Modelling potential presence of metazoan endoparasites of bobcats (*Lynx rufus*) using verified records

Shelby J. Hiestand^{1,2,3}, Clayton K. Nielsen^{2,4} and F. Agustín Jiménez¹

¹Department of Zoology, Southern Illinois University, Carbondale, Illinois, USA;

²Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, Illinois, USA;

³Wisconsin Department of Natural Resources, Merrill, Wisconsin, USA;

⁴Department of Forestry and Center for Ecology, Southern Illinois University, Carbondale, Illinois, USA

Abstract: Helminth parasites of wild and domestic felines pose a direct or potential threat to human health. Since helminths depend on multiple environmental factors that make their transmission possible, it is imperative to predict the areas where these parasites may complete the transmission to potential hosts. Bobcats, *Lynx rufus* (Schreber), are the most abundant and widely-distributed wild felid species in North America. The increase of population densities of bobcats raises concerns about their importance as reservoirs of pathogens and parasites that may affect wildlife, domestic animals and humans. Our objective was to predict the potential presence of the tapeworm *Taenia rileyi* Loewen, 1929, the fluke *Alaria marcianae* (La Rue, 1917) and the roundworm *Toxocara cati* (Schrunk, 1788) in southern Illinois. The empirical presence of these parasites in localities across the region was analysed in combination with a sampling bias layer (i.e. bobcat presence) and with environmental data: layers of water, soil, land cover, human density and climate variables in MAXENT to create maps of potential presence for these three species in an area of 46 436 km². All climatic variables were low contributors (0.0–2.0% contribution to model creation) whereas land cover surfaced as an important variable for the presence of *A. marcianae* (7.6%) and *T. cati* (6.3%); human density (4.8%) was of secondary importance for *T. rileyi*. Variables of importance likely represent habitat requirements necessary for the completion of parasite life cycles. Larger areas of potential presence were found for the feline specialist *T. rileyi* (85%) while potential presence was less likely for *A. marcianae* (73%), a parasite that requires multiple aquatic intermediate hosts. This study provides information to wildlife biologists and health officials regarding the potential impacts of growing bobcat populations in combination with complex and changing environmental factors.

Keywords: zoonosis, epizootic, MAXENT, niche-modelling, *Toxocara cati*, *Alaria marcianae*, *Taenia rileyi*

Several parasites of felines pose a direct or potential threat to human health (Gerhold and Jessup 2013). Species of digenetic trematodes included in the genus *Alaria* Schrunk, 1788, cysticerci of *Taenia* Linnaeus, 1758 and the roundworm *Toxocara cati* (Schrunk, 1788) are known to induce pathology in various organs of the definitive, intermediate, paratenic and accidental hosts (Fisher 2003, Mohl et al. 2009, Okulewicz et al. 2012). The chance of contracting these zoonoses increases proportionally with the growth of populations of suitable hosts, especially those in close proximity to humans.

In the USA, this includes feral domestic cats – *Felis catus* Linnaeus, estimated between 30–80 million individuals (Loss et al. 2013); bobcats – *Lynx rufus* (Schreber), estimated at about 2.3 million individuals (Roberts and Crimmins 2010), and cougars – *Puma concolor* (Linnaeus), which are expanding eastward (LaRue et al. 2012). The convergence of these three species of felines is important from an epidemiological perspective because prevalence of etiological agents of zoonotic disease in do-

mestic cats, bobcats and cougars is higher wherever these species are sympatric, and low in areas with no species overlap (Bevins et al. 2012). Thus, the potential occurrence of a zoonotic parasite may be estimated through the examination of any of the domestic or wild species.

The distribution of parasites in animals depends on multiple environmental and biological factors that determine the chance of the parasites to encounter and infect their hosts (Krasnov et al. 2004, Tseng 2006, Hegglin et al. 2007). Since transmission of parasites may be influenced by climate, population density, geological conditions and host activities (Euzet and Combes 1980, Combes 2001, Altizer et al. 2003), the identification of these characteristics makes it possible to detect and predict the presence of epizootic and zoonotic pathogens. Detection of the set of favourable environment conditions is especially relevant for heteroxenous parasites (species using several intermediate and definitive hosts), which may be introduced in new areas and become virulent in naïve hosts (Johnson and Thielges 2010), including native wildlife

or domestic animals (Daszak et al. 2000, Adams et al. 2010).

Models of species distribution are used to answer a diverse range of ecological and epidemiological questions (Guisan and Thuiller 2005, Jeschke and Strayer 2008), including predictions of environmental conditions that may promote parasite presence. A variety of methods are available to construct these models; however, appropriate model choice is often dependent on the scale and data availability (Elith et al. 2006, Peterson 2006, Elith and Graham 2009). Model choice often depends on sample size, data collection method (quantitative vs qualitative), and location specificity (Fielding and Bell 1997, Hernandez et al. 2008, Wisz et al. 2008, Royle et al. 2012). Geographic Information Systems and related technologies are increasingly used to analyse the geography of disease, specifically the relationships between pathological factors (Cromley 2003). Examples of mapping of disease inducing organisms and their vectors are abundant (Fuentes et al. 2001, Hendrickx et al. 2004, Slater and Michael 2010). These studies combine knowledge of vector and host requirements to define areas of potential high transmission risk.

