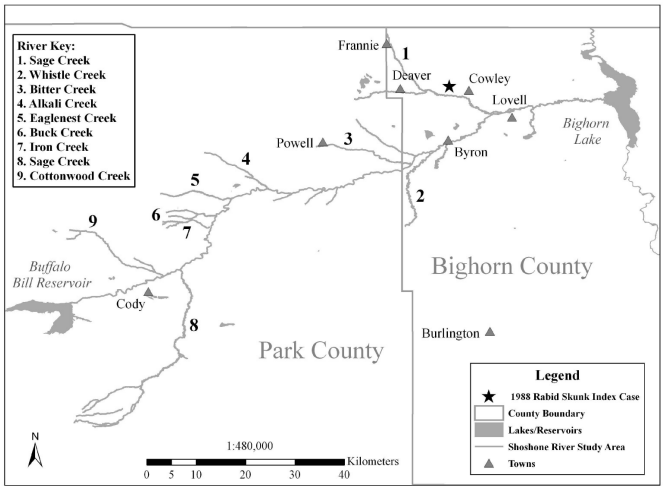

Figure 2. The lower Shoshone River Basin Study Area during the 1988-1993 Striped Skunk Rabies Epizootic illustrating its major tributaries, towns, and the Index Case.

The major landscape features affecting the rabies epizootic and surrounding the riparian areas were the irrigated farms and ranch lands first discussed in Ramey et al. (2009). Early settlers to the valley began to significantly change the valley's floor in the late 1800s using two federally funded projects, one for reclamation (Carey Act of 1894) and one for irrigation (Newlands Act of 1902). Both were spear-headed by "Buffalo Bill" Cody, among others. These two acts stimulated the valley's settlement, leading to growth of the city of Cody and an irrigation water distribution network throughout the valley that greatly assisted in the establishment of farms and ranches (Bonner 2002). The resultant canal network expanded irrigated lands in the lower SRB by nearly 8-fold. Just prior to the rabies epizootic in the 1980s, most of the irrigated lands were dedicated to alfalfa (*Medicago sativa*) production.

A significant by-product of the settler's irrigation activities was an increase in the skunk habitat in the valley, associated with the substantial expansion in crop and pasture lands, as has been similarly observed for skunks on farmlands in Illinois by Storm (1972). In addition, the actual irrigation ditches or canals provided skunks with a semi-aquatic environment, dense cover for dens, water, invertebrates and other food sources, and corridors for travel. As a result of the irrigation canals, the SRB's available skunk habitat had increased from <100 km^2 about 1900 to >800 km^2 in 1989 (Ramey et al. 2009).

The next significant landscape epidemiological feature above the valley floor was the valley's steep and arid slopes leading to gravel benches (Ritter 1975). Skunks were generally absent from these areas, which were composed of predominately saltbush fans, flats of desert shrubs, and gravel (Figure 3). Here, the dominant vegetation was the Wyoming big sagebrush (*Artemisia* sp.), and it was the dominant vegetation in the upper ¼ of the Shoshone River near Buffalo Bill Reservoir. The sagebrush, together with other western high plains xeric land features, had probably formed natural habitat (i.e., landscape epidemiological) barriers that may have isolated the valley's striped skunks and kept them rabies-free until the onset of this epizootic. The lower SRB study area has been described as marginal skunk habitat generally restricted to the river's flood plain (L. Dickerson, WS Superv. Wildl. Biologist, pers. commun., 1991).

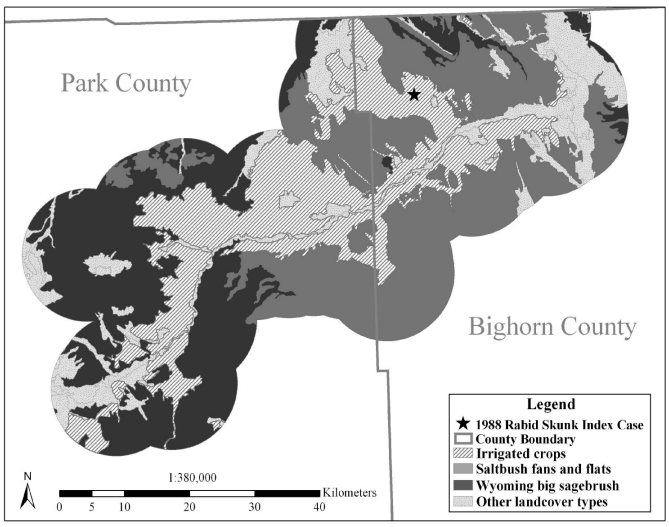

Figure 3. The Lower Shoshone River Basin illustrating the four major land cover types within a 10-km radius of all rabid skunk locations from 1988-1993.

