Evaluation of historical factors influencing the occurrence and distribution of *Mycobacterium bovis* infection among wildlife in Michigan

RoseAnn Miller, MS, and John B. Kaneene, DVM, MPH, PhD

**Objectives**—To determine historical events leading to establishment of bovine tuberculosis in the white-tailed deer population in the northeastern corner of the lower peninsula (NELP) of Michigan and describe factors relevant to the present outbreak of bovine tuberculosis in Michigan.

**Sample Population**—Cattle and white-tailed deer in Michigan from 1920 to 1990.

**Procedures**—A search of extant historical documents (eg, scientific journals, books, public reports, and correspondence and internal reports from governmental agencies) was conducted. Factors investigated included the number of cattle and prevalence of tuberculosis, deer population and density levels, and changes in regional environments affecting the population and management of cattle and wild deer.

**Results**—High deer numbers and severe winter feed shortages resulting from habitat destruction in the NELP in 1930 contributed to the transmission of tuberculosis from cattle to deer. Starvation increased the susceptibility of deer to infection and modified behavior such that exposure to infected cattle was increased. Relocation of deer resulted in spread of infection to other sites, including locations at which spatial clusters of tuberculosis presently exist. Ribotyping of *Mycobacterium bovis* from a human patient suggests that the strain of *M. bovis* presently infecting white-tailed deer in the region is the same strain that affected cattle farms at that time.

**Conclusions and Clinical Relevance**—Feeding deer to maintain numbers above the normal carrying capacity of the NELP led to deer depending on consumption of livestock feed for survival during winter and increased contact with domestic cattle. This practice should be avoided. (Am J Vet Res 2006;67:604–615)

The NELP of Michigan is the only locale in the continental United States where bovine tuberculosis is known to be endemic in a wildlife population. The first evidence that tuberculosis was affecting white-tailed deer (*Odocoileus virginianus*) in the region arose in 1975, when tuberculosis was diagnosed in a hunter-harvested deer from Oscoda County. Infection was considered to have resulted from exposure to local cattle with tuberculosis because tuberculosis had only recently been eradicated from the state. In 1979, after 5 years of livestock surveillance in which no additional cases of tuberculosis were discovered, Michigan was declared free of tuberculosis.

The discovery that tuberculosis was endemic among wild white-tailed deer in the NELP was made in 1994, when lesions consistent with the disseminated form of tuberculosis were observed in a deer harvested by a hunter on privately owned land in Alpena County. Surveillance of white-tailed deer in the 650-km² area around that location was initiated, and tuberculosis as an endemic infection in the wild deer population in that region of Michigan was confirmed. In 1996, the scope of surveillance was expanded to include elk (*Cervus elaphus*) and nonruminant mammal populations and the geographic area of surveillance was increased to include Alcona, Alpena, Montmorency, and Oscoda Counties (ie, the 4-county area; Figure 1).

Survey results revealed that there were infected wild deer near the boundary of the surveillance zone; the surveillance area was increased to include Presque Isle County, and statewide surveillance for tuberculosis in cattle and captive cervids has been in effect since 1999. Most cases of tuberculosis in wildlife species have been detected in wild white-tailed deer in the 4-county area in which the 1975 and 1994 cases in wild deer originated; the prevalence of tuberculosis in wild deer in adjacent counties (ie, Antrim, Crawford, Emmet, Iosco, Otsego, Presque Isle, and Roscommon Counties) is lower, and isolated cases have been detected in Osceola and Mecosta Counties. Infection is thought to be transmitted primarily within family bands. Since 1996, tuberculosis has been detected in 4 elk and several noncervid wildlife species, including coyotes (*Canis latrans*), raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), black bears (*Ursus americanus*), and bobcats (*Felis rufus*) originating from the 4-county area.

Presently, the geographic distribution of tuberculosis in the wild deer population can be characterized as a wide area of low prevalence (approx 0.3%) surrounding a central core area of higher prevalence (approx 2.3%). Within the high-prevalence core area, the prevalence of tuberculosis varies considerably, but

**Abbreviations**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>NELP</td>
<td>Northeastern lower peninsula</td>
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<tr>
<td>MDA</td>
<td>Michigan Department of Agriculture</td>
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<tr>
<td>MDNR</td>
<td>Michigan Department of Natural Resources</td>
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<td>MDC</td>
<td>Michigan Department of Conservation</td>
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<tr>
<td>MIRIS</td>
<td>Michigan Resource Inventory System</td>
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<td>NLP</td>
<td>Northern lower peninsula</td>
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</table>

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temporally stable spatial clusters of the infection in deer have been detected. The persistence of such spatial clusters was calculated on the basis of wildlife surveillance data obtained from 1995 to 2002; clusters were geographically stable over most of that time period, and the relative risk of tuberculosis in cluster areas was significantly higher than in noncluster areas, with an odds ratio ranging from 3.4 to 4.5. Clusters of tuberculosis in deer were associated with large expanses of deciduous forests on moraine ridges separated by low areas of forested wetlands and with areas containing numerous small lakes. Although specific reasons for the spatial clustering of infection have not been established, factors that promoted congregation of deer for extended periods of time (e.g., existence of the natural cover afforded by forests, access to water, availability of browse [i.e., the shoots, leaves, bud tips, and other vegetative materials that deer prefer to feed on] in forested wetlands, and lower frequency of human contact) appeared to be associated with higher prevalence of tuberculosis.