Understanding areas of potential parasite presence using environmental variables may facilitate future health initiatives and wildlife management decisions (Scott 1988). Using a well-studied species that is a potential host to a variety of parasites and adaptable to diverse ecosystems like the bobcat as an indicator for parasite presence may lead to understanding these relationships (Overstreet 1997). Because of their shared ancestry and similar physiology, sympatric North American felids share several species of pathogens (Shock et al. 2011, Bevins et al. 2012). Modelling the distribution of parasites in felids is important because it will enable health officials to identify areas where surveillance for the presence and spread of epizootic diseases should be more comprehensive.

Three species of parasites able to infect domestic and wild felines occur in high prevalence and abundance in bobcats: *Alaria marcianiae* (La Rue, 1917), *Taenia rileyi* Loewen, 1929 and *Toxocara cati*. All three species have very different life cycles and patterns of transmission (Mollhagen 1979, Mohl et al. 2009, Okulewicz et al. 2012). These species are of interest because all three have been reported in domestic animals (i.e. they are epizootic), congeneric species are known agents of zoonotic disease and occur in high prevalence in the bobcat (Hiestand et al. 2014). Herein we used MAXENT, a general-purpose machine learning method and maximum entropy approach (Phillips et al. 2004, 2006) to develop predictive maps for two agents of zoonotic disease, *T. cati* and *Alaria marcianae*, and the epizootic *T. rileyi*, a common parasite of bobcats. MAXENT has been shown to successfully map potential distribution in situations with low sample size (as few as 10 locations) and presence-only data (Baldwin

2009, Elith et al. 2011). The program has been used to predict the potential distribution of species of *Trichinella* Railliet, 1895 at a continental scale (Masuoka et al. 2009). The objective of developing these maps was threefold: (1) to model potential presence of *A. marcianae*, *T. rileyi* and *T. cati* in a small area; (2) to identify environmental variables of importance for potential parasite presence of monoxenous and heteroxenous species; and (3) to compare model confidence and validity with known ecology of these species.

MATERIALS AND METHODS

Study area

The potential presence of *Alaria marcianae*, *Taenia rileyi* and *Toxocara cati* was modelled across the 39 southernmost counties in Illinois (46436 km²). This region is human-dominated (ca 21.5 persons/km²) and comprises the southern till plain, Wabash border, Shawnee hills, Ozark, lower Mississippi river bottomlands and coastal plain natural divisions (Schwegman 1972, Neely and Heister 1987). Streams and roads are abundant on the landscape with densities of ca 1.1 km/km² and 1.5 km/km², respectively. Land cover consists primarily of closed-canopy mixed hardwood forests (44%), grasslands (21%) and cropland (19%) (Luman et al. 1996). Wetlands (8%), open water (6%) and urban (2%) cover types compose the remainder of the study area (Anonymous 1996a). Southern Illinois has a continental climate, with hot summers and cool winters. Average annual temperatures range from 10.2 to 14.4°C. Average annual precipitation is 810–1220 mm (Anonymous 2005). In Illinois, bobcats have been protected from legal harvest since 1971 and were considered threatened in the state until 1999 when they were assigned non-game species status (Woolf et al. 2002).

Parasite collection

Forty-three bobcats (34 adults, 9 juveniles) were collected in southern Illinois during July 2003–August 2012 with 95% collected from 2010–2012 (Fig. 1). Thirty-one roadkilled bobcats were collected in collaboration with the Illinois Department of Natural Resources (IDNR), Illinois Department of Transportation (IDOT) and the public. Twelve bobcats were trapped for the project (n = 8) or captured by licensed Illinois trappers seeking other species (n = 4). Data on individual bobcats were recorded (date, location and collector information); locations were recorded using a GPS or Google Earth (Google 2012). All methods were supported by the Institutional Animal Care and Use Committee at Southern Illinois University (Assurance Number A-3078-01).

The helminthological examination included inspection of body cavity and internal organs. Organ contents were sieved through 350 and 500 µm mesh. The filtered materials were processed by sedimentation and the sediment was examined to recuperate all parasites (Gardner 1996). Parasites were separated, washed, fixed and preserved immediately. Voucher specimens were deposited in the United States National Parasite Collection (USNPC, Beltsville, Maryland, USA; Hiestand et al. 2014).