TRAPPING RABID SKUNKS

The BCPB trapping methods for rabies specimens submitted for 1989 by WDA and for 1990 - 1992 by Wyoming WS were presented in Ramey et al. (2007) and will be only summarized here. The maximum number of traps utilized was ~70 in 1991 and 1992. Skunks and some foxes, porcupines, raccoons, coyotes, and domestic pets were caught predominantly in Tru-catch live traps (#30 Wildcat, 30 × 9 × 11 in) (Tru-Catch Traps, Manufacturing Systems, Inc., Belle Fourche, SD). The traps were generally baited with sardines with trapping results similar to those reported by Rosatte et al. (1986) and Rosatte (1985). The utilization of mainly live traps was done so that pets with proof of vaccination could be released. General trapping locations were determined by the trapper(s) in discussions with landowners, BCPB in 1989, and later with WS personnel in 1990 - 1992. The specific trapping locations were determined by observation of skunk tracks and signs. These trapping decisions were later supported by a 1991 literature review focusing on skunk habitat as discussed in Baer (1975), Charlton et al. (1991), Thorne and McLean (1982), and others.

Before initiating trapping, various trappers were consulted about skunk habitat characteristics (discussed above), normal and rabid skunk behavioral differences, and road-kills. Rabid skunk behavioral differences were generally surmised from the trapping results by the trappers themselves over time and in discussions with other trappers who had trapped rabid skunks. Pre-exposure rabies vaccinations were provided to all trappers, and they were taught capturing and handling techniques for potentially rabid mammals from CDC personnel.

Skunk-to-skunk rabies transmission had probably assisted in the spread of the disease during times of skunk dispersal by increasing the number of contacts (Schowalter and Gunson 1982). Greenwood et al. (1997) reported on normal and rabid skunk contacts during fall dispersals in North Dakota using radio-telemetry for tracking their movements. They concluded that fall was a critical time for surveillance and/or control, while others have suggested that spring surveillance is important (Heidt et al. 1982, Rosatte and Gunson 1984). Those who suggested the spring season was the most important period for the spread of rabies in striped skunks felt that in addition to dispersal contact activities, the skunks had spent the winter in communal/family den(s) in close proximity with one another, thus enhancing the spread of rabies.

By 1991, the epizootic's anticipatory movements for both surveillance and depopulation trapping had become so involved as to warrant additional analysis. Therefore, a NWRC scientist was asked to provide analytical input, and he developed descriptive concepts analogous to waves for explaining the rabies epizootic. For example, the dynamic (i.e., ever-changing) "leading edge(s)" were used to describe outlier locations, and "crest(s)" demonstrated area(s) with higher frequencies of rabies cases. Utilizing these constructs, some traps were placed in the epizootic's predicted path based on skunk habitat and associated hydrology; however, most were positioned in known rabies areas to lessen its impact. Predictions using the leading edge(s) alerted SRB citizens projected to be in the epizootic's path, while crests warned them of areas with the highest frequency of rabies. In addition, crests indicated possible areas for controlling rabies that may demonstrate synergistic effects resulting from interaction of depopulation trapping and the virulence of this rabies strain.

Over 1,100 potentially rabid skunks and other mammals were submitted to the WSVL for rabies testing. The standardized testing techniques and procedures used Fluorescent Antibody (FA) Testing after McQueen et al. (1960) and others (K. Mills, WSVL Director, pers. commun., 1995). The WSVL gave highest priority to the testing of potentially rabid animals, and thus a confirmation testing lag time was ~3 days in 1989 and 1990. It increased up to 3 weeks in 1991 and 1992, following sizable increases in the number of potentially rabid specimens received by the WSVL. This time period included logging information on the mammals received, storage time until testing, testing, and production of the Final Report. In summary, our trapping results were similar to those observed by Storm (1972) and Wade-Smith and Verts (1982), with the best habitat providing the majority of the skunks. In our study, the areas infrequently trapped had lacked skunk tracks and/or sign.

