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EVALUATION OF THE INFLUENCE OF SUPPLEMENTAL FEEDING OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) ON THE PREVALENCE OF BOVINE TUBERCULOSIS IN THE MICHIGAN WILD DEER POPULATION

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ABSTRACT: A retrospective study was conducted to test the hypothesis that supplemental feeding of white-tailed deer (*Odocoileus virginianus*) from 1995 to 1997 was associated with the prevalence of bovine tuberculosis (TB) in free-ranging deer in northeastern Michigan. Bovine TB prevalence data were obtained from an ongoing surveillance program, while data relating to supplemental feeding and other risk factors were collected via in-person interviews. A multivariable Poisson regression modeling approach was used to test the stated hypothesis while controlling for other risk factors. Of the 389 potential participants, 59% agreed to participate in the study. Results showed that supplemental feeding of deer was associated with bovine TB in white-tailed deer. Specific risk factors associated with increasing risk for bovine TB were locating feed sites in areas with high levels of hardwood forests (O.R.=1.8, 95% C.I.=1.3–2.4), other large-scale feeding sites in the area (O.R.=1.1, 95% C.I.=1.0–1.2), the number of deer fed per year (O.R.=3.9, 95% C.I.=1.4–11.4), the numbers of feed sites spreading grain (O.R.=14.7, 95% C.I.=2.2–98.9), the quantity of grains provided at the site (O.R.=1.4, 95% C. I.=1.1–1.7), and the quantity of fruits and vegetables provided (O.R.=1.4, 95% C.I.=1.2–1.7). Conversely, factors associated with decreasing risk of bovine TB were locating feed sites in areas with high levels of hardwood forests (O.R.=0.1, 95% C.I.=0.02–0.4), locating feed sites in forests (O.R.=0.05, 95% C.I.=0.01–0.4), and the level of sites providing grain (O.R.=0.1, 95% C.I.=0.01–0.3). The results of this study suggest that banning the practice of supplemental feeding is a valid policy for control of bovine tuberculosis in free-ranging white-tailed deer.

Key words: Bovine tuberculosis, epidemiology, feeding, *Mycobacterium bovis, Odocoileus virginianus,* prevalence, transmission, white-tailed deer.

INTRODUCTION

Mycobacterium bovis infection, or bovine tuberculosis (TB), in wild white-tailed deer (*Odocoileus virginianus*) in northeastern Michigan was first recognized in 1994 (Schmitt et al., 1997). Subsequent investigation revealed that *M. bovis* was endemic in deer in a 650-km^2 area.

Of initial concern was the question why was *M. bovis* endemic in wild white-tailed deer in Michigan considering that the state was accredited tuberculosis-free in 1979. Up until this point in time, there had been no previous example of self-sustaining *M. bovis* in a free-ranging white-tailed deer population. There have been reports of single deer with infection, presumably due to contact with cattle (Levine, 1934; Belli, 1962; Friend et al., 1963), and cases in farmed deer (Ferris et al., 1961). Normal white-tailed deer behavior was not believed to support the spread of *M. bovis* infection, therefore, factors unique to the area were sought that might be associated with maintenance of TB in free-ranging deer.

One possible factor associated with the maintenance of TB in free-ranging white-tailed deer was supplemental deer feeding. Supplemental or winter feeding of deer was commonly practiced in northeastern Michigan to help deer survive harsh winter conditions. In the 1970s and 1980s, individuals from the southern part of the state began to purchase land and form "hunt clubs," and the quantities of feed provided began to increase dramatically so as to increase the number and quality of deer for hunting. Feed increased from hundreds of kilograms per season to hundreds of thousands of kilograms per season (S. Schmitt, unpubl. data). The efforts of these programs to increase the deer population in northeastern Michigan has been relatively successful: deer density estimates based on pellet counts have increased from approximately 7–9 deer per km^2 in the 1960s to 19–23 per km^2 in the 1990s (Hill, 1999; O'Brien et al., 2002).

High levels of supplemental feeding may contribute to the transmission and maintenance of TB in deer in several ways. The primary way in which feeding influences *M. bovis* is through increased risk of spread through direct contact and increased population densities. Aerosol transmission is the most efficient form of transmission for *M. bovis* (Francis, 1958), and direct contact provides the best opportunities in outdoor conditions. Observers at feed sites have seen high deer density at feeding sites and increased direct contact between deer at feeding sites (Garner, 2001), and increasing local deer density has been implicated in the increased spread of TB (Lugton et al., 1998). There was also increased risk of spread of infection, through indirect contact via contamination of feed at these feed sites. Incomplete consumption of large feed items (e.g., sugar beets, potatoes, etc.) or consumption of small feed items (e.g., shelled corn, feed pellets, etc.) concentrated in bins, feeders, or piles by infected animals may contaminate the feed material with saliva and nasal secretions, which can then be ingested or inhaled by other uninfected animals, which are then exposed to infection.