Environmental variables

Environmental layers used to model the potential presence of parasite species included land cover, soil, distance to rivers, human density and climate variables. A cell size of 1 km² was

Fig. 1. Localities documenting the presence of 43 individual bobcats collected during 2003–2012 and infections caused by three prevalent helminth species. White dots denote infection caused by **A** – *Alaria marcianae*; **B** – *Taenia rileyi*; **C** – *Toxocara cati*.

used for all environmental layers and only animal locations known within that cell size were used as presence locations; several data layers were resampled to 10×10 -m pixels. Digital data layers downloaded from the internet (<http://www.mrlc.gov/index.php>; <http://www.worldclim.org/current>) were used to create geospatial datasets representative of southern Illinois. The 2006 National Landcover Dataset (Anonymous 2011) consisted of 15 classes in the study region; similar cover types were combined into 8 classes: developed/barren and open water, deciduous forest, mixed forest, evergreen forest, shrubland, grassland, agricultural land, and wetland. The soil layer (Anonymous 1996b) consisted of 11 classes of various sand, silt and clay soils. Digital elevation model (DEM) data and Arc Hydro Tools 2.0 (ESRI 2011) were used to create stream shapefiles by filling the DEM, calculating flow direction, and calculating flow accumulation. Subsequently, a layer including distance to river using Euclidean distance in ArcGIS was created. Human density (individuals/km²) was estimated by rasterising the enumeration area polygons based on U. S. census block groups (Anonymous 2010). Climate variables of annual mean temperature, annual precipitation and precipitation of seasonality (coefficient of variation) were downloaded from WorldClim – Global Climate Data (<http://www.worldclim.org/>). Precipitation of seasonality was the change of average precipitation among seasons with low values indicating little change, or consistency, between seasons and larger values indicating drastic changes between seasons. ArcGIS 10.0 (ESRI 2011, Redlands, California, USA) was used for geospatial operations.

Modelling procedure of maximum entropy (MAXENT)

Potential presence of parasites was modelled using MAXENT 3.3.3 beta (<http://www.cs.princeton.edu/~schapire/maxent/>). MAXENT utilises a general-purpose machine learning method and implements a maximum entropy approach to habitat modelling, estimating an unknown density distribution over a finite set of spatial units. It does this by maximising the entropy subject to unit-specific constraints (Phillips et al. 2006, Phillips and Dudik 2008). MAXENT is particularly useful when very few, presence-only data points are available and the program is capable of dealing with continuous and categorical variables simultaneously (Phillips et al. 2006). Calculation of the probability distribution is exponential, ranging from 0 to 1.0, and summing to 1.0. This is achieved by summing the weighted probability values by a scaling constant. Beginning with a uniform probability distribution with a ‘gain’ equal to 0, MAXENT alters the weight of variables in turn so that the probability of occurrence of source data is maximised (Elith et al. 2011). This increases the gain fitting an asymptote during a run of the model. This final gain is a measure of the likelihood of the sample dataset. MAXENT models were run with the selected output of ‘logistic’, where pixel values range from 0–1. Default values were used for convergence threshold (10^{-5}) maximum iterations (500) and a regularisation multiplier of 1 because these settings have been found to achieve good performance in comparison to altered variations (Phillips and Dudik 2008).

Model validation

To evaluate model fit, the receiver operating characteristic (ROC) and area under the curve (AUC) for both training and testing data were produced. The AUC value of the ROC plot is a method that does not require discrete presence/absence predictions, and is therefore a measure of accuracy that is threshold

Fig. 2. Potential suitability for *Alaria marcianae*, *Taenia rileyi* and *Toxocara cati* in southern Illinois using presence locations from 43 bobcats collected during 2003–2012 as training data for MAXENT. Maps show potential presence ranging from 0.0 (low) to 1.0 (high).

independent (Pearce and Ferrier 2000, McPherson et al. 2004). Area under the curve plots the model's sensitivity versus 1-specificity (Liu et al. 2005). Sensitivity quantifies the proportion of observed presences correctly predicted as presence, which is therefore considered the true positive fraction. Specificity quantifies the true negative fraction. These measures of accuracy require that probabilities of occurrence obtained by models are transformed into discrete presence or absence, where a threshold of 0.5 is commonly considered random (McPherson et al. 2004, Liu et al. 2005, Jiménez-Valverde and Lobo 2007). This method is widely employed in modelling (Swets 1992, Fielding and Bell 1997), including modelling species distributions (Phillips et al. 2006). It has been suggested that AUC should not be the only method of model validation (Lobo et al. 2008, Peterson et al. 2008). Thus, further model validation using a jackknife procedure for each presence location for all three models was performed. A jackknife removes one source of information, in this case a known presence location, and reruns the model. If the presence location is still detected, the model has successfully predicted an unknown location. Jackknife output has been shown to effectively calculate the probability of success in datasets of small sample sizes (< 25 observations) (Pearson et al. 2007).

MAXENT estimates the percentage relative contribution of each environmental variable to the overall model. However, the contributions may be altered by correlations between variables. To highlight these possible correlations MAXENT calculates a jackknife procedure for accuracy assessment and a combined p-value for significance testing of the species distribution models (Pearson et al. 2007). In the jackknife tests, the loss in regularised training gain of models with each predictor sequentially omitted was calculated. A constant low loss of gain compared with the complete model suggests that none of the predictors contain information contained in any other predictor. Subsequently, the gain for models containing each predictor was calculated separately. A large difference between the gain of these and the complete model supports that none of the predictors had sufficient explanatory power on their own. Highly correlated variables would have no loss of gain if they were left out of the model and would contribute equally if used alone.

