J. Parasitol., 95(4), 2009, pp. 829–837
© American Society of Parasitologists 2009

PREDICTED GEOGRAPHIC RANGES FOR NORTH AMERICAN SYLVATIC *TRICHINELLA* SPECIES

Penny M. Masuoka, Robin Burke, Michelle Colaccico, Hugo Razuri, Dolores Hill*, and K. Darwin Murrell
Department of Preventive Medicine and Biometrics, Uniformed Services, University of the Health Sciences, Bethesda, Maryland 20814. *e-mail: pmasuoka@usuhs.mil*

ABSTRACT: Because of a lack of comprehensive surveys, the geographic distributions of the North American species of encapsulating *Trichinella* (*T. nativa* and its variant T6, *T. murrelli*, and *T. spiralis*) are poorly characterized in detail. These species are potentially zoonotic; therefore, biogeographic information is critical to monitoring their status and any distribution changes due to climatic and man-made environmental impacts. The maximum entropy (Maxent) program was used to model predicted ranges for these sylvatic *Trichinella* spp., using a limited number of available location records with confirmed species identifications collected over 55 yr throughout North America. The resulting prediction models were shown to be robust, and the species maps created are presented. The predicted range of *T. nativa* is primarily north of the 48°–52° latitudes, overlapping the Tundra, sub-Arctic, and Warm Continental eco-regions. Its sympatric genotypic variant, T6, has a predicted range covering primarily the sub-Arctic and mountainous Temperate Steppe eco-regions, the latter extending below 48°N latitude. In the east, the T6 range includes the Warm Continental and the mountainous Hot Continental eco-regions; the T6 range is also predicted to extend to the Sierra Madre Mountains of Mexico. The most probable range of *T. murrelli* is centered in the Midwest within the Hot Continental and Prairie eco-regions, with an extension southward to the Subtropical and Tropical/Subtropical Steppe and Desert eco-regions. In the west, it exists in a restricted range characterized as mountainous Mediterranean. The most probable distribution of sylvatic *T. spiralis* is along the humid east North American coast (Hot Continental south to Subtropical), and along the coast of northwest North America (Marine) to Alaska (sub-Arctic and Tundra). Its most southerly range extends into central Mexico (Tropical/Subtropical Desert). The difference in relative freeze resistance between *T. nativa*/T6 and *T. murrelli* undoubtedly accounts for much of this geographic separation. However, the factors responsible for the absence of a more southerly distribution of *T. nativa* are not obvious, given the overlap in host range with *T. murrelli.* The maximum July temperature appears to have a significant effect on this distribution pattern. The results of the model building highlight subjects for future research on the biotic and abiotic factors important in determining *Trichinella* spp. distributions and directions for model validation research.

The recent era in the long history of trichinellosis and *Trichinella* spp. might be fairly characterized as the revolution of the parasite's systematics and ecology. Over the first 150 yr of its scientific recognition, *T. spiralis* was considered to be the sole member of the genus, with a host range of more than 100 species of mammals (Campbell, 1983). As reviewed by Pozio and Murrell (2006), the widely misunderstood taxonomy, host range, and epidemiology of *T. spiralis* persisted well into the 20th century, and it was not until the introduction of biochemical and molecular methods (particularly polymerase chain reaction [PCR]) to parasite taxonomy that the concept of a polytypic genus became accepted (Zarlenga et al., 1999). The modern paradigm for *Trichinella* spp. taxonomy was introduced in 1992 with 8 genotypes, including 5 named species (Pozio et al., 1992). Currently, the genus is composed of 2 clades, one formed by species that encapsulate in host muscle (5 species and 3 genotypes) and a non-encapsulating clade (3 species) (Pozio and Zarlenga, 2005; Pozio and Murrell, 2006).

Three species are endemic to North America and are confined to sylvatic mammals, i.e., *T. nativa* (and its closely related genotype T6), *T. murrelli*, and *T. pseudospiralis*. The cosmopolitan *T. spiralis* is also present in both domestic animals (pigs, dogs, cats, etc.) and sylvatic mammals. Recent analysis of the biogeography and phylogeny of *Trichinella* spp. has provided strong evidence that carnivores such as ursids, canids, and felids are principally responsible for the dispersal of Holarctic species, which appear to have expanded across western Europe and then across Beringia into North America (Zarlenga et al., 2006). Because human infection with the sylvatic *Trichinella* spp. from consumption of wild animals is an appreciable risk (Pozio and Murrell, 2006), the geographic and host ranges for these zoonotic parasites are of interest. Since the introduction of multiplex PCR methods (Zarlenga et al., 1999), the species identification of isolates of *Trichinella* has become more convenient and frequent, resulting in a growing database on the geographic locations and host species of the North American species.

The recent development of ecological niche modeling programs to model species' distributions (Elith et al., 2006) and the recent availability of improved global climate, land cover, and elevation datasets have increased the use of models in a variety of applications. Ecological niche models have been developed in conservation biology to guide population surveys (Bourg et al., 2005; Guisan et al., 2006), to predict the effects of global change on species (Pearson and Dawson, 2003; Pearson et al., 2004), and to find suitable habitats for the reintroduction of species (Pearce and Lindenmayer, 1998). Another application of species' distribution modeling is assessing disease risk. Peterson et al. (2006) modeled the potential distribution of Marburg virus in Africa. Peterson and Shaw (2003) predicted the geographic distribution of *Lutzomyia* spp. sand flies, the vector of leishmaniasis, in South America. Moffett et al. (2007) modeled the distribution of mosquitoes in Africa as part of an effort to predict malaria risk. Burke et al. (2008) used geographic information system (GIS) mapping to identify farm locations with risk for introduction of *T. spiralis* to domestic swine. Pozio et al. (2008) employed GIS tools to investigate the habitats and host ranges of *T. britovi* and *T. spiralis* in Europe and to identify potential host species suitable for surveillance.

In the present paper, we discuss our use of the Maxent approach to modeling (Phillips et al., 2004, 2006) to develop a predictive *Trichinella* spp. range map based on less-than-abundant confirmed species records from sylvatic hosts in North

Received 12 November 2008; revised 26 January 2009; accepted 12 February 2009.
* United States Department of Agriculture, Agricultural Research Service, Animal and Natural Resources Institute, Animal Parasitic Diseases Laboratory, Building 1044, BARC-East, Beltsville, Maryland 20705-2350.
DOI: 10.1645/GE-1952.1

America (Canada, United States, and Mexico) accumulated over the past 55 yr. The goal of this project was to create predictive maps based on the environmental conditions of limited *Trichinella* spp. occurrence data, which may assist future biogeographical investigations on *Trichinella* spp. endemic to North America by highlighting geographic regions with high probability for occurrence. The results obtained also call attention to certain enigmas related to the restriction of geographic ranges and the possible importance of the "free-living" stage of *Trichinella* spp.