Several factors have been linked with the maintenance of tuberculosis in the NELP of Michigan, including human activities (e.g., cattle-livestock management practices and large-scale supplemental winter feeding of wildlife) and environmental conditions (e.g., habitat conducive to the spread of disease among wild deer populations). However, those factors are not unique to the affected area and do not explain how tuberculosis became established in wild deer populations in the area. We hypothesized that unique circumstances in the area led to establishment of tuberculosis in the deer population and permitted prevalence of the infection to increase to levels detected in the 1990s.

The present study was conducted to determine historical factors related to the deer population, environmental changes, and human activity in the NELP of Michigan that may have permitted free-ranging white-tailed deer to become infected and maintain endemic infections of bovine tuberculosis. We also undertook to compare those factors, spatially and temporally, with other regions of the state in which there is no endemic bovine tuberculosis and to identify factors that were relevant to the present tuberculosis outbreak among wild white-tailed deer and cattle herds in the NELP.

Materials and Methods

A review of available historical documentation was conducted. Searches were conducted with an electronic library resource-sharing program that provides access to information from the Library of Michigan, the Archives of Michigan, and materials at several universities, colleges, and regional libraries in the state. Materials examined included articles from scientific journals; books; organizational proceedings; public and internal governmental reports; and correspondence to and from governmental agencies, including the MDA and MDNR. Before 1968, the MDNR was known as the MDC.

Documents were reviewed on the basis of focus on risk factors and circumstances associated with maintenance of tuberculosis in wild deer populations and transmission of Mycobacterium bovis between domestic cattle and wildlife. Topics concerning factors and events that increased contact or interaction between livestock and wildlife were of special interest.

Livestock risk factors included numbers of cattle and cattle herds, prevalence of bovine tuberculosis, and conditions that might have influenced disease transmission between cattle and wild deer. Data on cattle populations within and outside the tuberculosis-affected areas of Michigan were obtained from agricultural census reports dating from the 1920s to the present. The prevalence of tuberculosis among Michigan cattle was calculated on the basis of testing results obtained during the tuberculosis eradication program from data collected from MDA biennial reports.

Wildlife factors included deer numbers, deer management practices, hunter harvest records, and reports related to wild deer or the potential for disease transmission between livestock and wildlife. Historical data were gathered from the earliest available time until 1994, when endemic tuberculosis was detected.
and 1992 and are available to the public. \(^{17}\) Data in the MIRIS cover for the entire state were compiled by the MIRIS in 1979; information on land covers more accessible. Data on land cover recently, the use of remote sensing technologies has made land cover. \(^{18}\) region in 1978 and 1992 and described more than 40 types of system were derived from analysis of satellite imagery of the MIRIS data in these datasets contained data from surveys of native Michigan land cover conducted from 1816 to 1856. \(^{19}\) More recently, the use of remote sensing technologies has made information on land covers more accessible. Data on land cover for the entire state were compiled by the MIRIS in 1979 and 1992 and are available to the public. \(^{20}\) Data in the MIRIS system were derived from analysis of satellite imagery of the region in 1978 and 1992 and described more than 40 types of land cover. \(^{21}\)

After data were compiled, occurrence and timing of risk factors were compared between tuberculosis-affected and nonaffected areas and relative contributions of risk factors to development of bovine tuberculosis in wild white-tailed deer populations were assessed. Factors were examined by comparing historical data from the 4-county region presently affected by tuberculosis (ie, Alcona, Alpena, Montmorency, and Oscoda Counties) with an area presently unaffected by tuberculosis (ie, Allegan and Ottawa Counties; Figure 1). Two counties (Allegan and Ottawa) were selected for comparison with the affected 4-county area. Allegan County was selected because cattle populations were consistently maintained at high numbers, the prevalence of tuberculosis in livestock was high during the 1930s, the county is geographically separated from the 4-county area, and a severe winter in the early 1930s resulted in starvation of many deer. Ottawa County was selected for similar reasons, although that county did not experience the severe winter conditions resulting in substantial deer losses in the 1930s.

### Results

Cattle populations and bovine tuberculosis prior to 1994—The Michigan cattle population has fluctuated since the MDA commenced reporting agricultural statistics. \(^{22}\) The state cattle population declined from over 1.5 million to approximately 1.4 million in the mid-1920s but steadily increased to more than 2 million in 1944 and 1945 (Figure 2). After this peak in numbers, there were several 4- to 5-year declines in cattle populations followed by years of increasing numbers of cattle, but overall numbers decreased until 1988, when the cattle population appeared to stabilize and remained at approximately 1.2 million from that time until the mid-1990s. Changes in county cattle populations were similar (Table 1), with cyclic increases and decreases in numbers.