The purpose of this study was to test the hypothesis that supplemental feeding of free-ranging white-tailed deer is associated with the prevalence of *M. bovis* in the wild white-tailed deer population of northeastern Michigan. Specifically, the study was designed to describe wild deer supplemental feeding by residents in selected areas in northeastern Michigan, and to test associations between supplemental feeding practices and the prevalence of *M. bovis* in those wild deer populations.

MATERIALS AND METHODS

Study design

A retrospective study was conducted to assess levels of different supplemental feeding risk factors in areas with a wide range of TB prevalence. A retrospective study examining past feeding practices was necessary for several reasons. In an effort to take action to control the tuberculosis problem in wild white-tailed deer, the Michigan Department of Natural Resources (MDNR) instituted a voluntary ban on supplemental deer feeding in 1998, followed by a mandatory ban on deer feeding and restrictions on deer baiting (feeding during the hunting season, intended to attract deer to hunters) in the following year. The feeding bans would have changed supplemental feeding practices from that time forward. Additionally, considering the lengthy incubation period of *M. bovis,* with estimates of months to years before a case fully develops in a white-tailed deer (Clifton-Hadley and Wilesmith, 1999), levels of *M. bovis* seen in deer are likely the result of actions from the previous 2–3 yr.

Site selection

Four areas were selected for investigation (Fig. 1). These areas were located inside and outside the 'TB core' area, an area of approximately 650 square km around the site of the initial case of TB in a wild white-tailed deer, and were selected to represent a wide range of prevalence values. Each area was approximately 37,300 ha. Since one of the objectives was to describe feeding practices by residents in the TB-affected area, areas with high proportions of hunt clubs were specifically avoided in the selection of these blocks. While MDNR deer-related data were collected on single square mile (259 ha) township-range-section (TRS) blocks, the average home range of deer in the five county area has been estimated from 259 to 1,295 ha (Garner, 2001), the majority of deer enumerated in a 37,300 ha block should remain within the study areas for their entire lives.

Sample selection

Addresses of residents were taken from lists of Michigan driver's licenses and state identifi-

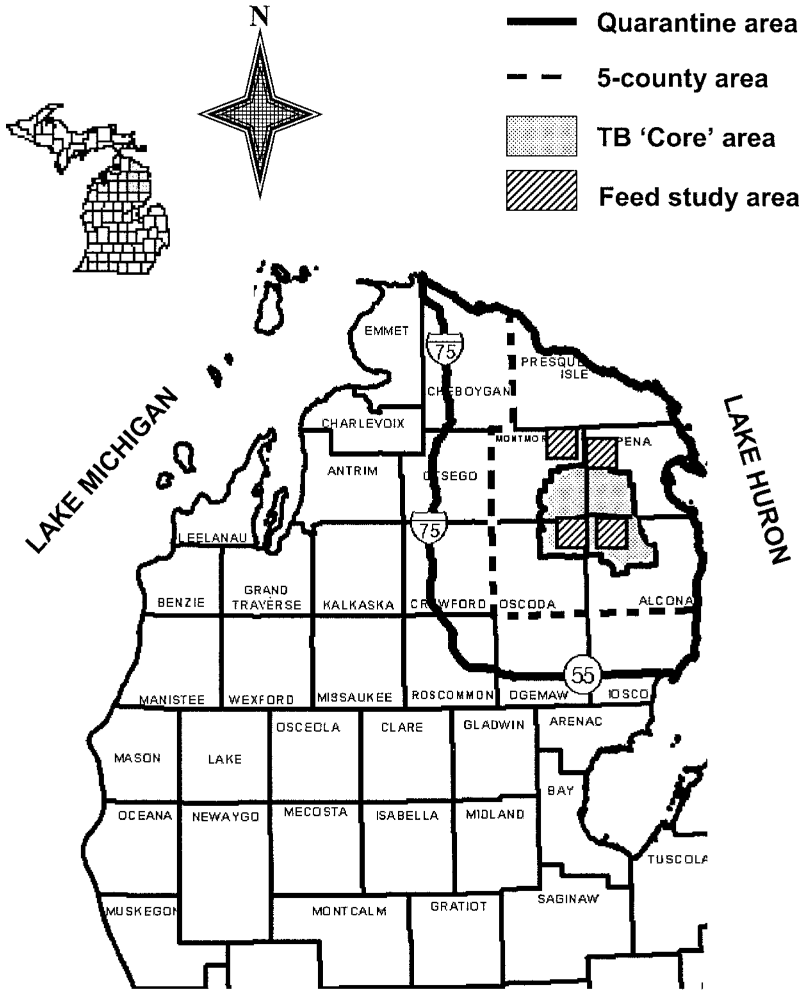

FIGURE 1. Map of bovine tuberculosis affected areas of Michigan and selected study areas.

cation cards from the Michigan Secretary of State's office. Street addresses located within the selected study areas were identified, and all residents of these locations were considered for participation in the study.