MATERIALS AND METHODS

Wild animal *Trichinella* spp. infection database

Records of *Trichinella* spp. isolated from sylvatic hosts in North America were compiled from published literature and from accession records on isolates deposited with the International *Trichinella* Reference Center (ITRC) in Rome. Two records of *T. pseudospiralis* were dropped from our database because these records are not sufficient to predict a geographic distribution of the species. In all but 16 of the 118 records included in the analysis, the *Trichinella* sp. was determined using molecular methods, either by the authors of the published records or at the ITRC, following methods approved by the International Trichinellosis Commission (FAO/WHO/OIE, 2007). The 16 non-molecularly identified *Trichinella* infections were assigned to species in the database based on the following criteria: 8 were designated *T. spiralis* based on host species. Seven records from rats (*Rattus* spp.) were so identified because of the very low susceptibility of this host species to other *Trichinella* spp. (Pozio and Murrell, 2006). One record was from a feral cat trapped near a farm with *T. spiralis*–infected pigs; the isolate was found to be highly infective for pigs in an unpublished experiment by one of the authors (K.D.M.), a biological character not shared by *T. murrelli*, *T. nativa*, or T6 (Kapel, 2000).

Eight records were from carnivores from Arctic areas (latitude greater than 52°) and designated as *T. nativa*, because no other species of *Trichinella* have been reported from these hosts in this region. Three of these records, from the Kootenay Peninsula, British Columbia (2 bobcats and 1 black bear), were also designated *T. nativa*, because only this genotype has been reported in this region. Location records for *T. spiralis* were utilized in the model building with and without rat (*Rattus* spp.) host records, because of the uncertainty of the role of rats as true sylvatic reservoir hosts (Pozio and Murrell, 2006).

When available, latitude and longitude data on host animal collection points were used. If not, the locations were extrapolated based on the coordinate points of the closest town or city to the collection point, using coordinates published in maps or on national databases. Records that contained a non-specific location (e.g., southeast Alaska) were not used. The final *Trichinella* spp. database was imported into ArcGIS 9, and location points were visually checked for location accuracy. The complete database with references is available from K.D.M. (kdmurrell@comcast.net) or P.M.M. (pmasuoka@usuhs.mil).

Table I summarizes the number of records and the host species used for model building and analysis in this study. One hundred and eighteen *Trichinella* records in 19 different host species were used in this study. An additional 39 records are included in parentheses; these records were added to illustrate the host range, but are not included in the geographic distribution models.

Environmental layers used in models

Environmental layers used to model the geographic ranges of sylvatic *Trichinella* spp. included elevation data, climate data, and land cover. The elevation data were obtained from the Global Land One-kilometer Base Elevation (GLOBE) digital elevation model (DEM) from the National Geophysical Data Center (NGDC) (Hastings and Dunbar, 1998) (http://www.ngdc.noaa.gov/mgg/topo/globe.html).

Climate data used for modeling consisted of January and July total precipitation, January mean minimum temperature, and July mean maximum temperature from the WorldClim Version 1.4 dataset (http://www.worldclim.org). WorldClim was created by interpolating average monthly climate data from weather stations. The resulting data layers are in raster format with 1^2-km grid cells. Weather data used to create WorldClim were collected from 1950 to 2000, which matches well with the *Trichinella* spp. data collected from 1950 to 2006. For a complete description of how the WorldClim dataset is compiled, see Hijmans et al. (2005).

Land cover was downloaded from the U.S. Geological Survey's Global Land Cover Characteristics Database (http://edcsns17.cr.usgs.gov/glcc/). This data set was produced from 1-km Advanced Very High Resolution Radiometer (AVHRR) data over a 12-mo period (April 1992–March 1993), using the seasonal changes in vegetation to aid the land cover identification process. The output database contains a number of classification schemes. The International Geosphere-Biosphere Programme (IGBP) land cover classification was selected for this study. This land cover classification uses 17 classes, which are listed in the first column of Table II. To simplify the statistical analysis, however, the original 17 classes were combined into the more generalized classes, as listed in the second column of Table II.

To determine which environmental layers should be included in the *Trichinella* spp. distribution analysis, a preliminary statistical analysis was made. Measurements of the temperature, precipitation, land cover, and elevation present within 20 km of *Trichinella* spp. locations were calculated from the environmental layers using the ArcGIS program. Associations between the location of *Trichinella* spp. and environmental variables were calculated using analysis of variance in SPSS 12.0.1 for Windows. Correlations that were statistically significant were then analyzed using Tukey's multiple comparison procedure. Statistical analysis revealed significant correlations between *Trichinella* spp. and: minimum January temperature ($P = 0.000$), maximum July temperature ($P = 0.000$), elevation ($P = 0.014$), and land cover ($P = 0.000$). No significant association was found between *Trichinella* spp. and precipitation and, as a result, precipitation was dropped from further analysis.

Species' distribution modeling

The maximum entropy method, Maxent 3.2.1 program for model building (Phillips et al., 2006), was used to model the *Trichinella* spp. geographic distribution for North America. Maxent takes a set of raster environmental layers (e.g., temperature and elevation) and a text file of species' occurrence locations and produces output maps that predict the potential range of each species. Maxent, which uses presence-only data rather than presence/absence data, has been shown to be a high-performing model-building program (Elith et al., 2006) and excels in using small numbers of occurrence points (Hernandez et al., 2006). Maxent is publicly available for download from http://www.cs.princeton.edu/~schapire/maxent/.

Twenty-five percent of the occurrence points were used for testing the accuracy of the model (testing points), and the remaining 75% were used for building the model (training points); training and testing points are randomly selected by the Maxent program. As measures of the accuracy of the models, Maxent calculates the receiver operating characteristic (ROC) and the area under the curve (AUC) of both the training and testing points. ROC and AUC methods have been discussed extensively in the literature and are widely employed in modeling (Swets, 1988; Fielding and Bell, 1997), including modeling of species' distributions (Phillips et al., 2006). Maxent estimates a relative contribution of each environmental variable to the overall model. However, the relative contributions of each variable can be affected by how correlated the environmental variables are to each other (see Results). As an alternative means to estimate the potential contribution of environmental variables to the model, the Maxent program was run multiple times, using only 1 environmental layer at a time (Moffett et al., 2007).