<table>
<thead>
<tr>
<th>Year</th>
<th>Alcona No.</th>
<th>Alcona tested (%)</th>
<th>Alcona No. tested</th>
<th>Montmorency No.</th>
<th>Montmorency tested (%)</th>
<th>Montmorency No. tested</th>
<th>Oscoda No.</th>
<th>Oscoda tested (%)</th>
<th>Oscoda No. tested</th>
<th>Allegan No.</th>
<th>Allegan tested (%)</th>
<th>Allegan No. tested</th>
<th>Ottawa No.</th>
<th>Ottawa tested (%)</th>
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<td>3,356</td>
<td>40,556</td>
<td>34,228</td>
<td>39,029</td>
<td>25,566</td>
<td>41,267</td>
<td>46,175</td>
<td>41,267</td>
<td>44,953</td>
<td>37,485</td>
<td>31,110</td>
<td>43,900</td>
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<td>13,046</td>
<td>3,869</td>
<td>2,498</td>
<td>13,855</td>
<td>9,588</td>
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<td>33,894</td>
<td>40,843</td>
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<td>45,715</td>
<td>38,093</td>
<td>32,400</td>
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</tbody>
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Table 2—Number (% of reactors) of cattle tested for bovine tuberculosis in Michigan from 1922 to 1936.
Control of bovine tuberculosis has been a priority in Michigan since the USDA began tuberculosis eradication efforts in 1917, at which time the state entered the bovine tuberculosis eradication program. Prior to development and implementation of the tuberculosis eradication program, tuberculosis was widespread throughout the United States and posed a serious threat to the livestock industry.\(^3\) The prevalence of tuberculosis among Michigan cattle prior to the eradication program is unknown. Earliest available data indicate that in 1922, tuberculosis reactor rates in cattle were 32% in Alcona County and 20% in Alpena County; those values represented the highest reactor rates in Michigan\(^5\) and were higher than the nationwide mean of 4.9% in 1917.\(^3\) Testing of livestock for tuberculosis in Michigan increased in the 1920s, with numbers of tests peaking in the early 1930s. As the prevalence of tuberculosis decreased in 1933 and 1934, the importance of reporting reactor rates decreased, and rates were no longer reported on a routine basis after 1934 (Table 2). By 1940, the overall reactor rate for tuberculosis in US cattle was 0.5%.

The tuberculosis testing program was greatly reduced during World War II, leading to an increase of tuberculosis in cattle in Michigan, and implementation of the program was resumed after the war. In the 1950s, the focus of tuberculosis control shifted from area testing, which had become inefficient at detection of the disease as prevalence decreased, to slaughter inspection, where epidemiologic investigations would be initiated when meat inspectors identified infected animals. At 1 point during the 1950s, Michigan cattle accounted for approximately 30% of all tuberculosis reactors in the United States.\(^3\) A renewed effort was made to eradicate bovine tuberculosis from Michigan, and the last apparent case of tuberculosis was detected in cattle from Ingham County in 1974; the state was granted tuberculosis-free status in 1979.

The livestock population in Michigan retained tuberculosis-free status until surveillance was reinstituted in 1995 after discovery of tuberculosis in wild deer. The new surveillance system detected the infection in animals at a captive cervid operation that recruited local deer for herd establishment in Presque Isle County in 1997\(^3\). Infection was detected in cattle herds beginning in 1998.\(^3\) Since that time, a total of 33 cattle herds with tuberculosis have been identified, all of which are located in the NELP.
White-tailed deer populations prior to 1994

White-tailed deer were common in Michigan forests in the 19th century, but the effects of conversion of deer habitat to farmland and unregulated hunting nearly exterminated white-tailed deer from southern Michigan. By the 1920s, deer populations were so low that deer hunting was banned in approximately 30% of Michigan counties. Regulation of hunting in northern Michigan allowed deer populations to rebound; surveys indicated that 320,000 deer (density, 7 deer/km²) inhabited the NLP region (an area that includes the 4-county area and Antrim, Crawford, Emmet, Iosco, Otsego, Presque Isle, and Roscommon Counties) and approximately 2,000 deer resided in southern Michigan (density, 0.03 deer/km²), including Allegan and Ottawa Counties, by the end of the 1920s. In a survey on hunting conditions in the 4-county area in 1932, hunters reported that deer numbers were increasing in that region. Aggressive deer-management measures, including the cutting of cedar browse from the Fletcher Swamp (located north of the center of the 4-county area) increased deer numbers in the 4-county area (Figure 3).