To classify resulting model predictions into unsuitable and suitable areas of potential presence for model validation and

interpretation the lowest presence threshold (LPT) was used. LPT is the lowest probability value assigned to any of the presence records analysed (Swanepoel et al. 2013). Lowest presence threshold maintains zero omission error in the model localities and also represents areas of habitat that are at least as suitable as to where the species were observed (Pearson et al. 2007). Maps of potential presence for *A. marcianae*, *T. cati* and *T. rileyi* were created using ArcGIS software (Bahn and McGill 2007).

To further test the resulting model, an independent MAXENT layer using presence locations of all sampled bobcats to account for sampling bias was created. It incorporated all bobcat presence locations with the previously mentioned environmental variables and displayed the proportional contribution of each variable. The layer was used as an additional habitat variable in MAXENT for all three species to produce maps of potential presence with comparative outputs. By including the 'bias layer', we accounted for the conditions influencing bobcat presence locations as the most important variable. The resulting environmental significance indicated variable importance after bias was accounted for. This enabled the detection of potential bias in the model output associated with the lack of a structured sampling design.

RESULTS

Models were developed with presence locations of three parasite species: *Alaria marcianae* ($n = 19$), *Taenia rileyi* ($n = 27$) and *Toxocara cati* ($n = 10$) (Fig. 1). These species occurred with abundance and mean intensity of: 81 and 193, 4 and 6, 4 and 14, respectively. *Taenia rileyi* had the greatest area of potential presence (39411 km², 85% of the study area), followed by *T. cati* (38110 km², 82%) and *A. marcianae* (34040 km², 73%) using the LPT of 0.1 (Fig. 2). Maps of *A. marcianae* and *T. rileyi* indicated clear concentrations of high potential presence towards southernmost Illinois, whereas the map of *T. cati* displayed more scattered areas of high potential presence across the study area. All species had high AUC values when compared to the ROC curve (0.85–0.88), indicating good model accuracy (see Swets 1988). The jackknife model validation demonstrated high predicted-presence

Table 1. Results of the jackknife validation method of model testing for *Alaria marcianae*, *Taenia rileyi* and *Toxocara cati* collected from bobcats in southern Illinois during 2003–2012, showing the number of presence locations used for modeling, the resulting area under the curve (AUC), lowest presence threshold (LPT) and percent success from jackknife model validation.

Species	No. of presence locations	No. of background locations	AUC	Regularised training gain	LPT	% success
<i>Alaria marcianae</i>	19	10016	0.87	0.93	0.12	75
<i>Taenia rileyi</i>	27	10015	0.88	0.59	0.25	100
<i>Toxocara cati</i>	10	10009	0.85	0.52	0.36	100

Table 2. Selected environmental variables and their percent contribution in MAXENT models for *Alaria marcianae*, *Taenia rileyi* and *Toxocara cati* collected from bobcats in southern Illinois during 2003–2012.

Environmental variable	% contribution for <i>Alaria marcianae</i>	% contribution for <i>Taenia rileyi</i>	% contribution for <i>Toxocara cati</i>
Average temperature	0.0	0.0	1.3
Average precipitation	14.3	13.3	11.2
Precipitation of seasonality	58.4	55.1	0.2
Human density	2.1	13.0	0.0
Land cover	12.3	1.2	40.6
Distance to rivers	5.5	1.9	19.1
Soil	7.4	15.5	27.6

success of omitted locations for all 3 species (75–100%; Table 1).

Of the environmental variables used to model potential presence, precipitation of seasonality was the most important contributing variable for *A. marcianae* (58.4% contribution to model creation) and *T. rileyi* (55.1%; Table 2). Land cover was the most important variable for *T. cati* (40.6%), but of relatively lower importance of the other two species (12.3 and 1.2%). Average precipitation was moderately important for all three species (14.3, 13.3 and 11.2) while average temperature was consistently unimportant (0.0, 0.0 and 1.3%). Human density was a higher contributor for *T. rileyi* (13.0%) but had a very low contribution for *A. marcianae* and *T. cati* (2.1 and 0.0%). Nearness to rivers was important for only *T. cati* (19.1%) with an increase of potential presence closer to rivers. The jackknife procedure for environmental variables for *A. marcianae*, *T. rileyi* and *T. cati* reflects these percentages and indicated the lack of correlation between environmental data layers used to build models (Fig. 3). No correlation was found between variables due to the consistent loss of gain when each variable was removed from the model. Regularised training gain created from the jackknife was highest in *A. marcianae* (0.93) and relatively low in both *T. rileyi* (0.59) and *T. cati* (0.53; Table 1).

In comparison, after the addition of the bias layer (Fig. 4), areas of potential suitability changed for each parasite species (Fig. 4). All species had increased AUC values when compared to the ROC curve (0.91–0.94) and regularised training gain (1.09–1.47) but the jackknife model validation demonstrated a slightly lower predicted-presence success of omitted locations for all three species

Fig. 3. Jackknife evaluation of the model reconstruction with MAXENT pondering the relative importance of predictor environmental variables for *Alaria marcianae*, *Taenia rileyi* and *Toxocara cati* collected from bobcats in southern Illinois during 2003–2012. The combination of all variables is summarised in the horizontal bar at the bottom of each graph.