To examine the input environmental values to Maxent for each species, we extracted the pixel values underneath each species occurrence location. For the elevation and temperature layers, these values were averaged. For land cover, the most frequent category was determined for each species.

Output from the model was compared to the eco-region types and characterizations described by Bailey (1996).

RESULTS

Geographic range prediction maps

Output images of predicted geographic distributions produced by the Maxent models are shown in Figure 1. The highest levels of

TABLE I. Confirmed *Trichinella* host species records included in the database and used in Maxent model. Those in parentheses were not included in the model but are discussed separately in the Results section.

Host species	*T. murrelli*	*T. nativa*	*T. nativa*	*T. spiralis* (T6)	Total*
Arctic fox (*Alopex lagopus*)	–	2	–	–	2
Black bear (*Ursus americanus*)	6	3	9	5	23
Bobcat (*Lynx rufus*)	1	2	–	1	4
Coyote (*Canis latrans*)	21	–	–	1	22
Feral cat (*Felis catus*)	–	–	–	2	2
Fisher (*Martes pennanti*)	–	–	1	–	1
Grey fox (*Urocyon cinereoargenteus*)	–	–	1	–	1
Grizzly bear (*Ursus arctos*)	–	1	3	–	4
Lynx (*Lynx canadensis*)	–	1	–	–	1
American Marten (*Martes americana*)	–	1	–	–	1
Mountain lion (*Felis concolor*)	–	–	3	–	3
Opossum (*Didelphis virginiana*)	–	–	–	(1)	–
Polar bear (*Ursus maritima*)	–	3	–	–	3
Raccoon (*Procyon lotor*)	12	–	–	(1)	12
Rat (*Rattus* sp.)	–	–	–	7	7
Red fox (*Vulpes vulpes*)	5	1	–	2	8
Striped skunk (*Mephitis mephitis*)	–	–	–	(1)	–
Walrus (*Odobenus osmarus*)	–	1	–	–	1
Wild boar/feral pig (*Sus scrofa*)	–	–	–	5	5
Wolf (*Canis lupus*)	–	11	6	–	17
Wolverine (*Gulo gulo*)	–	(3)	1 (33)	–	1
Total	45	26	24	23	118

* Records in parentheses not included in totals.

probability (more than 50%) for the range of *T. nativa* encompass the Tundra, sub-Arctic, and the Temperate Steppe (Rocky Mountains) eco-regions (Bailey, 1996). Its variant genotype T6 shares, at the same levels of probability, the sub-Arctic and mountainous Temperate Steppe eco-regions, its range in the latter extending below the 48°N latitude (mountainous is defined as mountains with altitudinal zonation). In the east, the T6 range extends from Quebec (Warm Continental) and down the mountainous Hot Continental eco-region (mountainous). It is has a predicted occurrence in the Sierra Madre Mountains of Mexico. The most probable range of *T. murrelli* is the Midwest within the Hot Continental (including mountainous) and Prairie eco-regions, with an extension southward to the Subtropical and Tropical/Subtropical Steppe and Desert eco-regions. In the West, it is predicted in a restricted range characterized as mountainous Mediterranean (California). The most probable distribution of *T. spiralis* is in the eastern United States (Hot Continental south to Subtropical), and along the coast of northwest North America (Marine) to Alaska (sub-Arctic and Tundra). A small region of the Rocky Mountains is included in the predicted ranges for *T. spirals* when records from rats are included. Its most southerly range extends into central Mexico (Tropical/Subtropical Desert).

The partitioning of the freeze-tolerant *T. nativa* and T6 from the freeze-sensitive species, *T. spiralis* and *T. murrelli*, is evident. The latter species are nearly completely restricted to the region below a latitude of 52°. In the alternate model, using *T. spiralis* records minus rat host records, the probability of *T. spiralis* occurrence drops in the Rocky Mountain region, but increases in the eastern United States.

Accuracy of the model

The reliability of the model was assessed by the AUC procedure. Table III lists the AUC calculated by Maxent for each of the output models. All of the generated models are above random (>0.5) and in the good (0.7–0.9) to very high (>0.9) accuracy range (Swets, 1988; Manel et al., 2001). Both *T. murrelli* and the *T. spiralis* models are above 0.9, while those for *T. nativa* and *T. nativa*/T6 are nearly as high, i.e., 0.854 and 0.885, respectively. The lower accuracy of the *T. spiralis* model when rat host records are omitted reflects the effect of a lower record number. However, because the training AUC is high (0.902), the model should be considered to have a reliability comparable to that of the model including rat records.

Effects of environmental variables on the model

The AUC values for models run using single environmental layers are shown in Table IV. The AUC values indicate that the models created with each of the environmental variables were good to very good for all species, with the exception of elevation for *T. spiralis*, *T. nativa*, and *T. nativa*/T6. For illustration, the output probability maps for *T. nativa* using individual environmental layers separately are shown in Figure 2. Elevation alone produces a predicted distribution that has a low probability (AUC 0.600). However, while a variable with an AUC <0.7 is considered to have low importance, if the variable is included in a multi-variable model, its contribution may be significant. For example, the AUC for elevation in the case of the *T. spiralis* model is only 0.632, but in the model with multiple environmental variables, elevation has a relative contribution to the species-

TABLE II. IGBP land cover legend.

Original IGBP land cover legend	Combined land cover classes
Evergreen needleleaf forest	Forest
Evergreen broadleaf forest	Forest
Deciduous needleleaf forest	Forest
Deciduous broadleaf forest	Forest
Mixed Forest	Forest
Closed shrublands	Shrublands
Open shrublands	Shrublands
Woody savannas	Grasslands
Savannas	Grasslands
Grasslands	Grasslands
Permanent wetlands	Wetlands
Croplands	Croplands
Urban and built-up	Barren land or urban areas
Cropland/natural vegetation mosaic	Croplands
Snow/ice	Snow/ice
Barren or sparsely vegetated	Barren land or urban areas
Water bodies	Water

predicted distribution (Fig. 1) of 21%. Further, because environmental layers may be correlated, e.g., higher elevations with cooler temperatures or low January temperatures are related to lower July temperatures, a particular environmental factor may be important to a species' biology, but may not contribute importantly to the model because of another correlated layer used in the model.

Table V summarizes the most frequent or significant environmental features associated with each species' location records. These were identified by determining the mean pixel value for the temperature and elevation variables and the most frequent land cover categories associated with the species' individual location records. Table V demonstrates that the temperature and land cover characteristics for *T. spiralis* and *T. murrelli* are distinctly different from those of *T. nativa* and T6, particularly in mean minimum January temperatures and maximum July temperatures.