RESULTS AND DISCUSSION OF EACH ANALYTICAL STAGE

Traditional CDC County Data

Traditional Wyoming surveillance data included suspiciously acting animals that had been shot or were road kills and that tested positive for rabies. Rabies cases were grouped by county (Figure 1) and the data were forwarded to CDC. Thus, they met the national reporting requirements established in 1938 for rabies (Rupprecht et al. 1995). In this study, the overall traditional county surveillance data were only a small part of the final epizootic sample (~3%), although the data did include the Index Case. Even though other rabid skunk cases were not found in 1988 using traditional surveillance techniques, beginning in February 1989 the BCPB decided to follow a "proactive strategy" of trapping skunks for rabies testing. They believed that if indeed this was the beginning of an epizootic, wildlife rabies would probably spread to other areas around Sage Creek including its primary tributary Polecat Creek. They used the Index Case as the central point for trapping skunks and other possible mammalian reservoirs including dogs and cats in order to provide for the early warning for SRB residents. Their supposition was later supported by the identification of a second rabid skunk caught nearby in mid-February. The BCPB trapper soon captured more rabid skunks, and trapping for rabies was given the highest priority. Unbeknownst to the BCPB members, the usefulness of these strategies for skunk rabies outbreaks had been suggested by others in the scientific literature including Rosatte (1985) and Rosatte and Gunson (1984).

By mid-summer of 1989, BCPB trapper(s) were trapping up to ~30 km radius from the Index Case including most of Polecat and Sage Creeks. By year's end, skunk rabies was occurring along the Shoshone River from its mouth at Bighorn Lake up to Lovell (Figure 2). Although feral animals and other mammals were submitted to the WSVL for analysis, rabies occurred only in skunks and bats. However, some of the early rabies data were not initially very

useful for epizootic analyses, because the rabid skunk locations were often recorded only by the name of the land owner or lease holder. These data met the requirements of the Bighorn County, Wyoming, and CDC to provide for monthly and annual county rabies reports for generating state and national rabies occurrence perspectives. However, with only one county involved in the epizootic in 1988 and 1989 and without any other location details, the worried citizens of the valley did not know where the rabies cases were occurring as 1990 progressed except by word of mouth and a few radio or newspaper accounts. When the NWRC became involved, various "new" analytical techniques were employed besides the traditional county summaries.

GPS and Computer Generated Locations

When an epidemiologist from NWRC was asked in 1991 by WS to analyze the rabies locations, he expressed the need for more precise locations for rabid animals. Thus, discussions were undertaken with the U.S. military that would provide rabies locations based on the use of Global Positioning Satellites (GPS). The NWRC believed that GPS generated data would provide more exact locations for captured rabid animals over the locations derived from landowners or lease holders addresses, compass readings, hand drawn maps, trapper's notes, and telemetry. Later, the advantages, disadvantages, and supplemental use of telemetry were discussed in relation to GPS locations by Lynch (1997).

NWRC sought GPS equipment on intergovernmental loan from the military to generate the latitudes and longitudes of rabies locations from satellites. However, before this could be accomplished, NWRC was able to purchase a Sony portable GPS unit (Model IPS-360, Sony Corp. of America, Park Ridge, NJ). This led to the first use of GPS equipment in investigations of wildlife disease, and it has been described in the movements of 5 rabid skunks out of 22 instrumented in 1991 (Ramey et al. 2007). The Sony GPS equipment generated locations using satellites, providing latitudes and longitudes with a global positional accuracy average of <50 meters, depending on the number of satellites available. Even though the trapper(s) believed that GPS locations would be helpful, they felt the process was too time-consuming for them to employ for every potential rabid animal captured. By September - October 1991, only 7 or 8 of the planned 24-satellite array for the fully GPS operational system had been deployed. Thus, the time to set up and initialize the equipment before determining a location was greater than anticipated, averaging about 20 minutes. Therefore, NWRC scientists agreed with the trappers that other means should be sought to produce the latitudes and longitudes for rabid skunk locations.

The first method employed was "digitization" of the rabid skunk locations in latitudes and longitudes using predominately the trapper's logs and computer-based topographic maps of the area. The 1991 data included detailed descriptions of the rabid skunk locations as recorded by the trappers on BLM 1987 edition 30 × 60-minute quadrangle maps of Cody and Powell, Wyoming. These trapper-generated map locations and their accompanying notes were converted to the global GPS latitude and longitude coordinate system using the "digitization process" first by a private company and shortly thereafter by NWRC personnel. The accuracy of the rabid locations were further increased by cross-checking them with the following information when available: telephone discussions with the landowners or lease holders about their recollections of rabid skunk locations, additional details in the original trapper's logs, copies of the WSVL testing results, veterinarian records, and WDA computer print-outs. In hindsight, most of the citizens of the SRB knew "exactly" where the one or few rabid skunks caught on their land were located, and they generally knew the locations of trapped rabid skunks of their closest neighbors.