Fig. 4. Effect of the potential presence of bobcats on the potential presence of three parasite species. The map on the upper left corner summarises the potential presence of bobcats in southern Illinois or 'bias layer'. This map was constructed using presence locations from 43 bobcats collected during 2003–2012 as training data for MAXENT. The probability for bobcat presence was then used to estimate the probability of finding *Alaria marciana*, *Taenia rileyi* and *Toxocara cati* in southern Illinois. Maps show potential presence ranging from 0.0 (low) to 1.0 (high).

Table 3. Results of the jackknife validation method of model testing with host-species bias layer for *Alaria marciana*, *Taenia rileyi* and *Toxocara cati* collected from bobcats in southern Illinois during 2003–2012, showing the number of presence locations used for modeling, the resulting area under the curve (AUC), lowest presence threshold (LPT) and percent success from jackknife model validation.

Species	No. of presence locations	No. of background locations	AUC	Regularised training gain	LPT	% success
<i>Alaria marciana</i>	19	10015	0.92	1.47	0.04	70
<i>Taenia rileyi</i>	27	10024	0.91	1.09	0.06	93
<i>Toxocara cati</i>	10	10009	0.94	1.33	0.01	90

Table 4. Selected environmental variables and their percent contribution in MAXENT models with parasite presence bias for *Alaria marciana*, *Taenia rileyi* and *Toxocara cati* collected from bobcats in southern Illinois during 2003–2012.

Environmental variable	% contribution for <i>Alaria marciana</i>	% contribution for <i>Taenia rileyi</i>	% contribution for <i>Toxocara cati</i>
Average temperature	0.0	0.0	0.0
Average precipitation	0.2	2.0	0.0
Precipitation of seasonality	0.1	0.8	0.0
Bobcat bias layer	90.9	89.7	83.6
Human density	0.1	4.8	0.8
Land cover	7.6	0.7	6.3
Distance to rivers	0.1	0.8	2.6
Soil	0.9	1.2	6.8

(70–93%; Table 3). The bobcat bias layer was of highest significance for presence of all three species (83.6–90.9%; Table 4). After accounting for the bias induced by the sole presence of the host, climatic variables such as precipitation of seasonality, average precipitation and average temperature were consistently low contributors to the model (0–2%). The variables of highest significance after accounting for sampling bias included: land cover for *A. marciana* (7.6%); soil and land cover for *T. cati* (6.8% and 6.3% respectively), and human density for *T. rileyi* (4.8%). A repeated jackknife of environmental variables for *A. marciana*, *T. rileyi* and *T. cati* with the bias layer

included reflected these percentages and indicated the lack of correlation between environmental data layers (Fig. 5).

DISCUSSION

As the first known study to spatially model potential presence of multiple parasite species for bobcats we found that land cover, soil and human density were indicator variables contributing to parasite presence for each parasite species studied. Model output had different training gain for each species, which was not consistent with the number of presence locations. The differences between the predicted presence of the parasites reflected

Fig. 5. Jackknife validations of the model reconstruction with MAXENT to model the relative importance of predictor environmental variables for *Alaria marciana* (upper graph), *Taenia rileyi* (middle graph) and *Toxocara cati* (lower graph) collected from bobcats in southern Illinois during 2003–2012. These environmental variables incorporate the probability of bobcat presence.

their specific environmental requirements, life cycles with varying intermediate hosts and free-living stages.

All three parasite species may be considered generalists and were found at high prevalence in the sampled bobcat population. *Alaria marciana*, for example, is commonly found in carnivores near wetland or semi-aquatic areas; known hosts include bobcats, domestic cats, red fox, *Vulpes vulpes* (Linnaeus), and coyotes, *Canis latrans* Say (U.S. National Parasite Collection <http://www.anri.barc.usda.gov/bnpcu/parasrch.asp>), all of which are present within our study area (McDonald et al. 2008). *Alaria marciana* depends on aquatic environments for successful transmission because the species features two aquatic free-living life stages: the miracidium that infects planorbid snails as first intermediate host and the cercaria released from sporocysts formed in snails, which infects tadpoles that act as second intermediate hosts (Johnson 1968).

Taenia rileyi, however, has no free-living life stage and the only intermediate host for the development of the cysticerci is in a small mammal such as the eastern cottontail, *Sylvilagus floridanus* (Allen), deer mouse, i.e. species of *Peromyscus* Glower, and hispid cotton rat, *Sigmodon hispidus* Say et Ord, which are ubiquitous across the southern Illinois landscape and common prey species for carnivore hosts (Mollhagen 1979). Definitive hosts of *T. rileyi* include the bobcat, domestic cat and lynx (*Lynx canadensis* Kerr). *Toxocara cati* is a nematode with a complex pattern of transmission that can be monoxenous or heteroxenous (Sprent 1956, Swerczek et al. 1971). However, *T. cati* has relatively strict host requirements preferring felids such as the domestic cat, bobcat, lynx and cougar (U.S. National Parasite Collection <http://www.anri.barc.usda.gov/bnpcu/parasrch.asp>).