DISCUSSION

Evaluation of Maxent models

All of the *Trichinella* spp. models had good to high accuracy assessments by the AUC measurement. In comparing the

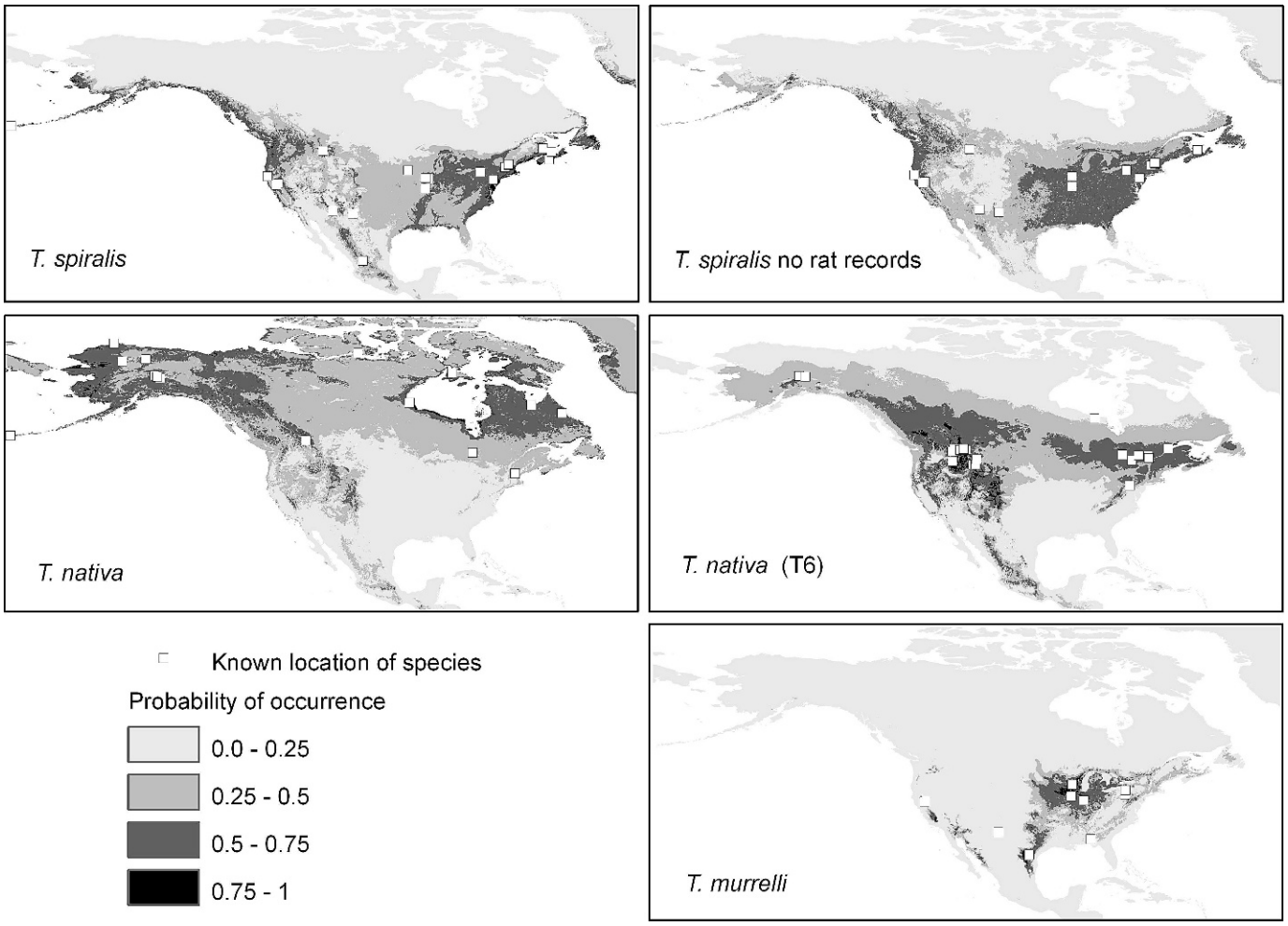

FIGURE 1. Predicted potential distributions of *Trichinella* spp. in North America. Each map was created using the Maxent program, with 4 inputs of environmental layers and known locations of each species.

TABLE III. Evaluation of *Trichinella* species Maxent models.

Species	Total number records	Number records used for training	Number records used for testing	AUC* training data	AUC* test data
T. murrelli	45	34	11	0.977	0.941
T. spiralis	23	18	5	0.932	0.905
T. spiralis (without rat)	16	12	4	0.906	0.737
T. nativa	26	20	6	0.828	0.854
T. nativa/T6	24	18	6	0.890	0.885

* AUC of 0.5 is a random prediction and a value greater than 0.9 indicates high reliability; an AUC of less than 0.7 indicates poor reliability. Training data (based on 75% of records) are the points used to build the model and the test data (25% of records) are used only for testing the model's accuracy.

accuracy of the models (Table III), the *T. murrelli* model had the highest accuracy (AUC 0.977) and also had the most records for the model development. The increased accuracy of the prediction may be due to the larger number of records.

The *T. spiralis* model that included rat records was more accurate (AUC 0.932) than that in which rat host records were omitted (AUC 0.906) (Table III), possibly a result of reducing the total number of records from 23 to 16. The environmental records for these 2 datasets have the same or very close values for mean January and July temperatures, mean elevation, and land cover (Table V). This yields probability maps (Fig. 1) that are similar, but which have local differences in the probability of occurrence in the Rocky Mountain region and the eastern half of the United States. One record for *T. spiralis* north of latitude 51° is due to an infected rat on the Aleutian Islands, which are within the temperate, rainy Marine eco-region (Bailey, 1996). This record may be spurious because it cannot be ruled out that these infections resulted from consumption of infected pork scraps in garbage produced by local settlements or towns, rather than the reflection of a true sylvatic cycle. The role of rats as a reservoir host is problematic, and little conclusive evidence has been produced to support such a role (Madsen, 1961; Pozio and Murrell, 2006). However, their importance in a domestic cycle that involves infection of swine is well established (Madsen, 1961; Schad et al., 1987; Leiby et al., 1990).

In the models using all 4 environmental layers, several environmental variables had low contributions to the models, possibly a result of being correlated with other variables. However, analysis of the AUC of the models constructed using single variables reveals that some of these variables are associated with the distribution of the species. Table IV shows that temperature and land cover are most closely associated with the distribution of *Trichinella* spp. based on AUC values, while elevation by itself is essentially unimportant for *T. spiralis*, *T. nativa*, and T6. Land cover had higher AUC values than temperature, which seems surprising given the emphasis on freeze resistance in the literature. However, land cover is shaped by a combination of factors, and the minimum and maximum temperature and the elevation all influence the land use/land cover in an area. Furthermore, the ranges of the *Trichinella* spp. hosts are all affected by land cover, which may add additional significance to land cover in the model.