The second method used, when BLM rabid map locations and/or trapper's logs were unavailable or incomplete, was referred to as "geocoding". These geocoded locations were defined as the placement of the rabid skunk's location in the center of the owner's or lease holder's lands using computerized maps (Ramey et al. 2007). Geocoding was used whenever only the land owner's or lease holder's name or addresses were recorded in the trapping logs or a more precise location was unavailable in follow-up telephone calls. Another geocoding convention was established for a few residents of the valley that could not be located to clarify their land holdings or the more precise trapping data was lost (~7%). Employing primarily digitized locations and a few geocoded locations, the NWRC location database was developed.

NWRC Databases and Landscape Epidemiology

The first of many NWRC Geographic Information Systems (GIS) databases were constructed in 1992, and they have continued up to the present day. Ramey et al. (1992) analyzed the Shoshone River skunk rabies epizootic using the spatial-temporal data (i.e., location and date caught) for each rabid animal. Using our current context, these locations became the first GIS data "layer" and included the date of capture and the specific rabid skunk's GPS, digitized GPS, or geocoded location (Figure 4) (yearly data being published elsewhere).

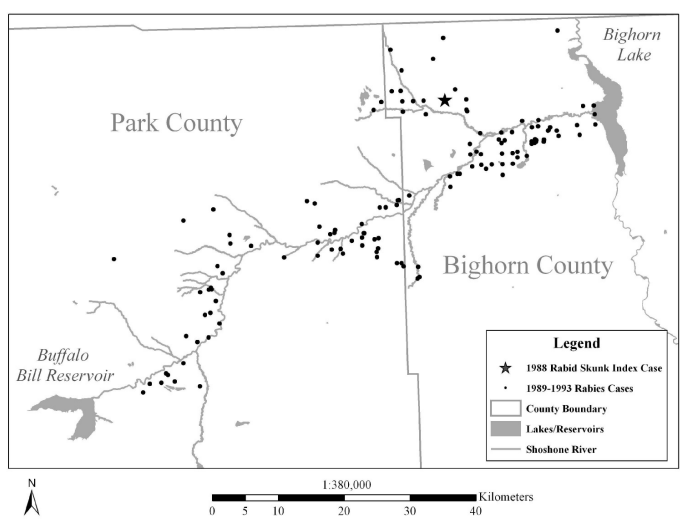

Figure 4. Rabid striped skunk capture locations and some multiple capture locations used to analyze the lower Shoshone River Basin's rabies epizootic from 1988-1993.

The second data layer included the major river sections or tributaries of the SRB. During 1991-1993, we further developed this database by analyzing the Shoshone River skunk rabies epizootic's movements by the addition of computer generated hydrology. These two data layers formed the first "geographic information system" (GIS) utilized in computerized mapping of a wildlife disease epizootic (Ramey et al. 1992) and analyses of its movements (Ramey et al. 1994, Ramey and Mills 1995). In addition, this novel epizootic database in later years included land use features of the valley which were also useful in describing epidemiological features, including naturally occurring habitat "bottlenecks".

The construct of "landscape epidemiology" after Audy (1958), Carey et al. (1978), and more recently Meade and Earickson (2005) was used to also analyze these rabies locations. The result was that movement trends were analyzed in relation to skunk habitat abundance and constraints (i.e., niches and geological bottlenecks) (Figure 3) (Ramey et al. 2008). Utilizing early GIS land use and especially geographic hydrology maps with all documented rabid skunk locations (Figure 4) and their capture dates, information on the spreading skunk rabies epizootic was presented at a national meeting (Ramey et al. 1992), annual conference (Ramey et al. 1994), and international meeting (Ramey and Mills 1995).

The evolution of these early GIS versions of the SRB rabid skunk epizootic was later chronicled by Ramey et al. (2007). Although our computer generated epizootic maps from the early 1990s proved to be useful, they did not approach the detail and usefulness of our more recent maps derived by "new" analytical methods described below. This rapidly evolving area of wildlife disease analysis has made significant progress; for instance, Blanton et al. (2006) developed a GIS-based, real-time Internet mapping tool for rabies surveillance.