The life cycles of the three parasite species were reflected by (1) the environmental and habitat variables chosen as layers for MAXENT and (2) the resulting importance of variable contribution. For *A. marciana*, precipitation and land cover were the highest percent contributors for the model indicating selection for the free-living water stages as well as aquatic intermediate hosts (Johnson 1968). However, after accounting for bias with the addition of the bobcat collection layer, land cover alone was of higher contribution. The highest areas of potential presence were in the Shawnee National Forest where bottomland hardwood forests and other wetlands are a more prominent land cover type than the more agricultural northern areas of the range of *A. marciana* (Telford 1926).

For *T. rileyi*, precipitation and soil likely represented the need for eggs in the environment to avoid desiccation (Coman 1975). However, with the addition of the bias layer human density was the most important additional contributor. As *T. rileyi* is commonly found in domestic carnivores such as dogs and cats, higher human density may indicate a greater abundance of these domestic animals, increasing the density of potential hosts and thus increasing potential presence (Robertson et al. 2000). *Toxocara cati* had little change with and without the bias layer with land cover and soil being the most important contributors in both models. The results of the final map showing relatively few areas of high potential presence in combination with its low training gain indicate that *T. cati* is likely found throughout the study area and is less reliant on environmental factors within the study area.

The variation between models reflects not the habitat or host, but the unique parasite species. Only temperature was consistently of low importance for all models, likely due to the relatively small study area and limited variation that could be potentially influential. With the bias layer included, all climatic variables were of low importance, possibly indicating that in a smaller study area minimal climatic variations were not important con-

tributors to parasite presence. Scale may be an important factor to consider when modelling potential presence of parasite species. An increase in sample area for parasites of bobcats may provide more accurate models especially for generalist parasites that are not as dependent on environmental factors for infection to occur. Localised studies appear to work optimally with parasites that have specific environmental requirements like species of *Alaria* that require aquatic planorbid snails to complete their life cycle. However, modelling species like *T. cati* may provide more informative output only with a larger sample area.

In the present study, some parasite species had widespread, scattered areas of high potential presence across the entire study area like *T. cati*, whereas others displayed more concentrated areas (*A. marciana*). This difference is likely a result of the species dependence on the environmental factors that were used for modelling. Whereas sample locations were low for all species, the best model had the intermediate number of training data (19), indicating that small sample size was not the best indicator of model confidence. Other successful MAXENT models used low numbers of presence locations, as low as 10 (Pearson et al. 2007). Regardless of the modelling techniques used, it is important to consider the possibility of over representative models that are based on too many underlying assumptions. Researchers must employ caution when using them to make recommendations for management decisions (Bart 1995).

All parasite locations were collected from road killed or trapped bobcat hosts, which may cause a sampling bias. To this effect, Kadmon et al. (2003) showed how environmental biases, expressed as the degree of sampling bias with respect to the environmental conditions under which a species is known to occur, had a significant negative effect on the predictive accuracy of species distribution models like MAXENT. However, the same method was

used to compare the effectiveness of MAXENT between multiple parasite species that were sampled using the same techniques. Therefore, in our study all models were subject to the same amount of error indicating the differences between models were relevant.

To account for the effect of sampling using road killed organisms, the addition of the sampling bias layer displayed more restricted areas of potential presence and improved information for variable contribution. While this technique is not yet widely used in the literature, it provides quantifiable differences and is useful as a comparative tool. It should be recommended to further studies considering multiple or systematic sampling strategies which can be combined in MAXENT. More rigorous sampling design can decrease the chance of locational or environmental bias.

In general, this study can help guide wildlife biologists and health officials interested in using MAXENT and GIS as tools for predicting presence of parasites across a relatively small region (< 50 000 km²). Understanding parasite dynamics is becoming increasingly relevant with the growing impacts of climate change, anthropogenic landscape alterations and expanding populations of potential host species (Daszak et al. 2000, Walther et al. 2002, Carver et al. 2012, LaRue et al. 2012, Loss et al. 2013). With shifts such as these, understanding parasite biodiversity in wildlife in terms of conservation, the role of wildlife as reservoirs of parasite infection and the role of parasites within the broader ecosystem is of growing importance (Thompson et al. 2010).

Acknowledgements. Funding for this project was provided by the Cooperative Wildlife Research Laboratory and Department of Zoology at Southern Illinois University. A special thanks for modelling assistance to Julia Smith, Christopher Robinson, and Ramiro Crego.