The *T. nativa* distribution maps based on individual environmental variables (Fig. 2) illustrate how the individual variables contribute to the prediction model for a species. Maps of this sort might be helpful in biogeographic studies and in future investigations intending to explore the effect of individual environmental variables on the model.

It is important to emphasize that the models built for this study are predictions of the suitability of habitat for the *Trichinella* spp. and their mammalian hosts as a first approximation of the potential ranges and may not represent, when future research data are accumulated, the actual ranges of the species. The actual range of a species can be affected by conditions other than environmental suitability, including geographic barriers and interactions with other species. Further, the assumption cannot be made that a species fills all available potential habitat, has a range that is constant over time, or remains genetically stable (Jeschke and Strayer, 2008). Until a systematic survey that includes all of North America is carried out, modeling remains the best predictor for identifying potential areas of *Trichinella* spp. infection in sylvatic host species and geographic areas.

Geographic distribution of *Trichinella* spp.

The predicted range for *T. nativa* (Fig. 1) can be characterized as latitudes above 46° and/or high elevations (T6), with mean minimum January temperatures of −18 to −27 C (Table V). These predictions conform well to previously published range descriptions based on records (Pozio, 2001; Pozio and Murrell, 2006). The recent proposals on the post-Miocene expansion and speciation in species of *Trichinella* (Zarlenga et al., 2006) suggest that the invasion of the Nearctic during the Pilocene and Pleistocene periods led to species diversification, resulting in the colonization of the high arctic habitats of Canada by *T. nativa*

TABLE IV. AUC* comparisons of models built on single environmental variables.

Species	Land cover	Minimum January temperature	Maximum July temperature	Elevation
T. murrelli	0.940	0.925	0.929	0.805
T. spiralis	0.875	0.849	0.810	0.632
T. nativa	0.886	0.742	0.760	0.600
T. nativa/T6	0.870	0.808	0.833	0.682

* AUC of 0.5 is a random prediction and a value greater than 0.9 indicates high reliability; an AUC of less than 0.7 indicates poor reliability.

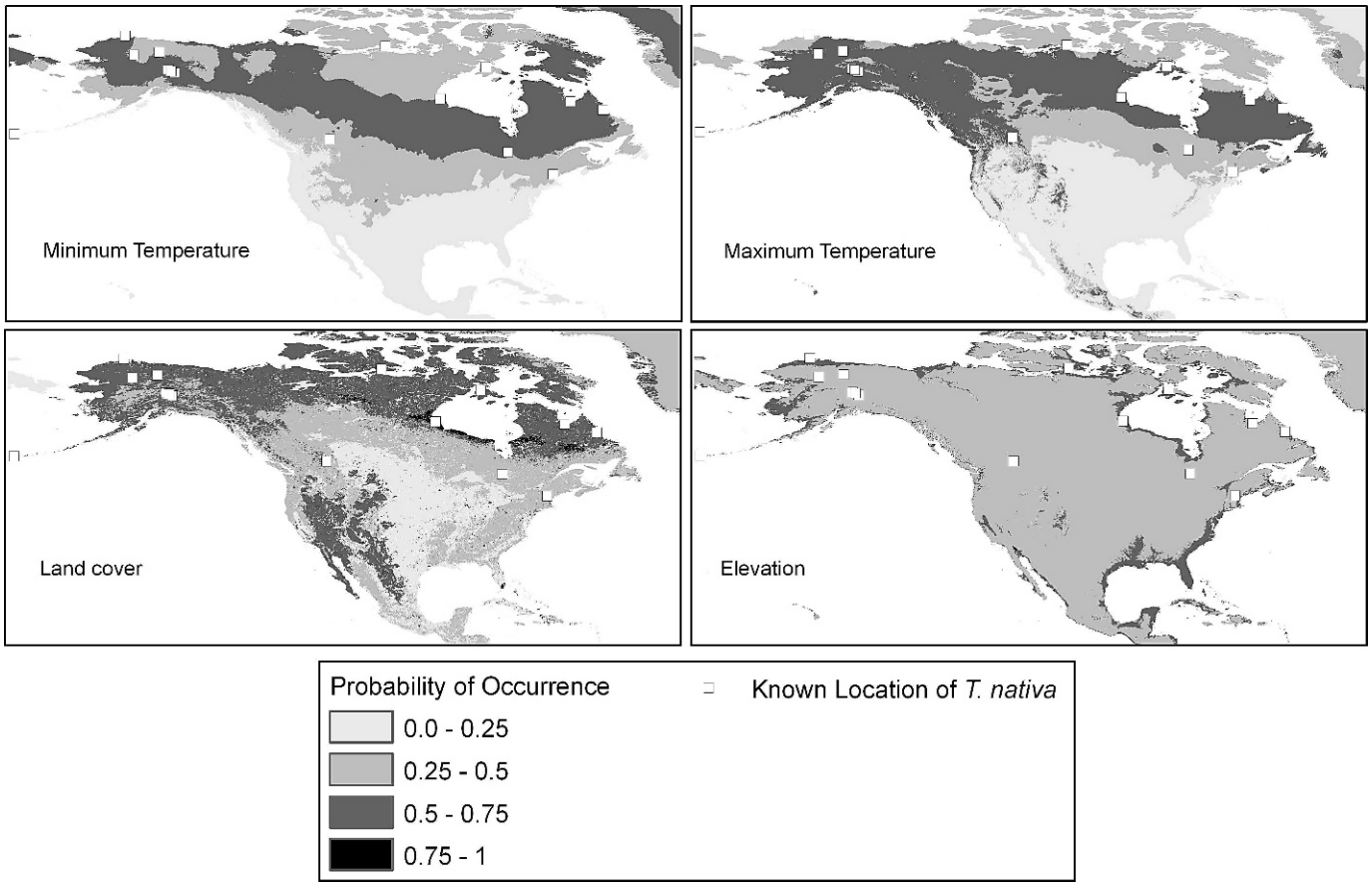

FIGURE 2. Predicted range of *T. nativa* using 1 environmental layer to create each map.

and a more southerly colonization by *T. murrelli.* The introduction of *T. spiralis* to North America occurred relatively recently through the immigration and colonization by humans and their domestic animals (Pozio and Murrell, 2006; Rosenthal, 2008). The permanent establishment of *T. spiralis* in wild animals in the absence of reintroduction from the domestic habitat is uncertain (Pozio, 2001; Burke et al., 2008), but until conclusive evidence that it is not sustainable in a sylvatic cycle is obtained, its occurrence in wild animals should be taken as an indication of a circulation in sylvatic animals.