A decrease in the number of deer in the NELP was recognized in 1950; starvation was deemed the major cause because there was insufficient feed in certain areas to sustain deer during the winter. Notes from the chief of the Game Division to the director of the MDC indicated that a 20-year program had been implemented to address the problem. Despite fluctuations in the severity of winters and changes in hunting laws, the effectiveness of the efforts by the MDC (MDNR) to increase the deer population was evident: the state deer population increased to 759,000 in 1960 and increased from 500,000 in 1972 to 1,721,000 in 1998. Estimates of deer populations in the 4-county area in 1955 indicated that there were a mean of 5 (range, 3 to 8) deer/km² in most of Alpena County, 11 (5 to 14)/km² in most of Montmorency County and the northwest portion of Oscoda County, and 23 (8 to 37)/km² in the center of the 4-county area and the northern portion of Alcona County.

In addition to efforts by the MDNR to increase deer numbers in the NLP, the actions of individuals residing or vacationing in the region also contributed to increased numbers. Several hunt clubs (organizations with lands purchased specifically for hunting) were operating in the 4-county area, some of which had been established at the turn of the century. In the period of economic and industrial growth after World War II, numerous employment opportunities arose in southern Michigan. Many residents of the NLP moved to the industrialized southern part of the state in pursuit of more lucrative jobs. By the 1970s, many of those workers were retiring from the workforce and returning, with job pensions, to the NLP. In a survey of intrastate migrants over the age of 65 who were moving to the NLP region of Michigan, 28% had been born in the area, 31% had spent their childhood years in the area, 38% had family living in the area, and 78% had recently moved there from urban areas in the southern part of the state.

The practice of supplemental feeding of deer during harsh winters had been practiced in the past, and it was known that well-nourished male deer developed larger antlers and fed females often produced twin fawns instead of singletons. Supplemental winter feeding to improve the quality of deer available for hunting became common in the NLP, despite reti-
ence of the MDC and MDNR to approve the practice.\textsuperscript{41} The quantity and quality of feed set out for deer increased substantially from hundreds of kilograms per season to hundreds of tons per season.\textsuperscript{4} During this period of large-scale supplemental feeding, the density of deer in the northeastern portion of the NLP increased from approximately 7 to 9 deer/km\textsuperscript{2} in the 1960s to 19 to 23 deer/km\textsuperscript{2} in the 1990s.\textsuperscript{3,42}

During the particularly harsh winter of 1930 to 1931, a shortage of natural feed resulted in severe loss of deer from starvation throughout the state of Michigan, especially in the 4-county region. The 3 locations in the 4-county area most affected by starvation in the 1930s were the Fletcher Swamp, Turtle Lake, and Beaver Swamp areas\textsuperscript{40} (Figure 4). The impact of the food shortage was severe enough that a special report\textsuperscript{40} was generated by the MDC to describe the extent of the problem. A summary of findings from that region during the winter of 1930 to 1931 was published in 1938\textsuperscript{43}:

"Despite the mild weather the population was too great in at least two areas; and by mid-March dead deer were being reported in the Turtle Lake region in Alpena, Alcona, Montmorency and Oscoda Counties. Dead deer census drives on small areas totaling 2.5 square miles in this territory revealed nearly 200 dead deer. It is estimated that well over 2,000 dead deer died of starvation on the 25 square miles of similar area in this region."\textsuperscript{43} Many of the dead deer were also infected with parasites, particularly nose bots (Cephenomyia phobifer) and lungworms (Protostrongylus rufescens).\textsuperscript{44}

To reduce the density of local deer populations and provide long-term relief from starvation, deer were moved from the Fletcher Swamp area to a nearby area with greater food availability.\textsuperscript{44} That site was < 8 km away, and the move was ultimately unsuccessful because most relocated deer returned to their home ranges despite the better habitat and quality of browse in the new site. Starving deer were captured and relocated again to more distant locations (Turtle Lake area, Beaver Swamp, and a location 9 km west-southwest of the city of Alpena), with more lasting success (Figure 5). Additional measures taken to reduce deer starvation in the 1930s included plantings and provision of supplemental feed. Rye grass was planted to provide food plots, but the plantings were of little use because they were unavailable to the deer when buried by snow. Alfalfa hay fed to deer in wildlife areas provided immediate relief from starvation.\textsuperscript{40,45}

Habitat changes prior to 1994—Surveys of native Michigan land covers were conducted from 1816 to 1856\textsuperscript{16} (Table 3). The 4-county area was primarily covered in forests and cedar swamps, whereas the southern counties (eg, Allegan and Ottawa) were mostly covered by hardwood and mixed hardwood-conifer forests. In the MDNR Deer Management Unit 452 (a 650-km\textsuperscript{2} area that encompasses the center of the 4-county area; Figure 5), the predominant land covers were white pine-red pine forests (24% of the area), cedar swamps (20%), beech-sugar maple-hemlock forests (20%), jack pine-red pine forests (16%), and mixed conifer swamps (10%). The largest expanses of cedar swamps and mixed conifer swamps were in the Fletcher Swamp, the Beaver Lake

![Figure 6](image-url)
Swamp, a cedar swamp west of Hubbard Lake, and an area of swampland to the west and north of Turtle Lake (Figure 4). These swamps were interconnected by forested swamplands that followed perennial streams through poorly drained broad glacial outwash plains. During the 19th century, much of the state of Michigan underwent substantial changes in land cover as agricultural and lumbering activity increased.