REFERENCES

- ADAMS M.J., CHELGREN N.D., REINITZ D., COLE R.A., RACHOWICZ L.J., GALVAN S., MCCREARY B., PEARL C.A., BAILEY L.L., BETTASO J., BULL E.L., LEU M. 2010: Using occupancy models to understand the distribution of an amphibian pathogen, *Batrachochytrium dendrobatidis*. *Ecol. Appl.* 20: 289–302.
- ALTIZER S., NUNN C.L., THRALL P.H., GITTLEMAN J.L., ANTONOVICS J., CUNNINGHAM A.A., DOBSON A.P., EZENWA V., JONES K.E., PEDERSEN A.B., POSS M., PULLIAM J.R.C. 2003: Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annu. Rev. Ecol. Evol. Syst.* 34: 517–547.
- ANONYMOUS. 1996a: Digital Data Set of Illinois, CD-ROM. Illinois Department of Natural Resources Springfield, Illinois, USA.
- ANONYMOUS. 1996b: Illinois soil survey shapefile World Wide Web electronic publication, <http://websoilsurvey.nrcs.usda.gov>
- ANONYMOUS. 2005: Climate of Illinois. World Wide Web electronic publication, http://hurricane.ncdc.noaa.gov/climate/normals/clim60/states/Clim_IL_01.pdf, 04/2013.
- ANONYMOUS. 2010: TIGER/Line® shapefiles: block groups. United States Census Bureau.
- ANONYMOUS. 2011: National Land Cover Dataset. World Wide Web electronic publication, <http://www.mrlc.gov/index.php>, 08/2013.
- BAHN V., MCGILL B.J. 2007: Can niche-based distribution models outperform spatial interpolation? *Global Ecol. Biogeogr.* 16: 733–742.
- BALDWIN R.A. 2009: Use of maximum entropy modeling in wildlife research. *Entropy* 11: 854–866.
- BART J. 1995: Acceptance criteria for using individual-based models to make management decisions. *Ecol. Appl.* 5: 411–420.
- BEVINS S.N., CARVER S., BOYDSTON E.E., LYREN L.M., ALLDREDGE M., LOGAN K.A., RILEY S.P., FISHER R.N., VICKERS T.W., BOYCE W., SALMAN M., LAPPIN M.R.,