The Maxent model predicts an infrequent and restricted occurrence of T6 in the Canadian Arctic and sub-Arctic, but recently Reichard et al. (2008) have recovered both T6 and *T. nativa* from wolverines at a latitude of 66°–67°, with prevalence of over 91% for T6. (This information was not available until after completion of the present study.) The sympatry of *T. nativa* and T6 has also been demonstrated by others (Zarnke et al., 1995; La Rosa et al., 2003; Zarlenga et al., 2006) and suggests to us that the distinction of T6 from *T. nativa*, at least in regard to geographic distribution and host preferences, is problematic. Until further research resolves this issue, however, we follow current convention (Pozio and Murrell, 2006) and consider T6 as a genotypic variant or subspecies of *T. nativa*.

The occurrence of only *T. nativa* and T6 in the most northern latitudes of North America is believed to be due to the high resistance of the muscle larvae to freezing (Dick and Pozio, 2001), in contrast to *T. spiralis* and *T. murrelli*, which are relatively intolerant to freezing. This intolerance in *T. murrelli* and *T.*

TABLE V. Environmental variables associated with species.*

Species	Most frequent land cover categories	Mean Elevation (meters)	Mean maximum temperature July (°C)	Mean minimum temperature January (°C)
T. murrelli	cropland/forest†	288	30.6	−7.7
T. spiralis	forest/croplands	584	26.4	−8.5
T. spiralis (without rat records)	forest/croplands	601	27.6	−8.5
T. nativa	scrublands/forest	577	17.6	−26.6
T. nativa/T6	forest/shrublands	1059	22.6	−18.6

* Data were extracted from the environmental layers at each of the 118 occurrence locations.
† Most frequent/second most frequent category.

spiralis is probably a critical factor in restricting their ranges to southern latitudes with mean minimum January temperatures not lower than −7 to −8 C. The predicted ranges for *T. nativa* and T6, however, do raise the question of why they appear to be rare in those non-mountainous southern latitudes (below 48° latitude), which are occupied only by *T. murrelli* and *T. spiralis* and where adaptation to freezing may not be important. This question is underscored by the overlap of host ranges for all of these species. As shown in Table I, black bears, grizzly bears, bobcats, and red foxes are hosts for all of the 4 encapsulated *Trichinella* genotypes in North America (*T. spiralis* has been isolated from all but grizzly bears). The major land cover types associated with these species, especially the forest category, are also very similar. Among the possible reasons for this apparent enigma are sampling problems, ecological/environmental factors affecting the muscle larvae, and host-related factors.

Sampling limitations

The data used for these models are, for the most part, convenience samples and are not from comprehensive national or regional surveys. Most result from area-limited or point-prevalence surveys, leaving large areas of North America inadequately surveyed. Many known host species are also under-represented (Table I). Prevalence surveys targeted toward filling these geographic and host species gaps may reveal, for example, that the geographic distribution of *T. nativa* and T6 extends further south in North America than the high probability ranges predicted by the Maxent model. Maxent-built models using a small number of location records, however, have been shown to be useful and reliable (Hernandez et al., 2006; Papes and Gaubert, 2007; Pearson et al., 2007), especially in identifying survey targets for model validation efforts.

Ecological factors

It is generally agreed that carrion is a major vehicle in the transfer of *Trichinella* spp. between hosts and that the muscle larvae in carrion can be considered a "free-living stage," adapted for survival in decomposing carcasses (Madsen, 1961; Pozio, 2000; Zarlenga et al., 2006). The free-living larvae, however, are vulnerable to environmental factors such as temperature and desiccation (Pozio and Murrell, 2006). The host species records used in this Maxent model building are nearly all documented carrion-eaters (Table I), particularly so when under severe stress like that experienced in severe winters (Ingles, 1954; Kurta, 1995; Wilson and Ruff, 1999). Because freeze resistance may be less important in the more southerly latitudes, tolerance for high temperatures, e.g., maximum July temperatures (Table V), may play a significant role, similar to that of freeze resistance for *T. nativa* and T6. There was a statistically significant correlation between the occurrence of specific *Trichinella* genotypes and maximum July temperatures. The eco-regions of the geographic range of *T. nativa* can be characterized as humid, with cold winters and short, cool summers. For example, the sub-Arctic experiences only 1 mo with temperatures above 10 C, and the most southerly eco-region in *T. nativa*'s predicted range, the Warm Continental, is humid, but the warmest month's temperature does not exceed 22 C. In contrast, the predicted range for *T. murrelli* includes a highly variable spectrum of eco-regions, which can be generalized as humid, with cool winters and hot summers. The major eco-regions over this species' range, i.e., Hot Continental, Prairie, and Subtropical regions, have summers of 3–5 mo, with average temperatures above 22 C. The most arid eco-regions for *T. murrelli*, the Tropical/Subtropical and Mediterranean (mountainous), characteristically have hot summers with low precipitation.

These climate differences may help to explain the constraints on the distribution of *T. nativa.* High temperatures may speed carcass putrification, exposing the muscle larvae to decomposition by-products that are harmful. There has been a great deal of research on the ability of various *Trichinella* spp. muscle larvae, especially *T. nativa*, to remain viable in frozen muscle for extended periods of time (Kapel, 2000), and a recent report by Davidson et al. (2008) provides evidence that there is intraspecific variation in freeze resistance of different geographic isolates of *T. nativa*. In contrast, there has been little research on the effect of high temperatures and carcass decomposition on the viability of muscle larvae. An unpublished report suggests that *T. nelsoni*, endemic in Africa south of the Sahara, survives better in decaying meat, compared with other species (cited in Kapel, 2000), and is more resistant to elevated temperatures (Sokolova, 1979). An evaluation of the role for high temperature tolerance in *Trichinella* spp. viability and geographic distributions is needed.