Monthly Mean Epizootic Movements

Adding more detailed GIS information for land cover (i.e., habitat), hydrology, and human populations from 1999 - 2006, we employed a new method of analysis in 2007 which we named "monthly mean location" (MML). Although some months did not follow the general trends discussed below, most months demonstrated rabies movements out from the Index Case into new skunk habitat along the SRB. For example, the MML for August 1988 - June 1989, demonstrated the epizootic had established itself in Sage and Polecat Creeks in Bighorn County. By July 1989, the epizootic had reached the mainstream of the Shoshone River, and it began moving both downstream towards Lovell and the Bighorn Lake and Canyon and upstream towards Byron (Ramey et al. 2009). During 1990, the epizootic's monthly mean movements continued to spread into more streams, creeks, and irrigation canals around Sage Creek and the area of the SRB east of Lovell and west of Byron. By 1991, the epizootic's upstream movements had reached areas of the Shoshone River south of Powell. In 1992, the skunk rabies epizootic continued to move west up river reaching the area around Heart Mountain between Powell and Cody (Figure 5). However, in 1993 with only surveillance data (n = 4) available, the epizootic seemed to cover the entire lower SRB; however, by the following year the rabies epizootic seems to have ended and has not reappeared in lower SRB.

In summary, the MMLs provided several analytical advantages over our previous analyses. First, by averaging rabid locations in monthly groups, the resulting MMLs provided a more fluid epizootic movement summary from 1988 to 1993 irrespective of the helter-skelter diversity of locations demonstrated by using only the daily trapping results. Second, the MMLs sometimes brought our focus away from the Shoshone River and major streams to a closer examination the entire water system of the valley. Thus, we identified a maze of smaller streams, creeks, and the extensive irrigation system not illustrated in Figure 5, because it would produce an over whelming abundance of detail. Third and most important, the MMLs indicated the directions and movements of the epizootic and suggested the areas in "harm's way".

Negative aspects of this analytical method have been associated with the loss of the specific information associated with each location. Although the MMLs were helpful in overcoming the helter-skelter appearance of daily rabies trapping maps, some epizootic information associated with each individual rabid location such as associated with outliers and areas with a higher frequency of rabies was not displayed. This detailed information was helpful to the trappers and those planning to possibly control of the rabies epizootic in 1989 - 1991. So another method of analysis was tried.

Spatial Ellipsoid Movements

Positive cases were next analyzed in 2008 utilizing the "Directional Distribution: Standard Deviational Ellipse (Spatial Statistics) (Release 9.1, April 25, 2005). The most common way of measuring the trends in geographically scattered data points is by calculating standard distances separately in the x and y directions. These two measures define the long and short axes of an ellipse encompassing the data distribution of interest: for example, rabid skunk locations on an epizootic map. The ellipse formed is referred to as the "standard deviational ellipse" (SDE); calculating it using ArcGIS 9.2 (ESRI, Redlands, CA) and displaying it on a GIS map made the epizootic trends clearer. This ellipse allows you to see if the distribution is elongated; hence, it has a particular directional orientation (Kent and Leitner 2008).

One use of the SDEs in Spatial Statistics has been to plot ellipses demonstrating the landscape epidemiology of disease in models depicting its movements over space and time (Meade and Earickson 2005). For example: 1) mapping the distributional trends related to a particular physiographic feature such as the Shoshone River with its narrow but elongated skunk habitat, and 2) plotting landscape epidemiology features such as habitat bottlenecks for the spreading rabies epizootic over time. Our output maps illustrated: the ellipse polygon using two standard distances (long and short axes); the orientation of the ellipse in the study area; the rabid case locations; and the number of standard deviations used to determine the ellipse (Figure 6). By specifying the number of standard deviations (e.g., 1 or 3), different distributional maps were produced which highlighted different attributes of the epizootic. With randomly distributed features, 1 standard deviation (the

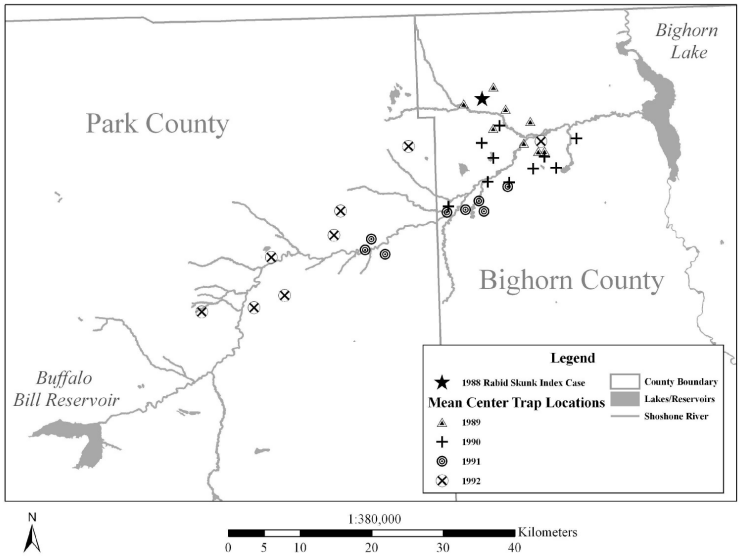

Figure 5. The Monthly Mean Locations of captured rabid skunks along the lower Shoshone River Basin from 1989 to 1992.