Data collection

All deer-related data were collected under the white-tailed deer TB surveillance program. The program, which has been in place since 1995, was designed specifically for TB surveillance and involves examination of white-tailed deer heads from throughout the state of Michigan. Only data on the deer in the aforementioned study area were utilized for this study. Data from the TB surveillance included the year the deer was collected, the geographic location in which the deer was taken (to TRS when possible), and each animal's age, sex, and *M. bovis* infection status. Details on the methodology used to determine an animal's TB status have been described (Schmitt et al., 1997; Fitzgerald et al., 2000). The outcome of interest for statistical analysis was the prevalence of bovine TB in white-tailed deer within specific township-ranges by year.

Supplemental feeding data were collected on pre-tested questionnaires through in-person interviews with trained data collectors. Information was sought on winter supplemental feeding by residents of the area for three periods: fall 1995 to winter 1996, fall 1996 to winter 1997, and fall 1997 to winter 1998. These periods preceded the restrictions on supplemental feeding and baiting. This information was broken down into three general categories:

1. Site-related features, including the number of years the site was continuously in use;

the area of the feed site in which deer could congregate around feed (m^2); whether the site was located in natural fields, hardwood forests, coniferous forests, or cedar swamps (yes/no for each); whether the site was adjacent to an agricultural crop field not intended for deer feeding (yes/no) and, if it was, the area of the agricultural crop field (km^2); whether the site was located on grounds that were wet, dry, or both (yes/no to one only); and the estimated number of deer that were fed at that site during the year.

2. Quantities of feeds present, expressed as kilograms of feed per square meter of feed site area, at each site. These feeds were categorized into groups: grains (primarily corn, but including other grains and pelleted feeds); fruits and vegetables (mostly sugar beets, carrots, potatoes, pumpkins); food plots planted specifically for use by wildlife (e.g., rye, oat, alfalfa fields); and forages (grass hay, alfalfa hay). These feed quantities were computed both by feed type and overall. It was believed that increasing feed quantities would increase the risk of TB, since providing feed in high quantities would increase the likelihood that deer would not be able to completely consume the feed at one feeding, and increase the risk of contamination from partial consumption. Feed quantity, expressed in kg/m^2, was computed as:

$$\mathrm{FeedQuant}_{ai} = \frac{\sum_{i=1}^{R_a} \mathrm{FeedWt}_{ai}}{\mathrm{FeedArea}_a}$$

where:

$\mathrm{FeedQuant}_{ai}$ = Feed quantity, for feed type i at site a
FeedWt_a = Total weight of specific type of feed provided at site a
R_a = Number of types of feed provided at site a
$\mathrm{FeedArea}_a$ = Area of feed site a, in square meters

3. The methods of providing feed used at the feed site, expressed as the percentage of feeding sites providing feeds by spreading feed at the site, leaving feeds in heaps or piles, or providing feeds in feeders. Feeding method levels were computed as:

$$\mathrm{FeedMeth}_{ai} = \frac{\sum_{k=1}^{M_a} \mathrm{FeedWt}_{aik}}{\sum_{j=1}^{T_a} \mathrm{FeedWt}_{aij}}$$

where

$\mathrm{FeedMeth}_{ai}$ = Feeding method index for feed type i at site a
FeedWt_{ai} = Total weight of feed type i provided at site a each year
M_a = Number of types of feeding methods for feed type i at site a
T_a = Total number of types of feed provided at site a each season

The feeding method level had values ranging from 0 (no feeding using the particular method at the site) to 1.0 (that particular feeding method was used for 100% of feeds at that site).

The location of each feed site, by TRS, was requested during the interview process. Since some participants were reluctant to disclose the location of their feed sites (even to the square mile level of the TRS), the township-range block (TR), a 6×6 block of contiguous TRS areas, was used as the geographical unit of analysis for this study. The TR areas encompassing the selected study areas were utilized in the analysis.

Data on general environmental conditions within each TRS block were collected from a geographic environmental dataset of land coverages generated by the MDNR, based on 1993 LandSat® satellite imagery (30 m^2 resolution). Land coverages were classified into the following general categories: hardwood forests, coniferous forests, mixed hardwood/conifer forests, swamps and wetlands, agricultural use areas, natural open fields and shrublands, open water, and other uses (primarily human habitation and industrial use). Levels of each land type per TR were calculated as the total acreage of each coverage type in the TR divided by the total acreage of the TR.

Statistical methods

Since TB can take relatively long periods of time from exposure to the development of detectable infection, with periods from 6 mo up to 2 yr, prevalence data were assessed with this in mind. Two separate analyses were conducted to test associations between supplemental feeding data in one specific year with TB prevalence lagged either 1 or 2 yr. For the 1 yr lag analysis, associations were tested between supplemental feeding data from 1995 with TB prevalence and deer-related data from 1996, and supplemental feeding data from 1996 and 1997 with deer-related data from 1997 and 1998, respectively. Supplemental feeding data from 1995, 1996, and 1997 were assessed with deer data from 1997, 1998, and 1999 (respectively) for the 2 yr lag analysis.