Host-related factors

According to Zarlenga et al. (2006), the diversification of Nearctic *Trichinella* spp. during the late Pilocene and Quarternary periods was driven by the isolation and dispersal of their carnivore hosts (ursids, mustelids, canids, and felids), a result of the episodic glacial-interglacial periods. Consequently, long association with these hosts, particularly by *T. nativa*, may have resulted in a level of host species adaptation not easily detectable by typical prevalence surveys. Even subtle differences in a *Trichinella* species' adaptation to a particular host species, e.g., greater adult worm reproductive capacity and longevity of the muscle larvae, could yield a competitive edge over other *Trichinella* species for that host. The geographic range of a preferred host species then would influence the species' distribution. A possible example of a difference in carnivore host species adaptation is the large number of coyote infections with *T. murrelli* (21/45 records for this species; Table I). In contrast, although the range for coyotes extends well into the range of *T. nativa* and T6 (Wilson and Ruff, 1999), there are no confirmed records for these genotypes in coyotes (0/50). Differences in host suitability are also seen in the greater infectivity of *T. spiralis* for swine (*Sus scrofa*) compared to that of sylvatic species (Kapel et al., 1998; Kapel and Gamble, 2000). Only a few detailed comparative studies on *Trichinella* spp. infectivity for carnivore hosts have been reported (reviewed by Kapel, 2000). Webster and Kapel (2005) observed only slight differences in infectivity and reproduction between 4 species of *Trichinella* in infections of foxes (*Vulpes vulpes*), either in single or mixed infections. Although differences in host adaptation cannot explain the restricted distribution of *T. nativa* to higher latitudes (the ranges of its hosts such as black bears and red foxes extend far below the 42°N line), research utilizing a broader array of carnivore host species and infection sizes with the Nearctic *Trichinella* spp. is needed. Relevant information would also be provided if, in wild animal surveys, muscle larvae

densities (larvae/g) could be made; such data can be used to help assess host susceptibility and parasite reproductive capacity in various host species.

In general, GIS models have value for mapping the current distribution of a species based on actual records. The Maxent model is attractive because, with limited location records, it can make predictions of geographic ranges and can direct attention to locations for validation of these predictions (Guisan et al., 2006). While the identification of geographic ranges for zoonotic parasites can facilitate epidemiological studies and efforts to implement preventive measures (Burke et al., 2008), we emphasize that these tools can have great value in monitoring the impact of climate changes and man-made landscape alterations on parasite distributions. Recently, Rausch et al. (2007) called attention to the potential impact of climate change on *T. nativa* transmission in the arctic walrus and the infection-risk consequences for humans residing in that habitat. Non-climate influences such as habitat destruction are also causing significant population declines in important *T. nativa* hosts such as wolves and brown bears (Schipper et al., 2008). The development of geographic maps for animal species (including parasites) with the assistance of models such as Maxent will enhance the ability to develop effective conservation strategies and to facilitate the detection of evidence on how a species is responding to relevant environmental variables (Svenning and Condit, 2008). The results of the present study also illustrate the ability of predictive modeling to identify interesting research questions relating to parasite biogeography.

ACKNOWLEDGMENTS

We thank Dr. Edoardo Pozio and the staff of the International *Trichinella* Reference Centre in Rome, Italy, for their generous and expert assistance on submissions of *Trichinella* isolates from North America and for confirming record location data. Appreciation is also expressed to Drs. Eric Hoberg, Dan Zarlenga, and Ben Rosenthal of the Beltsville Agricultural Research Center for their provocative and helpful discussions on parasite genetics and biogeography. We are also grateful to the Department of Defense Global Emerging Infections Surveillance and Response System (DoD-GEIS) for funding the computers and software needed to complete this project.

LITERATURE CITED

Bailey, R. G. 1996. Ecosystem Geography. Springer, New York, New York, p. 204.

Bourg, N. A., W. J. McShea, and D. E. Gill. 2005. Putting a cart before the search: Successful habitat prediction for a rare forest herb. Ecology **86:** 2793–2804.

Burke, R., P. Masuoka, and K. D. Murrell. 2008. Swine *Trichinella* infection and geographic information system tools. Emerging Infectious Diseases **14:** 1109–1111.

Campbell, W. C. 1983. Epidemiology. *In* Trichinella and trichinosis, W. C. Campbell (ed.). Plenum Press, New York, New York, p. 425–444.

Davidson, R. K., K. Handeland, and C. M. Kapel. 2008. High tolerance to repeated cycles of freezing and thawing in different *Trichinella nativa* isolates. Parasitology Research **103:** 1005–1010.

Dick, T. A., and E. Pozio. 2001. *Trichinella spp.* and trichinellosis. *In* Parasitic diseases of wild mammals, W. M. Samuel, M. J. Pybus, and A. A. Kocan (eds.). Iowa State University Press, Ames, Iowa, p. 380–396.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Lethwick, A. Lehmann, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29:** 129–151.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24:** 38–49.

Guisan, A., O. Broennimann, R. Engler, M. Vust, N. G. Yoccoz, A. Lehman, and N. E. Zimmermann. 2006. Using niche-based models to improve the sampling of rare species. Conservation Biology **20:** 501–511.

Hastings, D. A., and P. K. Dunbar. 1998. Development and assessment of the Global Land One-km Base Elevation Digital Elevation Model (GLOBE). ISPRS Archives **32:** 218–221. (http://www.ngdc.noaa.gov/mgg/topo/isprsdem.html)

Hernandez, P., C. Graham, L. Master, and D. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography **29:** 773–785.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology **25:** 1965–1978.

Ingles, L. G. 1954. Mammals of California. Stanford University Press, Stanford, California, 396 p.

Jeschke, J., and D. Strayer. 2008. Usefulness of bioclimatic models for studying climate change and invasive species. Annals of the New York Academy of Sciences **1134:** 1–24.

Kapel, C. M. O. 2000. Host diversity and biological characteristics of the *Trichinella* genotypes and their effect on transmision. Veterinary Parsitology **93:** 263–278.

———, and H. R. Gamble. 2000. Infectivity, persistence, and antibody response to domestic and sylvatic *Trichinella* spp. in experimentally infected pigs. International Journal for Parasitology **30:** 215–221.

———, P. Webster, P. Lind, E. Pozio, S. A. Henriksen, K. D. Murrell, and P. Nansen. 1998. *Trichinella spiralis, Trichinella britovi,* and *Trichinella nativa*: Infectivity, larval distribution in muscle, and antibody response after experimental infection of pigs. Parasitology Research **84:** 264–271.

Kurta, A. 1995. Mammals of the Great Lakes region. University of Michigan Press, Ann Arbor, Michigan, 376 p.

La Rosa, G., G. Marucci, D. S. Zarlenga, A. Casulli, R. L. Zarnke, and E. Pozio. 2003. Molecular identification of natural hybrids between *Trichinella nativa* and *Trichinella* T6 provides evidence of gene flow and ongoing genetic divergente. International Journal for Parasitology **33:** 209–216.