Information was available on changes in deer habitat in the 4-county area in the 1920s and early 1930s. In the 1920s, hunt clubs cut down cedar trees in Fletcher Swamp to provide browse for deer. Although the cutting of cedar trees provided short-term relief from starvation, the long-term effect was a 45% reduction in the area of Fletcher Swamp that was useful for thermal cover and winter browse. This caused deer to become more concentrated in the area and overbrowse the area. A survey of the Fletcher Swamp in 1930 revealed that 39% of the area had been browsed heavily, 78% of the area had little or no feed available for deer, and only 5% of the area had medium-to-good-quality browse. The Beaver Creek Swamp was in worse condition, with virtually no browse available in the entire swamp. In 1932, damming of the south branch of the Thunder Bay River resulted in covering much of the area that comprised Fletcher Swamp with water.

Land use data from the MIRIS were available for the counties of interest for 1979 and 1992, covering the interval from when the state's livestock population was declared free of tuberculosis to the time prior to detection of tuberculosis in white-tailed deer (Table 4). During that period (ie, the 1970s to the 1990s), the area under deciduous trees and forests in the 4-county area was substantially reduced (from 72% to 37% of total land in the 4-county area), the area of forested wetlands increased (from 4% to 17%), and agricultural land use decreased slightly (from 10% to 9%). In Allegan and Ottawa Counties, forested areas were reduced (from 33% to 18% and 23% to 20%, respectively) and forested wetlands increased (from 2% to 5% and 1% to 4%, respectively), whereas land under agricultural use increased (from 52% to 69% and 55% to 37%, respectively).

**Discussion**

The review of historical data revealed that there was a unique combination of events and conditions in the central portion of the 4-county area that may have provided the opportunity for wild deer in the region to first acquire tuberculosis from livestock. The harsh winter of 1930 to 1931, coupled with habitat destruction, appears to be the precipitating event for introduction of the disease into the deer population. The geographic location of the areas affected in the present outbreak coincides with locations where deer were affected by severe winter conditions in 1930 to 1931; measures to aid the affected deer population at that time may have introduced or encouraged spread of tuberculosis and appear to be associated with the locations of spatial clusters detected in the present outbreak.

Our study is subject to certain shortcomings innate to retrospective studies and use of historical documents. Although statistical analysis of the variables possibly associated with transmission, maintenance, and spread of tuberculosis through the deer population would have been ideal, it was impossible to collect sufficient appropriate data. The number of observations used for determination of susceptible populations was limited; the rates of disease, measures of exposure, and types and quality of data that were reported varied over time, making comparison of variables between time periods difficult. A particular example is the data regarding tuberculosis reactor rates among cattle: the number of cattle tested and reactors detected were available at the beginning of the tuberculosis control program in the 1920s, but the detail regarding test results decreased as priorities for control shifted in the late 1930s. It is only as a result of the recent outbreak of tuberculosis in wildlife and cattle that data on numbers of animals tested and rate of positive reactors detected became readily available. Our data were extracted from information in documents and personal correspondences written more than 80 years ago; such communications were not intended for use in data compilation and did not contain sufficient detailed information for analysis. Finally, there is an absence of direct evidence of causality, and it cannot definitively be determined where, when, or how tuberculosis was established in the deer population. The historical records provide evidence for the temporal sequencing of events but do not clearly delineate the order of events critical to the development of this disease problem. However, results suggest that there was a series of conditions that could plausibly be associated with establishment of tuberculosis in the white-tailed deer population in the 4-county area, and that information provides a starting point from which to conduct further research into the history of the problem.

Viewed in an epidemiologic context of agent, host, and environment, a necessary condition for infection of wild deer was exposure to the disease agent. Bovine tuberculosis was endemic in Michigan in the 1920s and 1930s. The prevalence of tuberculosis in cattle was very high in 2 counties (Alpena and Alcona; 20.2% and 31.9%, respectively) within the 4-county area, but the finding was not unique to that portion of the state. The prevalence of tuberculosis in cattle in Ottawa County was 10.7% in the 1920s, and the prevalence in Allegan County was higher than the state mean of 4%, but there is no historical or present evidence of tuberculosis in wild white-tailed deer in that part of the state. This suggests that high prevalence of the disease alone would not be sufficient cause for transmission between cattle and deer.

Use of molecular techniques for detection of infective sources has practical applications in various contemporary situations, but the applicability of such techniques in investigations of historical events is limited. All isolates of *M. bovis* collected during the present outbreak in Michigan share an identical restriction fragment length polymorphism pattern, including isolates collected from cattle, deer, and other wildlife; a domestic cat; and a hunter with a cutaneous infection acquired while dressing the carcass of a tuberculosis deer. This strain of *M. bovis* is unique to the tuberculosis...
sis-affected area of Michigan.\textsuperscript{50} Because \textit{Mycobacterium tuberculosis} is a stable organism in terms of genetic mutation\textsuperscript{51} and \textit{M bovis} has 99.9\% homology with \textit{M tuberculosis} at the DNA level,\textsuperscript{52} if \textit{M bovis} from the present outbreak in deer originated from the strain that infected cattle in the 1930s, a high percentage of genetic similarity between isolates from both times and specimens would be expected. Unfortunately, no bacterial specimens from tuberculous cattle from the 1930s exist, and such comparisons are impossible.