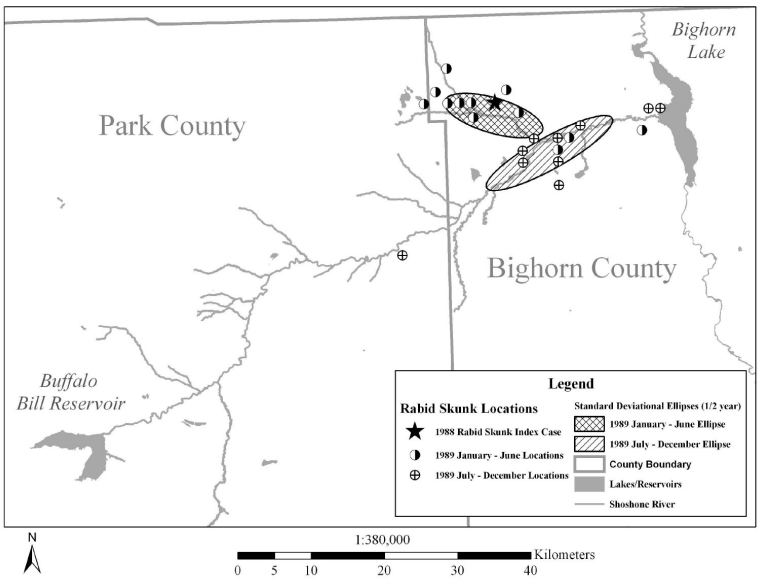

Figure 6. Illustrations of rabid skunk locations from 1989 indicating 6-month standard ellipses using one standard deviation.

default value) covered ~60 % of all input data whereas 3 standard deviations produced a distributional map using 99%. Even though the rabid SRB locations were not randomly distributed, the ellipsoid maps that were produced using 3 standard deviations were helpful in identifying distributional outliers. In contrast, maps produced using 1 standard deviation illustrated ellipsoid areas with higher incidences of skunk rabies and higher rabies exposures for both man and animals (Figure 6). Thus, researchers may select the parameter of interest (e.g., outlier cases versus high frequency crests) for investigation and various illustrative uses. Such analyses and illustrations were particularly helpful in the retrospective identification of the potential barrier sites suggested by Ramey et al. (2009) in a "case study" that could have potentially thwarted the epizootic's spread if they had been used in early 1989.

However, a drawback in the utilization of this technique was that often the area within the ellipsoid seemed to indicate the occurrence of rabies was similar throughout the ellipse, but in actuality the areas with the highest incidence of rabies occurred at the edge of the ellipsoids, which were viewed as crests. Therefore, the interiors of the ellipses may have had very low frequency of rabies because of depopulation effect of trapping and/or inferred "virulence" of this strain. Because these factors were not directly studied, they can only be inferred by the lack of skunks captured behind the crests. Our need to better understand and illustrate these multivariate results led to development of a novel method of analysis which we named "multivariate movement maps".

Multivariate Movement Maps

In 2009, we developed another novel approach, "Multivariate Movement Maps" (MMM). To overcome many of the previous shortcomings presented above in other

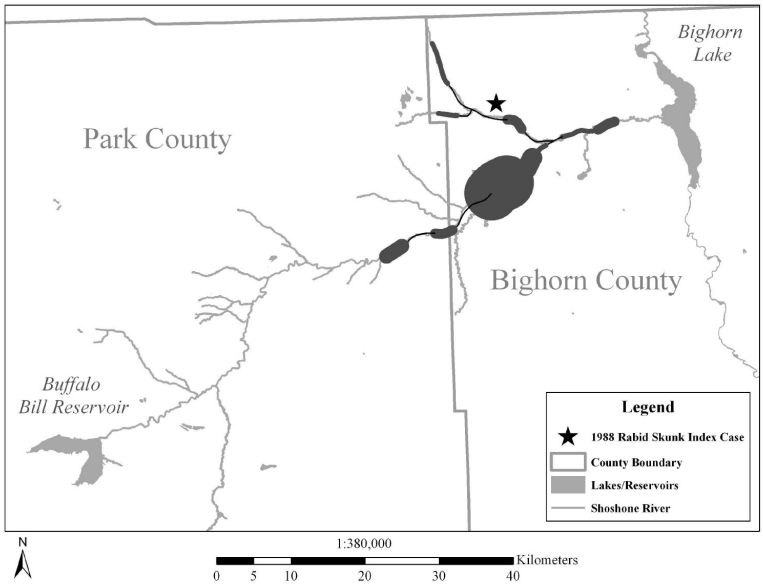

Figure 7. The Multivariate Movement Map for January - June 1990 from the Shoshone River Basin's striped skunk epizootic illustrating the density at four leading edges and one crest.