Leiby, D. A., C. H. Fuffy, K. D. Murrell, and G. A. Schad. 1990. *Trichinella spiralis* in an agricultural ecosystem: Transmission in the rat population. Journal of Parasitology **76:** 360–364.

Madsen, H. 1961. The distribution of *Trichinella spiralis* in sledge dogs and wild animals in Greenland. Meddelser om Gronland **159:** 1–124.

Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: The need to account for prevalence. Journal of Applied Ecology **38:** 921–931.

Moffett, A., N. Shackelford, and S. Sarkar. 2007. Malaria in Africa: Vector species' niche models and relative rick maps. PLoSOne **2(9):** e824. doi:10.1371/journal.pone.0000824

Papes, M., and P. Baubert. 2007. Modeling ecological niches from low numbers of occurrences: Assessment of the conservation status of poorly known viverrids (Mammalia, Carnivora) across two continents. Diversity and Distributions **13:** 890–902.

Pearce, J., and D. B. Lindenmayer. 1998. Bioclimatic analysis to enhance reintroduction biology of the endangered helmeted honeyeater (*Lichenostomus melanops cassidix*) in southeastern Australia. Restoration Ecology **6:** 238–243.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography **12:** 361–371.

———, ———, and C. Liu. 2004. Modeling species distributions in Britain: A hierarchical integration of climate and land-cover data. Ecography **27:** 285–298.

———, C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species' distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. Journal of Biogeography **34:** 102–117.

Peterson, A. T., R. R. Lash, D. S. Carroll, and K. M. Johnson. 2006. Geographic potential for outbreaks of Marburg hemorrhagic fever. American Journal of Tropical Medicine & Hygiene **75:** 9–15.

———, AND J. J. SHAW. 2003. *Lutzomyia* vectors for cutaneous leishmaniasis in southern Brazil: Ecological niche models, predicted geographic distributions, and climate change effects. International Journal for Parasitology **33:** 919–931.

PHILLIPS, S. J., R. P. ANDERSON, AND R. E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling **190:** 231–259.

———, M. DUDIK, AND R. E. SCHAPIRE. 2004. A maximum entropy approach to species distribution modeling. *In* Proceedings of the 21st international conference on machine learning. Carla Brodley (ed.). AMC Press, New York, New York, p. 655–662.

POZIO, E. 2000. Factors affecting the flow among domestic, synanthropic and sylvatic cycles of *Trichinella*. Veterinary Parasitology **93:** 241–262.

———. 2001. New patterns of *Trichinella* infection. Veterinary Parasitology **98:** 133–198.

———, G. LA ROSA, K. D. MURRELL, AND J. R. LICHTENFELS. 1992. Taxonomic revision of the genus *Trichinella.* Journal of Parasitology **78:** 654–659.

———, AND K. D. MURRELL. 2006. Systematics and epidemiology of *Trichinella.* Advances in Parasitology **63:** 368–439.

———, C. RINALDI, G. MARUCCI, V. MUSELLA, F. GALATI, G. GRINOLGI, P. BOIREAU, AND G. LA ROSA. 2008. Hosts and habitats of *Trichinella spiralis* and *Trichinella britovi* in Europe. International Journal for Parasitology, doi: 10.1016/j.para.2008.06.006.

———, AND D. S. ZARLENGA. 2005. Recent advances on the taxonomy, systematics and epidemiology of *Trichinella*. International Journal for Parasitology **35:** 1191–1204.

RAUSCH, R. L., J. C. GEORGE, AND H. K. BROWER. 2007. Effect of climatic warming on the Pacific Walrus, and potential modification of its helminth fauna. Journal of Parasitology **93:** 1247–1251.

REICHARD, M. V., L. TORRETTI, T. A. SNIDER, J. M. GARVON, G. MARUCCI, AND E. POZIO. 2008. *Trichinella* T6 and *Trichinella nativa* in wolverines (*Gulo gulo*) from Nunavut, Canada. Parasitology Research **103:** 657–661.

ROSENTHAL, B. M., G. LA ROSA, D. S. ZARLENGA, D. DUNAMS, Y. CHUNYU, L. MINGYUAN, AND E. POZIO. 2008. Human dispersal of *Trichinella spiralis* in domesticated pigs. Infection, Genetics, and Evolution **8:** 799–805.

SCHAD, G. A., C. H. DUFFY, D. A. LEIBY, K. D. MURRELL, AND E. W. ZIRKLE. 1987. *Trichinella spiralis* in an agricultural ecosystem: Transmission under natural and experimentally modified on-farm conditions. Journal of Parasitology **73:** 95–102.

SCHIPPER, J., J. S. CHANSON, F. CHIOZZA, N. A. COX, M. HOFFMANN, V. KATARIYA, J. LAMOREUX, A. S. L. RODRIGUES, S. N. STUART, H. J. TEMPLE, et al. 2008. The status of the world's land and marine mammals: Diversity, threat, and knowledge. Science **322:** 225–230.

SOKOLOVA, J. B. 1979. The effect of temperature on the viability of different species of *Trichinella.* Voprosy Prirodnoi Ochagovosti Boleznei **10:** 185–187.

SVENNING, J.-C., AND R. CONDIT. 2008. Biodiversity in a warmer world. Science **322:** 206–207.

SWETS, J. A. 1988. Measuring the accuracy of diagnostic systems. Science **240:** 1285–1293.

WEBSTER, P., AND C. M. O. KAPEL. 2005. Intestinal establishment and reproduction of adult *Trichinella* spp. in single and mixed species infections in foxes (*Vulpes vulpes*). Veterinary Parasitology **130:** 245–253.

WILSON, D. E., AND S. RUFF. 1999. The Smithsonian book of North American mammals. Smithsonian Institution Press, Washington, D.C., 750 p.

ZARLENGA, D. S., M. B. CHUTE, A. MARTIN, AND C. M. KAPEL. 1999. A multiplex PCR for unequivocal differentiation of all encapsulated and non-encapsulated genotypes of *Trichinella.* International Journal for Parasitology **29:** 1859–1867.

———, B. M. ROSENTHAL, G. LA ROSA, E. POZIO, AND E. P. HOBERG. 2006. Post-Miocene expansion, colonization, and host switching drove speciation among extant nematodes of the archaic genus *Trichinella.* Proceedings of the National Academy of Sciences U S A **103:** 7354–7359.

ZARNKE, R. L., A. A. GAJADHAR, G. B. TIFFIN, AND J. M. VER HOEF. 1995. Prevalence of *Trichinella nativa* in lynx (*Felis lynx)* from Alaska, 1988–1993. Journal of Wildlife Diseases **31:** 314–318.