Although direct evidence for causality is lacking, a case of \textit{M bovis} infection in an elderly human patient from Michigan has provided evidence linking the strain of the pathogen affecting northeastern Michigan in the 1930s with the contemporaneous strain affecting the 4-county area. In 2002, a 74-year-old male resident of the 4-county area was diagnosed with \textit{M bovis} infection while undergoing treatment for another condition.\textsuperscript{53} Analysis of the isolate (obtained from a bronchial wash specimen) revealed a restriction fragment length polymorphism pattern indistinguishable from that of \textit{M bovis} isolates collected from cattle and wild white-tailed deer in the 4-county area since 1995.

That patient died before a complete exposure history was obtained, but he had lived in the 4-county area during the time when tuberculosis in livestock was common and had a history of consuming unpasteurized milk and hunting deer. The patient had moved to the Detroit area and remained there until retirement, when he returned to the 4-county area. It is unlikely that he was exposed to tuberculosis after his return to northern Michigan because he did not participate in hunting or consume unpasteurized milk during that period of his life.

Recrudescent of latent \textit{M bovis} infection is a well-described phenomenon, and a number of cases of tuberculosis in humans have been attributed to recrudescence.\textsuperscript{14,35} Recrudescence is facilitated by immunocompromising events such as concurrent disease or decreases in immune response associated with age. In 1 study,\textsuperscript{66} investigators found that \textit{M tuberculosis} was genetically stable for as long as 39 years after initial infection, particularly if the latency of infection had lasted for longer than 2 decades, and that the rate of change of the genome was estimated to be only 1.9\% per year. If \textit{M bovis} also has long periods of genomic stability, it is likely that the aforementioned patient was exposed to \textit{M bovis} more than 50 years previously and that his recrudescent infection represented a sample of \textit{M bovis} contracted from cattle infected in the 1930s. That finding would suggest that the human patient and the white-tailed deer population in the 4-county area contracted \textit{M bovis} from a common source. Hunting deer with tuberculosis is less likely to result in infection than consumption of unpasteurized milk from cows with tuberculosis.

In addition to exposure to the disease agent, susceptible hosts are also necessary for transmission of infection. Two factors that increased the susceptibility of deer in the NLP to infection were high population densities in the 1920s to 1930s and 1970s to 1990s and immune compromise associated with starvation conditions in the winter of 1930 to 1931.

There have been 2 peaks in deer numbers in the 4-county area during the last century. Despite the decline in deer populations throughout the state in the early 1920s, regulation of hunting and deer management increased deer numbers by the end of the decade.\textsuperscript{12} Many of the more aggressive deer management practices, including browse cutting, were commonly practiced on hunt club lands in the 4-county area.\textsuperscript{13} The density of deer in those 4 counties in the 1920s and 1930s was approximately 200 times higher than that in the counties outside the area presently affected (7 deer/km\textsuperscript{2} vs 0.03/km\textsuperscript{2}, respectively). Increases in the practice of supplemental winter feeding in the 1970s and 1980s nearly tripled the region's deer population in the 1990s.\textsuperscript{42}

Increased animal numbers increase transmission of communicable diseases; as animal density increases, direct contact among individual animals increases and the probability of direct disease transmission increases.\textsuperscript{4} Large-scale supplemental feeding in the 4-county area, practiced in the 1920s and 1970s, created focal concentrations of animals around feed piles, further facilitating the spread of tuberculosis in deer.\textsuperscript{14} In the 1990s, large feed piles created an environment in which several matrilineal family groups, which typically would seldom mix, were simultaneously drawn to feeding sites, and increased contact between such groups facilitated transmission of \textit{M bovis} via direct contact or contamination of feed by infected animals.\textsuperscript{7}

The susceptibility of deer to \textit{M bovis} infection was increased in the winter of 1930 to 1931 by starvation. Starving deer were observed in Allegan County and in the 4-county area, but the severity of the problem in the 4-county area was much worse. Starvation has substantial and deleterious effects on immune system function, and exposure to small quantities of \textit{M bovis} via contaminated feed may be sufficient to cause infection under such conditions. The poor immune status of starved deer in the 4-county area was evident in the heavy parasite infestations observed, particularly nose bots and lungworms.\textsuperscript{9} Nose bots are a common parasite of deer and are well-tolerated in healthy hosts,\textsuperscript{16} but the numbers observed in starved animals by wildlife biologists indicated that parasite loads were much higher than usual and were consistent with a state of low immunity. Interestingly, the species of lungworm detected in those deer were not the usual deer lungworm (\textit{Dictyocaulus viviparus}) but rather were \textit{P rufescens}, the species that commonly infested sheep in the region.\textsuperscript{17} Because lungworm transmission occurs via ingestion of larvae, that finding suggested that deer consumed feed from nearby farms to compensate for the absence of natural feedstuffs in the area.