types of epizootic movement illustrations, we developed MMMs that will be presented in detail in another scientific outlet. MMM illustrations indicate the disease front with the instantaneous and spatially described density of cases and the directional flow of the spreading disease (R. Engemann, NWRC statistician, pers. commun., 2009). MMMs were analyzed for spatial and temporal patterns using the general ideas of Carey et al. (1978) and Recuenco et al. (2007). Our new epizootic movements were depicted in daily, monthly, 6-month, and annual group illustrations.

MMMs analyses were generated from a new "GIS data layer" depicting the frequency of rabies in short river segments. The base line was created by tracing the primary Shoshone River between Buffalo Bill Reservoir and Bighorn Lake as well as Sage Creek from the Wyoming/Montana state line to its convergence with the Shoshone River. This base line was then split into 2.5-km segments. All rabid skunk locations within the appropriate baseline segment were summed to determine number of locations that were to be assigned to each line segment for the appropriate dates. The thickness of each line segment was modified in relation to the number of rabid skunk points assigned to it. Although the line segments were arbitrary in size (e.g., length and thickness), they were selected mindful of the overall rabid skunks locations and preferred skunk habitat. This method seemed to work especially well in this narrow band of riparian habitat along the Shoshone River and extensive canal system limited by the narrow valley floor.

Figure 7 provides an example of a MMM illustrating a one-half year grouping of rabid skunks from January - June 1990 indicating the location of four rabies wave fronts (i.e., "leading edges" of the spreading epizootic) followed by one wave "crest" during this 6-month period. This spatial and temporal pattern was generated from the 4 computerized data layers including the MMM, and it demonstrated the instantaneous and spatially described density of rabies cases. Also, whenever these maps were viewed in temporal sequencing, they indicated the directional flow of the rabies epizootic and its path.

In summary, all of our previous analytical methods were included in the use of MMMs in some respect. For instance, individual rabid locations were not indicated in the black-and-white illustration used here; however, on our color coded maps they were indicated as well as land use and epidemiological landscape features. For this black-and-white MMM illustration (Figure 7), we excluded specific data locations, land use, and epidemiological landscape features described above, to make it easier to identify the epizootic wave characteristics in 1990. Such figures, if they had been available during the epizootic, would certainly have better answered the public's requests for epizootic information, but awaited our novel use of a multivariate illustrative methodology.

DISCUSSION

The Index Case was identified by a homeowner and his family who found this skunk in their backyard. After observing it for a few hours, they telephoned the local veterinarian and described its behavior as unusually "friendly", ambulating erratically, and not spraying. In consultation with a veterinarian, they were instructed on how to kill and transport it to the veterinarian for forwarding to the WSVL. When the family was contacted by NWRC personnel, besides discussing the information presented above, they stated that it may have been a recently released pet. Similar instances of wild caught and "domesticated" skunks or pet store purchases have been documented where the "owners" had a change of heart and decided to release these skunks into the wild. Such activities have been discussed as a serious source of rabies contact with humans (Hattwick and Gregg 1975).

Without a viable skunk rabies vaccine (Slate et al. 2005), the citizens of the SRB were amenable to trapping and shooting for surveillance and depopulation. Because of the precautionary foresight of the BCPB and the capture of more rabid skunks, more groups/agencies became involved with the outbreak of rabies in the valley (e.g., WSVL, veterinarians, WDA, WS, NWRC, Wyoming Game and Fish

Department, Sheriff's Offices, Public Health Officials, and others). The precautionary trapping campaign started by the BCPB in 1989 was successful in obtaining surveillance information during the epizootic, and WS continued this surveillance during 1990 - 1992. However, the success of the other goal, to limit or stop the spread of rabies, was unclear. Although >1,100 mammals were captured from ~800 km^2 of skunk habitat, of which >200 were rabid skunks (Ramey et al. 2009), the depopulation effect of trapping was not studied. The Wyoming Wildlife Services' State Director believed that they had insufficient personnel and funds to meet this goal, but he believed that they had certainly influenced the epizootic's outcome (W. Rightmire, WS State Director, pers. commun., 1992).