Statistical analyses were conducted to determine whether associations existed between prevalence and historic feeding practices and other risk factors. All statistical tests were con-

TABLE 1. Descriptive statistics for deer-related data from 27 TR areas included in models.

Variable	Mean	Variance	95% C.I.	Median	Quartiles
Over all years					
Number deer/TR	100.04	1,520.11	84.61–115.46	96.0	69.00, 96.00, 130.00
TB cases/TR	1.56	6.72	0.53–2.58	1.0	0.00, 1.00, 2.00
Prevalence/100	1.68	0.06	0.68–2.69	0	0.00, 0.62, 2.14
Percent males	52.99	1.33	48.42–57.56	52.17	43.40, 52.20, 62.40
Average age (yr)	2.69	0.17	2.52–2.86	2.70	2.33, 2.70, 2.99
1997					
Number deer/TR	65.11	316.36	51.44–78.78	67.0	37.0, 67.0, 76.0
TB cases/TR	2.11	6.86	0.10–4.12	1.0	0.0, 1.0, 3.0
Prevalence	3.12	0.12	0.49–5.75	2.41	0.0, 2.41, 3.95
Percent males	64.08	0.44	58.97–69.18	63.16	62.16, 63.16, 66.67
Average age (yr)	2.75	0.15	2.45–3.05	2.65	2.53, 2.65, 2.85
1998					
Number deer/TR	125.33	1,685.00	93.78–156.89	128.0	119.0, 128.0, 161.0
TB cases/TR	2.00	12.50	−0.72–4.72	1.0	0.0, 1.0, 2.0
Prevalence	1.43	0.04	−0.20–3.05	0.62	0, 0.62, 2.0
Percent males	43.90	0.56	38.14–49.67	42.68	42.19, 42.68, 50.42
Average age (yr)	2.93	0.08	2.71–3.15	2.99	2.70, 2.99, 3.06
1999					
Number deer/TR	109.67	742.50	88.72–130.61	99.0	96.0, 99.0, 130.0
TB cases/TR	0.56	0.78	−0.12–1.23	0.0	0.0, 0.0, 1.0
Prevalence	0.48	0.01	−0.12–1.08	0.0	0.0, 0.0, 0.81
Percent males	51.00	0.98	43.41–58.59	47.83	43.79, 47.83, 56.12
Average age (yr)	2.39	0.18	2.07–2.72	2.16	2.11, 2.16, 2.88

sidered significant for $P \leq 0.05$. At the univariable level, analysis of variance was used for simple assessment of associations. Because the occurrence of TB in wild deer was relatively rare and followed a Poisson distribution, multivariable Poisson regression models were developed for supplemental feeding and TB prevalence from each TR, for feeding by type, method and feed quantity, controlling for deer age, gender, and year. Variables with very rare occurrences (less than five uses from 347 feeding sites), or variables with high levels of missing data (more than 50% of sites missing data) were not included in the analyses. Any sets of highly correlated variables were examined, and the one variable which best captured the effect of the set of variables on the outcome was selected for inclusion in the models. All eligible risk factors, with any interaction terms, were included in the full model. Backwards model building was used to develop a final model, using the Aikaike Information Criteria statistic to compare models between different stages of development. Associations between selected risk factors and TB prevalence were reported as odds ratios with 95% confidence intervals. Odds ratios for continuous variables were adjusted for significant increments of change (i.e., odds for a 10 kg change in quantity of feed provided). If, during model development, the removal of a potential confounder resulted in a 10% or more change in the odds ratio of the risk factor of interest, the variable was retained in the model to control for confounding.

RESULTS

There were 200 cases of *M. bovis* seen in 18,560 deer from 1997 to 1999. Table 1 shows deer-related data used in the multivariable models, overall and by year, from 1997 to 1999. Land cover data for the 27 TR study areas are presented in Table 2. The most common features present in the study area were mixed hardwood/conifer forests, hardwood forests, agricultural land use, and natural open areas/shrublands.

A total of 1,359 individuals were asked to participate by mail and 677 (50%) responses were received. Of these, 76 addresses had expired, 27 were no longer residents of the area, and 12 were deceased. Of the 562 responses left, 173 (31%) did not feed deer and were not interviewed. Of the 389 remaining, 173 (44%) refused to participate. Reasons for

TABLE 2. Descriptive statistics for general land use data from 27 TR areas included in models.

Coverage type	Mean	SD	Range
Mixed forest	30.92	11.91	9.89–48.50
Hardwood forest	23.89	16.12	6.36–58.21
Coniferous forest	9.62	10.36	1.19–43.82
Natural open areas, shrublands	10.33	3.41	5.37–16.32
Wetlands	2.72	1.46	0.71–5.52
Open water	2.68	4.14	0.02–18.02
Agricultural use	13.91	8.4	0.95–28.22
Other uses	5.78	4.08	0.69–14.25

refusal to participate included 30 (8%) for not hunting, 41 (11%) for no reason, and 102 (26%) for other reasons. Of the 216 participating, 128 (59.3%) were successfully interviewed. Unsuccessful interviews were due to participants changing their minds, inability of interviewer to make contact, death, or finding the participant ineligible for participation during the interview.