Compared with the 4-county area, deer populations in southern Michigan have historically been maintained at lower densities. Lower deer numbers in Allegan, Ottawa, and other southern counties were attributed to unregulated hunting in that region and loss of habitat, which prompted changes in hunting regulations and adoption of the Pittman-Robertson Act for Federal Aid in Wildlife Restoration, under which federal excise taxes levied on hunting, firearms, and...
ammunition were collected for use in wildlife research, land acquisition, and habitat development.36

Habitat changes have affected the 4-county area and southern counties differently. Comparison of pre-settlement land covers and recent land-cover data indicated that there are important differences between land cover in the 4-county and southern county areas. The rates of conversion of land cover (primarily forests in both areas) into agricultural land differ: more than 50% of the land in Allegan and Ottawa Counties was converted to agricultural use, whereas less than 10% of land in the 4-county area is presently used for agriculture. The extent of forested swampslands decreased over time in both areas, but that change has not been as substantial as the conversion of forested land cover to agricultural use. Conversion of forested land to agricultural land has continued in Allegan and Ottawa Counties, and the loss of deer habitat in wide areas of southern Michigan has contributed substantially to reducing deer numbers in that region.

Given the similarities in prevalence of tuberculosis in livestock in the past and the differences in deer densities between the 4-county and southern county areas, it appears that high concentrations of infected livestock alone were not sufficient for the development of M bovis infection in wild deer populations. The density of deer in certain areas also appears to have been an important component in the transmission of tuberculosis from livestock to wildlife.

The final component of the agent-host-environment complex was an environment in which contact between susceptible deer hosts and the infectious agent was facilitated. It appears that the severe winter of 1930 to 1931 was likely the precipitating event for extension of M bovis infection from domestic livestock into the wild deer population and that increases in deer numbers and the practice of supplemental feeding in the 1970s and 1990s led to an increase in the prevalence of M bovis infection to detectable levels.

Normal behavior patterns of wild deer in the NLP were conducive to the spread of disease. The survival of deer during winter is dependent on their access to food and habitat that affords thermal protection, such as areas with cedar and conifer swamps (i.e., deer yards). These conditions were available in the 4-county area, and the Fletcher Swamp was one of the largest cedar swamps in the area until the mid-1930s. Although the tendency to congregate in deer yards during winter leads to access to food and shelter for deer, it also contributes to the spread of disease.38 Deer in yards spend long periods of time in close proximity, increasing direct contact among individual animals and contamination of browse by infected animals. However, in the southern counties, there was much less area suitable for deer. In such situations, deer seek out wooded areas and marshes for thermal protection but move regularly in the search for food. Under those circumstances, it is unlikely that deer would congregate in the large numbers observed in deer yards, the effect of which would be to reduce the spread of disease.

Human attempts to support deer populations during the severe winter in 1930 to 1931 may have facilitated transmission of M bovis to wild deer in the 4-county area. The impact of the severe weather conditions on the deer population was most severe in the 4-county area and in Allegan County. Because deer numbers in Allegan County were low, there were fewer starving deer and less public concern was elicited. However, in the 4-county area, the severity of the situation prompted implementation of mitigation strategies, including provision of supplemental feedstuffs to deer and translocation of deer to areas with more available browse. None of these actions were implemented in Allegan County, an agricultural area in which deer were considered a nuisance. Because these mitigation strategies were only implemented in areas where tuberculosis is presently established in the wild deer population, it is possible that the practices were important contributing factors to the transmission of tuberculosis from cattle to deer and among deer.

Supplemental feeding of deer with locally purchased alfalfa hay during the winter of 1930 to 1931 likely contributed to introduction of M bovis into wild deer populations. Livestock feedstuffs have been implicated as a mode of transmission of tuberculosis among cervids38 and between cervids and cattle.62,65 Studies have revealed that M bovis can survive for as long as 3 months on alfalfa hay, shelled corn, sugar beets, apples, and potatoes held at a temperature of 46°F66 which is rarely exceeded during Michigan winters. In addition, provision of such feedstuffs may have habituated deer to these types of feed and increased the likelihood that deer would seek such feeds in the future, increasing their exposure to infected cattle and contaminated feed. Problems associated with disease transmission, disruption of movement patterns, changes in spatial distribution, reduction of biodiversity and abundance, introduction of and invasion by exotic plant species, and general habitat degradation have lead wildlife agencies to discourage or cease supplemental feeding of wildlife.61,62,65