NWRC's ever-evolving surveillance illustrations as described herein have provided a variety of perspectives on this skunk rabies epizootic. Using traditional county surveillance data summaries in 1988 and 1989, it was almost impossible to answer the public's concerns about the epizootics movements and potential areas of human and domestic animal contact. The BCPB's surveillance trapping program began the process of identifying much more specifically rabid skunk locations and answering some of the public's need for rabid animals' locations. However, as the number of daily trapping results increased, they provided a rather helter-skelter data set of locations when viewed on a daily basis. Illustrative rabid skunk analyses awaited the involvement of the NWRC in 1991. Also, by co-mingling rabies location data from various sources, its accuracy and reliability was increased for analyses of spatial and temporal patterns.

Important NWRC accomplishments included being the first to gather rabies location data using the GPS technology (1991) and to utilize GPS, digitized, and geocoded locations for the study of wildlife disease in GIS maps (1992). When the epizootic ended in 1993, we focused even more on the analysis of epizootic patterns from our data to understand what had occurred. Each additional analytical methodology seemed to provide some new perspective of the epizootic. From the study in 2007 of the movement of the monthly mean locations of rabid skunks, we observed epizootic trends that had been somewhat lost by trapping of multiple SRB locations. The daily helter-skelter appearance of new rabid skunk locations was replaced by movement trends. Next, we utilized standard deviational ellipses of the rabies epizootic that seemed to demonstrate some descriptive characteristics of waves, such as "wave fronts" and "crests". Although the ellipsoids were useful in analyzing the skunk habitat along the SRB, we derived a new and novel multivariate movement maps (MMM) approach that is being published in detail elsewhere. Besides using these maps to illustrate both the rabies fronts and the instantaneous and spatially described density of cases in the crest(s) over various time sequences, we were able to demonstrate the directional flows of spreading disease.

Some scientists have stated that the epizootiology of rabies seems to be insufficient to reduce the vector population density to a low enough level to curb an outbreak by itself (Winkler 1975); however, many believe that combined with other control efforts the result may be more positive (Linhart 1960). Our post-hoc review of patterns in the spreading rabies epizootic led to discussions about some possible strategies to slow or even halt its spread. Trapping and shooting such as was employed during this epizootic have been reported in the literature to have generally positive results when utilized early in control (Rosatte et al. 1986, Rosatte 1985, Seyler and Niemeyer 1974). Other emergency population reduction strategies for controlling potential rabies vectors have been reported to be successful by Schnurrenberger et al. (1964) for controlling a skunk rabies outbreak in Ohio using den gassing and poison. Trapping, shooting, night-lighting, and poisoning were also utilized successfully to control rabies from 1980 - 1983 by taking ~2,400 skunks in southern Alberta, Canada of which 110 were rabid (Rosatte et al. 1986). However, the timing of intervention is also very important, as was observed in the emergency control of skunk rabies in Montana by Seyler and Niemeyer (1974). They reported their success was due in part to the rapid response of biologists using strychnine eggs; however, the use of strychnine eggs was illegal in 1988 in Wyoming. Even having a multi-agency rabies control committee already established and necessary paperwork completed to quickly respond to any outbreaks certainly adds to the likelihood of a positive outcome as was demonstrated with skunks in Alberta (Gurba 1974). However, the control of rabies by reducing potential vectors continues to be a controversial matter that may not be decided until vaccines are available for all "major" vectors.

MANAGEMENT IMPLICATIONS

In summary, none of the groups and agencies involved in the Shoshone River striped skunk epizootic had foreseen all that would be involved following the testing of a "friendly skunk" for rabies. During the epizootic, some "futuristic" discussions occurred at NWRC that foresaw the need for the further development of GIS, and particularly for a real-time GIS-based mapping tool for rabies surveillance. Also, we felt National Wildlife Research Center of Wildlife Services should become a leader in the study and control of wildlife diseases and become a partner in a national perspective and initiative on the prevention and control of rabies. Since then, all of these thoughts and ideas have become reality; see Hanlon et al. (1999) and Blanton et al. (2006), among others. Lastly, a more positive rabies management outlook has occurred with new trends in the prevention, control and possible eradication of wildlife rabies (Dietzschold et al. 2003, Rupprecht et al. 2006). The development of a skunk rabies vaccine seems nearer, as well as progress in some delivery systems discussed nearly 20 years ago including aerial baiting in rural settings (Johnston et al. 1988) or trap-vaccinate-release in urban settings (Rosatte et al. 1992).

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