Through interviews with 128 participants, data were collected on 347 separate feeding sites being used from the winter of 1995–96 to the winter of 1997–1998 in the 27 TR areas. Tables 3 and 4 show description of feeding sites maintained by participants in the study, by study area. Types of feeds provided are described in Table 5.

Results of multivariable analyses using both the 1- and 2-yr lag periods were similar, so the results of only one series of analyses are presented. Table 6 shows the results of the final multivariable Poisson regression model for feed type and feeding method, and feed site risk factors, adjusted for deer age, sex, and study year using the 2 yr lag period. Several risk factors were significantly associated with the prevalence of TB within a TR area in the reduced model: risk factors associated with decreasing risk were level of open natural areas (O.R.=0.07, 95% C.I.=0.02–0.36), locating sites in or near hardwood forests (O.R.=0.05, 95% C.I.=0.01–0.41), and the percent of feed site providing grains (O.R.=0.06, 95% C.I.=0.01–0.26). Conversely, risk factors associated with increasing risk were the levels of hardwood forests in the TR area (O.R.=1.76, 95% C.I.=1.31–2.36), the number of large feed sites identified through aerial surveillance (O.R.=1.11, 95% C.I.=1.00–1.23), the average number of deer fed per year (O.R.=3.91, 95% C.I.=1.35–11.37), percentage of sites spreading grain (O.R.=14.7, 95% C.I.=2.19–98.85), kg of grain fed at the site (O.R.=1.37, 95% C.I.=1.10–1.71), and the kg of fruits and vegetables provided at the site per m^2 (O.R.=1.43, 95% C.I.=1.19–1.71).

DISCUSSION

The basic hypothesis this study tested was that supplemental feeding practices

TABLE 3. Descriptive statistics for general site-related data from 347 feeding sites in 27 TR areas included in models.

Variable	Mean	Variance	95% C.I.	Median	Quartiles
Number of feeding sites	27.44	74.56	24.03–30.86	27.00	20.0, 27.0, 34.0
Total feed site area (km^2)	414.31	7.3×10^8	77.24–751.38	23.95	6.88, 23.95, 264.81
Average feed site area (km^2)	11.96	558,250.48	2.61–21.31	1.20	0.28, 1.20, 9.13
Number of years site used	12.17	16.35	10.57–13.77	12.18	9.37, 12.18, 12.50
Average number of deer fed/year	17.00	244.59	10.81–23.19	12.04	7.90, 12.04, 16.31
Total number of deer fed/year	34.00	978.36	21.63–46.37	24.08	15.80, 24.08, 32.62

TABLE 4. Descriptive statistics for site location data from 27 TR areas included in models.

Variable	Mean	Variance	95% C.I.	Median	Quartiles
In hardwood forest	10.00	30.23	7.82–12.18	10.0	7.0, 10.0, 12.0
In coniferous forest	6.11	91.26	2.33–9.89	4.0	1.0, 4.0, 5.0
In cedar swamp	10.11	58.95	7.07–13.15	8.0	6.0, 8.0, 13.0
Site with dry soils	9.33	17.31	7.69–10.98	9.0	7.0, 9.0, 13.0
Site with wet soils	10.67	78.0	7.17–14.16	8.0	8.0, 8.0, 12.0
Site with variable soils	6.88	26.87	4.84–8.94	8.0	1.0, 8.0, 10.0

influenced the levels of TB in the wild white-tailed deer population. The results of our study show that certain supplemental feeding practices were associated with the prevalence of bovine TB, presumably by increasing the risk of transmission of *M. bovis* between wild white-tailed deer. Supplemental feeding appears to play an important role in the epidemiology of bovine TB in the deer population, but no doubt there are other forces contributing to the maintenance of this infection including local deer density, level of infection in the population, and deer behavior patterns. While it would be desirable to be able to measure the effects of these different factors on the prevalence of TB, the logistics of conducting such a study would be considerable, and are well beyond the scope of this study.

There are two biologically plausible methods which might increase the likelihood of disease transmission: by increasing direct contact between animals at feeding sites and by increasing the spread of disease through contaminated feed sources used by large numbers of animals. While direct contact and aerosol transmission are the most efficient methods of spreading *M. bovis* from animal to animal (Francis, 1971), oral transmission of *M. bovis* has been demonstrated in cervids (de Lisle et

TABLE 5. Feed types provided at feeding sites from 27 TR areas included in models.