Deer were captured in the heavily affected Fletcher Swamp and moved to locations with lower numbers and better natural food sources. Areas (i.e., the Turtle Lake area, Beaver Swamp, and a location 9 km west-southwest of the city of Alpena) that received deer from Fletcher Swamp are correlated with the present spatial clusters of tuberculosis in white-tailed deer, as indicated by results of surveillance measures conducted from 1995 to 2002.5 The relocation of deer (intentionally by MDC personnel and unintentionally as a result of flooding of Fletcher Swamp) likely aided spread of the disease from the most severely affected area to other locations where clusters of tuberculosis now exist. The MDNR does not support translocation of deer as a means of population control.36

Loss of habitat in the 4-county area after the winter of 1930 to 1931 may have served to maintain the disease among wild deer. Flooding of the Fletcher Swamp in the mid-1930s would have forced deer into remaining swamp areas, increasing deer concentrations at those yards and facilitating transmission of tuberculosis among deer. Loss of habitat to flooding also provided a strong impetus for deer to move into farming
areas adjacent to the swamp, resulting in greater contact between wild deer and livestock.

The effects of selective harvest may also have contributed to the increase in tuberculosis in the deer population. A common practice among hunters and hunting clubs was to limit the harvest of females and young male deer with the intention of improving the quality of bucks for hunting (antler size tends to increase with age). The increase in numbers of older males in the population may have further increased the prevalence of tuberculosis because older deer, especially males, are more likely to be infected.3

The spatial clusters of tuberculosis observed recently are coincident with the areas affected by the severe winter food shortages of 1930 and 1931, other areas connected by swamplands to this area, and locations where infected deer may have been relocated. This suggests that relocated deer were infected with M bovis prior to being moved. Relocation of infected deer and the ability of M bovis infection to be maintained at a low prevalence in a population could account for the present foci of tuberculosis infections. Translocated deer have higher mortality and dispersal rates than nontranslocated deer.66

Two sites used for deer relocation (ie, relocation sites 1 and 2) are not inside the boundaries of present tuberculosis clusters, although 1 site (relocation site 1) was located at the end of a forested swamp that stretched from the release site to the area around Hubbard Lake, which is the present site of a tuberculosis cluster. It is possible that the relocated animals left the area of the release point to establish new home ranges or that none of the relocated deer had tuberculosis when they were moved, but infected deer may have naturally migrated there from the Fletcher Swamp area to take advantage of the better habitat.

Relocation site 3 is located in a contemporaneous tuberculosis cluster that is not spatially linked to other clusters or corridors of forested swampland. The isolation of this site makes it likely that the disease developed in the deer that were brought to the area, as opposed to entering the area by migration of infected deer from other present cluster areas. Another release point (site 2) in the southern section of Montmorency County, was in an area that was not swampland or connected to forested swampland. That site is not part of a contemporaneous tuberculosis cluster. It is possible that deer released at the site may have left in search of more desirable habitats or that a cluster did not develop because the deer relocated to this site were not infected.

Regardless of the original source of tuberculosis in deer in the 4-county area, there are problems associated with detection of disease in the present outbreak. As previously mentioned, endemic M bovis infection was only confirmed after geographically targeted surveillance of hunter-harvested deer was conducted near the location where a hunter-harvested deer was found to have tuberculosis lesions.3

There had been no perceived need for wildlife tuberculosis surveillance in Michigan until that time, and information available at the time indicated that normal behavior patterns in white-tailed deer did not support the spread of M bovis infection.67 Additionally, tuberculosis in North American white-tailed deer had previously been associated with proximity to cattle with a high prevalence of infection; it was assumed that infected deer were a result of spillover of the disease from cattle.62,63 In Michigan, the infected deer harvested in the 4-county area in 1975 were presumed to represent the spillover effect from infected cattle in the area; however, cattle in the area were presumed tuberculosis-free when infection in the deer in 1994 was detected. The absence of an apparent bovine source of tuberculosis for the infection in wild deer led to the mandating of surveillance measures to determine the extent of the problem.

The temporal sequence of the spread of tuberculosis among wild deer is unclear. It is possible that the prevalence of tuberculosis had been maintained at very low values (eg, <1%) in the deer population from the 1930s until the 1970s, at which time increases in deer populations in the 4-county area increased disease transmission rates and prevalence of the disease, or that tuberculosis had been maintained at the same prevalence detected during the mid-1990s (2% to 4%) since the 1930s but that low numbers of deer made detection difficult until the population explosion in the 1970s. Information regarding transmission rates of tuberculosis in wild deer populations would be necessary for determining which scenario is most plausible. However, estimation of disease and transmission rates among wildlife is not as efficient or thorough as is possible for captive or domestic animals. Difficulties in enumeration of wildlife populations at risk make it difficult to determine rates of disease in those animals.65-77

In the present outbreak of tuberculosis in the NL, most infected deer do not have clinical signs of the disease,14 making detection of infected free-ranging deer difficult without diagnostic testing. The respiratory tract and oral cavity are important routes of transmission of infection, but most studies63,78 concern captive deer populations and results may not be reflective of actual transmission in free-ranging animals.

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References