Feed group (most common)	Variable	Sum	Mean	95% C.I.	Quartiles
Grains (corn, oats, wheat)	Number sites using	258	15.5	12.2–18.9	3.0, 18.5, 22.5
	Number sites spreading	199	11.8	9–14.6	3.0, 11.5, 18.0
	Number sites heaping	62	3.7	2.4–4.9	0, 2.0, 7.0
	Total fed per year[a]	1,732.3	32.7	2.6–62.8	0.9, 3.0, 13.7
	Total fed at a time[a]	19.6	1.1	0.5–1.6	0.1, 0.4, 1.3
Fruits and vegetables (sugar beets, carrots, apples)	Number sites using	278	38.4	31.2–45.5	9.0, 43.0, 53.0
	Number sites spreading	224	29.2	23.1–35.3	7.0, 27.0, 40.0
	Number sites heaping	81	11.0	7.6–14.4	0.0, 5.0, 25.0
	Total fed per year[a]	1,697.5	32.6	7.8–57.4	2.0, 4.8, 29.3
	Total fed at a time[a]	341.1	6.2	1.2–11.2	0.1, 1.0, 3.0
Forages (hay)	Number sites using	98	5.5	4.3–6.7	2.0, 4.0, 9.0
	Number sites spreading	77	3.9	3.0–4.8	1.0, 3.0, 5.0
	Number sites heaping	18	0.9	0.4–1.4	0, 0, 1
	Total fed per year[a]	385.6	7.3	2.4–12.1	0.7, 1.5, 4.0
	Total fed at a time[a]	38.2	0.7	0.4–1.1	0.1, 0.3, 1.1
Other fed items (salt)	Number sites using	17	6.3	3.3–9.4	2.0, 6.0, 7.0
	Number sites spreading	8	3.1	1.8–4.3	1.0, 3.0, 6.0
	Number sites heaping	11	1.9	0.5–3.3	0, 0, 4.0
	Total fed per year[a]	NR	NR	NR	NR
Crop fields (rye, clover)	Number sites using	27	6.3	3.3–9.4	2.0, 6.0, 7.0

[a] In 1,000 kg. NR=weights not reported.

TABLE 6. Final multivariable Poisson regression model for supplemental feeding risk factors, controlling for deer age, gender, and study year, for 27 TR areas included in models.

Risk factor	P	Odds ratio	95% C.I.
Level of TR area covered by hardwoods	0.0002	1.76[a]	1.31–2.36
Level of TR area covered by open areas	0.0012	0.07[a]	0.02–0.36
Large feed sites (by aerial surveillance)	0.0461	1.11	1.00–1.23
Average years feed site used	0.1071	1.74[b]	0.89–3.39
Average number of deer fed per year	0.0123	3.91[c]	1.35–11.37
% Sites in/near hardwood forests	0.0054	0.05	0.01–0.41
% Sites feeding grains	0.0002	0.06	0.01–0.26
% Sites spreading grain	0.0057	14.70	2.19–98.85
Kg of grain per m^2	0.0050	1.37[d]	1.10–1.71
% Sites feeding fruits and vegetables	0.7968	1.09	0.55–2.16
Kg of fruits and vegetables per m^2	0.0001	1.43[d]	1.19–1.71
Interaction terms			
% Sites feeding vegetables, fruit × kg of vegetables, fruits per m^2	<0.0001	—	—
Model AIC=1,012.90, Likelihood Ratio=148.02, 16 df, $P<0.0001$, Estimated Model $R^2=2.89$			

[a] Odds ratio for 10% change in percentage of TR covered.
[b] Odds ratio for 10 year change in average number of years sites were used.
[c] Odds ratio for 1,000 animal change in estimated numbers of deer fed.
[d] Odds ratio for 10 kg change in kg of feed per m^2.

al., 1983; Lugton et al., 1997). Past reports have indicated that, under climatic conditions similar to Michigan, *M. bovis* can persist in the environments for weeks or months (Williams and Hoy, 1930; Chiondi and Van Kruiningen, 1983), and experimental studies have shown that *M. bovis* can survive for extended periods of time on different types of animal feeds used for deer in Michigan (Whipple and Palmer, 2000), indicating that contamination of feed materials can form an important source of infection at deer feeding sites. These concepts have formed the basis for TB control programs to date, and, while these ideas are well-reasoned and logical, providing scientifically valid support for these concepts was needed to assist in garnering public support for the control programs.

The use of a lag period between feeding data and TB prevalence data was used to account for period of time from a wild deer's exposure to *M. bovis* to the development of gross lesions detectable under the current TB surveillance program. Earlier references have indicated that an incubation period of 6 mo to years has been seen in various cervids (Clifton-Hadley and Wilesmith, 1999). There have been experimental infection studies with white-tailed deer demonstrating development of lesions within 100 days (Palmer et al., 2001), but these have been conducted in circumstances where the subjects received relatively large doses of TB to induce infection, were housed in biohazard level 3 confinement facilities, and were probably under high levels of stress. As in cattle, an animal's innate disease resistance, health, stocking density, and size of the infecting dose influence the rate that *M. bovis* grows and spreads in the deer's body (de Lisle et al., 1985), so experimental animals kept under these circumstances would be more likely to develop signs of infection more rapidly than in animals in the wild where the stresses and infectious doses would likely be much lower.

Given the geographic scale at which these data were analyzed (TR area—approximately 9,300 ha each), it was assumed that, in the case of an adult, 1) it was likely that a deer probably spent a significant portion of its life in the same TR capture area, and 2) that deer had been exposed to the feeding practices in the TR for that same portion of its life. The average ages of deer collected during surveillance in 1997, 1998, and 1999 were 2.8, 2.9, and 2.4, respectively, and if these deer had remained in the same TR area in which they were born, the lag between feeding practice and prevalence would associate supplemental feeding from the deer's earlier life, possibly when *M. bovis* was initially contracted through contact with other deer. Interestingly, by age group, 2- to 3-yr-old white-tailed deer had higher levels of *M. bovis* infection than other age groups, based on information from ongoing TB surveillance in Michigan (O'Brien et al., 2002) and data from a TB-positive captive cervid herd in the same area (Palmer et al., 2000).

Several risk factors that would increase the likelihood of direct transmission of *M. bovis* were identified. Increasing the quantity of feeds provided at the site was associated with increasing risk of tuberculosis in the area deer population. If the feed is present in high quantities or high densities in a given area in a feeding site, it will take longer for deer to consume the feed in that area than if feeds were there in lower quantities. This will increase the amount of time deer spend in that particular area, which will increase direct contact between animals. When feeds are concentrated there is increased risk of other deer being exposed to feed contaminated by oral and nasal secretions. One situation has been commonly seen in northeastern Michigan when the outer surfaces of the feed piles become frozen in the winter. One deer will break a small 'hole' through the frozen surface of the feed pile, just large enough to accommodate its muzzle, and will feed at that spot. After this 'hole' is made, other deer will consume feed from the pile from the same 'hole'. If an infected deer contaminated feed in one of these 'holes', other deer feeding from this 'hole' could either ingest *M. bovis* on the feed, or inhale the organism on dust or particulate materials in the 'hole'.

Increasing numbers of large feed sites identified through aerial surveillance in the TR area were associated with increasing TB prevalence. While there were no significant associations between these very large sites and the supplemental feeding reported by participants in this study, the presence of these large sites would serve as areas where large numbers of deer could become exposed to *M. bovis*, either through direct contact or through ingestion of contaminated feed.

Increased percentage of sites that provided fruits and vegetables was associated with increased prevalence. Large numbers of sites providing more desirable feed (such as apples, carrots and sugar beets) will draw more deer into the general area where these sites and feeds are available. Conversely, increased percentage of sites providing grain was associated with decreased prevalence. While grains were provided at fewer feeding sites than vegetables and fruits, the quantities provided (in kg) were greater (Table 4). Increasing the number of feeding sites in a geographic area will provide deer with a greater number of feeding places, which will help disperse deer among these sites. On the other hand, if there were only a few feeding sites in the same geographic area, more animals would concentrate at the few sites available. The differences seen between feeding grains and fruits and vegetables may be explained by their physical attributes. Grains and other granular-type feeds can be dispersed to the point where only a few grains lie close enough to be consumed in one bite by deer. On the other hand, no matter how widely spread they are at a feed site, some of the more common fruits and vegetables (sugar beets, carrots, potatoes, and pumpkins) come in sizes that cannot be consumed in a single bite. In situations like this an infected deer could partially consume a single sugar beet and contaminate it with saliva or nasal secretions, providing a source of infection for an uninfected deer.

The years feeding sites were used was also associated with increased prevalence (O.R.=1.74), but this was not statistically significant. Deer become habituated to feed sites that are used repeatedly over time. Does returning to the same site year after year will introduce their offspring to these sites, increasing the number of deer routinely visiting these feed sites. A two-stage model of disease transmission for white-tailed deer has been proposed (O'Brien et al., 2002), in which 1) TB is maintained at low levels in matriarchal groups and 2) dissemination of disease is due to movement of infected bucks. Repeated visits could be a factor supporting *M. bovis* infection in matriarchal bands.

Increased TB prevalence was seen in TR areas with higher percentages of hardwood forests. These areas include those used by deer as bedding areas, providing cover from potential predators. It has also been reported that deer continue to utilize browse as a source of food even in the presence of supplemental feed sources (Doenier et al., 1997), so locating feed sites in areas with woodlands would provide conditions where deer would have access to both sources of food. Also, if environmental contamination by infected deer occurred, the presence of canopy cover and leaf litter in these locations would provide shady, moist conditions in which *M. bovis* might survive longer in the environment.

Feeding larger numbers of deer at a site was also associated with increasing TB prevalences. Larger numbers of animals at a single site provide greater opportunities for spread of disease, either through direct or indirect contact, by simply increasing the numbers of animals available for exposure to *M. bovis* at the site.

In addition to factors associated with increased prevalence of TB in wild deer, several factors were identified with decreased disease prevalence. Declining levels of TB were found in areas with increased natural open area. Deer may not spend as much time in open areas in comparison to forested areas due to the lack of natural cover for hiding, and possibly due to decreased availability of browse.

Feeding sites in or near forested areas were associated with lower disease rates. The presence of trees and undergrowth might keep deer from congregating in large numbers at feed sites in hardwood forests, and the cover provided by the forest would allow deer to enter and leave the feed site without the hazard of exposure, as would be the case if the feed site were located in an open field.

One unexpected effect seen was that increasing the percentage of sites spreading grain was associated with increasing risk of tuberculosis. We expected that dispersing feed at a site would reduce the risk of disease transmission by avoiding situations in which nose-to-nose contact between deer at the site would be more likely. However, the process of spreading feed may not be as important as the density of the feed material after spreading. For both feed types by weight, the majority of feeds were spread (97% of grain, and 96% of vegetables and fruits). However, when looking at feed density for feeds that were spread, the feed density of grains were 0.16 kg/m^2, compared to only 0.05 kg/m^2 for fruits and vegetables. Even though the grains were not provided in heaps or feeders, the density of spread grains was notably higher than for fruits and vegetables. This increased density of feed may be more important than efforts to relatively disperse grains at feed sites. Interestingly, the feed densities of both feed types that were not spread were fairly similar: 0.59 kg/m^2 for grains, and 0.51 kg/m^2 for vegetables and fruits.

Prevalences of TB from the study area varied over the study period, from 3.12 per 100 deer in 1997, to 0.48 in 1999. There are two likely causes for the variability seen: 1) actual changes in the prevalence of TB in the white-tailed deer population, and 2) limitations of the surveillance techniques. It is interesting to note that, since the advent of feeding/baiting restrictions and increased hunting in the region since 1999, the prevalence of TB has been dropping in the study areas. This decline in prevalence may be due to control measures implemented in 1998 (Table 1) (O'Brien et al., 2002), particularly the aggressive harvesting of deer to reduce the overall deer population, and the ban on supplemental feeding. Whether the declines in prevalence seen were entirely due to the control programs or other factors has not been conclusively determined (O'Brien et al., 2002). The effect of the state-imposed feeding/baiting restrictions on supplemental feeding is not easily quantifiable, and is beyond the scope of this study. While the deer-related data from this study falls into the time period after the feeding restrictions began, it was felt that the effects of feeding in years prior to when a deer was collected under surveillance was more important than feeding practices during the year of surveillance.

The surveillance program, under which deer-related data for this study were gathered, relied heavily on the voluntary submission of deer heads taken during the firearm deer season in the study area (Schmitt et al., 1997; O'Brien et al., 2002). Unfortunately, this method of sampling the deer population in the area does not ensure a proportional and representative sample of the overall population, and may have biased both the numbers of deer and number of TB cases identified through surveillance, though there is little evidence to suggest that hunters intentionally withheld TB-lesioned deer from surveillance (O'Brien et al., 2002). The decline in prevalence may have been an artifact of the increasing intensity of hunting in the area (collecting more deer that were less likely to be infected), but since age and gender have been highly associated with TB (older deer and males being at higher risk of infection) (O'Brien et al., 2002) and the age and gender profiles of deer did not change significantly from year to year, this suggests that decreasing prevalence was not due to changes in the demographics of the population collected through hunter harvesting, and contributes to the argument that changes in deer management (feeding/baiting restrictions) have affected the TB prevalence.

Another source of bias could be related to methods used to identify *M. bovis* infection in the submitted specimens. Since testing (histopathology, acid-fast staining, mycobacterial culture, and PCR) was limited to specimens with gross lesions suspicious for TB, there was the possibility that the prevalence of TB could have been underestimated by as much as 57% (Palmer et al., 2001). However, results of histopathology and acid-fast staining on tissues from deer without gross lesions taken in 1995 suggest that the numbers of cases missed may not be significant (Fitzgerald et al., 2000).

In summary, there was evidence that some aspects of supplemental feeding were associated with the prevalence of *M. bovis* in the wild white-tailed deer population of northeastern Michigan. Risk factors associated with concentrating deer were associated with increasing prevalence of TB, while risk factors associated with dispersing deer were associated with decreasing prevalence of TB. Those factors which concentrated deer in a limited area could increase the frequency and probability of both direct and indirect transmission of *M. bovis.* Conversely, factors which dispersed deer could reduce the probability of direct contact between infected and uninfected animals, and decrease the frequency and probability of indirect transmission through environmental contamination. While supplemental feeding practices are not the only force behind the TB epidemic in the white-tailed deer population, their contribution to the problem should not be overlooked. Stopping or curtailing supplemental feeding practices associated with increased disease transmission should help to reduce the problem of bovine TB in the deer herd. Finally, the outbreak of bovine TB in Michigan and the role of supplemental feeding in support of the outbreak should serve as a cautionary example of an unintended effect of a human intervention in the ecology of a wildlife species.

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