- CROOKS K.R., VANDEWOUDE S. 2012: Three pathogens in sympatric populations of pumas, bobcats, and domestic cats: implications for infectious disease transmission. *PloS One* 7: e31403.
- CARVER S., SCORZA A.V., BEVINS S.N., RILEY S.P., CROOKS K.R., VANDEWOUDE S., LAPPIN M.R. 2012: Zoonotic parasites of bobcats around human landscapes. *J. Clin. Microbiol.* 50: 3080–3083.
- COMAN B.J. 1975: The survival of *Taenia pisiformis* eggs under laboratory conditions and in the field environment. *Aust. Vet. J.* 51: 560–565.
- COMBES C. 2001: Parasitism: the Ecology and Evolution of Intimate Interactions. University of Chicago Press, Chicago, 728 pp.
- CROMLEY E.K. 2003: GIS and disease. *Annu. Rev. Public Hlth.* 24: 7–24.
- DASZAK P., CUNNINGHAM A.A., HYATT A.D. 2000: Wildlife ecology: emerging infectious diseases of wildlife – threats to biodiversity and human health. *Science* 287: 443–449.
- ELITH J., GRAHAM C.H. 2009: Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography* 32: 66–77.
- ELITH J., GRAHAM C.H., ANDERSON R.P., DUDIK M., FERRIER S., GUISAN A., HIJMAN R.J., HUETTMANN F., LEATHWICK J.R., LEHMANN A., LI J., LOHMANN L.G., LOISELLE B.A., MANION G., MORITZ C., NAKAMURA M., NAKAZAWA Y., OVERTON J.M., PETERSON A.T., PHILLIPS S.J., RICHARDSON K., SCACHETTI-PEREIRA R., SCHAPIRE R.E., SOBERÓN J., WILLIAMS S., WISZ M.S., ZIMMERMANN N.E. 2006: Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.
- ELITH J., PHILLIPS S.J., HASTIE T., DUDIK M., CHEE Y.E., YATES C.J. 2011: A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17: 43–57.
- ESRI. 2011: ArcGIS Desktop. Version 10. Environmental Systems Research Institute, Redlands, California.
- EUZET L., COMBES C. 1980: Les problèmes de l'espèce chez les animaux parasites. *Mém. Soc. Zool. France* 40: 239–285.
- FIELDING A.H., BELL J.F. 1997: A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24: 38–49.
- FISHER M. 2003: *Toxocara cati*: an underestimated zoonotic agent. *Trends Parasitol.* 19: 167–170.
- FUENTES M.V., MALONE J.B., MAS-COMA S. 2001: Validation of a mapping and prediction model for human fasciolosis transmission in Andean very high altitude endemic areas using remote sensing data. *Acta Trop.* 79: 87–95.
- GARDNER S.L. 1996: Essential techniques for collection of parasites during surveys of mammals. In: D. Wilson, R. Cole, J.D. Nichols, R. Rudran and M. Foster (Eds.), *Measuring and Monitoring Biological Diversity. Standard Methods for Mammals*. Smithsonian Institution Press, Washington, D.C., pp. 291–298.
- GERHOLD R.W., JESSUP D.A. 2013: Zoonotic diseases associated with free-roaming cats. *Zoonoses Publ. Hlth.* 60: 189–195.
- GOOGLE INC. 2012: Google Earth (Version 7.0). World Wide Web electronic publication, www.google.com/earth/, 02/2014.
- GUISAN A., THUILLER W. 2005: Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8: 993–1009.
- HEGGLIN D., BONTADINA F., CONTESSA P., GLOOR S., DEPLAZES P. 2007: Plasticity of predation behaviour as a putative driving force for parasite life-cycle dynamics: the case of urban foxes and *Echinococcus multilocularis* tapeworm. *Funct. Ecol.* 21: 552–560.
- HENDRICKX G., BIESEMANS J., DEKEN R.D. 2004: The use of GIS in veterinary parasitology. In: P. Durr and A. Gatrell (Eds.), *GIS and Spatial Analysis in Veterinary Medicine*. CABI Publishing, Oxfordshire, pp. 145–176.
- HERNANDEZ P.A., FRANKE I., HERZOG S.K., PACHECO V., PANIAGUA L., QUINTANA H.L., SOTO A., SWENSON J.J., TOVAR C., VALQUI T.H., VARGAS J., YOUNG B.E. 2008: Predicting species distributions in poorly-studied landscapes. *Biodivers. Conserv.* 17: 1353–1366.
- HIESTAND S.J., NIELSEN C., JIMÉNEZ F.A. 2014: Epizootic and zoonotic helminths of the bobcat (*Lynx rufus*) in Illinois and a comparison of helminth component communities across the American Midwest. *Parasite* 21: 4.
- JESCHKE J.M., STRAYER D.L. 2008: Usefulness of bioclimatic models for studying climate change and invasive species. *Ann. N.Y. Acad. Sci.* 1134: 1–24.
- JIMÉNEZ-VALVERDE A., LOBO J.M. 2007: Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecol.* 31: 361–369.
- JOHNSON A.D. 1968: Life history of *Alaria marcianae* (La Rue, 1917) Walton, 1949 (Trematoda: Diplostomatidae). *J. Parasitol.* 52: 324–332.
- JOHNSON P.T.J., THIELTGES D.W. 2010: Diversity, decoys and the dilution effect: how ecological communities affect disease risk. *J. Exp. Biol.* 213: 961–970.
- KADMON R., FARBER O., DANIN A. 2003: A systematic analysis of factors affecting the performance of climatic envelope models. *Ecol. Appl.* 13: 853–867.
- KRASNOV B.R., MOUILLOT D., SHENBROT G.I., KHOKHLOVA I.S., POULIN R. 2004: Geographical variation in host specificity of fleas (Siphonaptera) parasitic on small mammals: the influence of phylogeny and local environmental conditions. *Ecography* 27: 787–797.
- LARUE M.A., NIELSEN C.K., DOWLING M., MILLER K., WILSON B., SHAW H., ANDERSON C.R. 2012: Cougars are recolonizing the Midwest: analysis of cougar confirmations during 1990–2008. *J. Wildl. Manage.* 76: 1364–1369.
- LIU C.R., BERRY P.M., DAWSON T.P., PEARSON R.G. 2005: Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28: 385–393.
- LOBO J.M., JIMÉNEZ-VALVERDE A., REAL R. 2008: AUC: a misleading measure of the performance of predictive distribution models. *Global Ecol. Biogeogr.* 17: 145–151.
- LOSS S.R., WILL T., MARRA P.P. 2013: The impact of free-ranging domestic cats on wildlife of the United States. *Nat Commun.* 4: 1396.
- LUMAN D.M., JOSELYN M., SULOWAY L. 1996: Critical trends assessment project: landcover database World Wide Web electronic publication, <http://dnr.state.il.us/orep/ctap/map/land.htm>, 02/2014.
- MASUOKA P.M., BURKE R., COLACCICO M., RAZURI H., HILL D., MURRELL K.D. 2009: Predicted geographic ranges for North American sylvatic *Trichinella* species. *J. Parasitol.* 95: 829–837.
- MCDONALD P.T., NIELSEN C.K., OYANA T.J., SUN W.X. 2008: Modelling habitat overlap among sympatric mesocarnivores in southern Illinois, USA. *Ecol. Model.* 215: 276–286.
- MCPHERSON J.M., JETZ W., ROGERS D.J. 2004: The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *J. Appl. Ecol.* 41: 811–823.

- MOHL K., GROSSE K., HAMEDY A., WUSTE T., KABELITZ P., LUCKER E. 2009: Biology of *Alaria* spp. and human exposition risk to *Alaria* mesocercariae – a review. *Parasitol. Res.* 105: 1–15.
- MOLLHAGEN T. 1979: *Cysticercus of Taenia rileyi* Loewen, 1929. *Proc. Helminthol. Soc. Wash.* 46: 98–101.
- NEELY R.D., HEISTER C.G. 1987: The Natural Resources of Illinois: Introductions and Guide. Illinois Natural History Survey, Champaign, Illinois, 224 pp.
- OKULEWICZ A., PEREC-MATYSIAK A., BUNKOWSKA K., HILDEBRAND J. 2012: *Toxocara canis*, *Toxocara cati* and *Toxascaris leonina* in wild and domestic carnivores. *Helminthologia* 49: 3–10.
- OVERSTREET R.M. 1997: Parasitological data as monitors of environmental health. *Parassitologia* 39: 169–175.
- PEARCE J., FERRIER S. 2000: Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* 133: 225–245.
- PEARSON R.G., RAXWORTHY C.J., NAKAMURA M., PETERSON A.T. 2007: Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* 34: 102–117.
- PETERSON A.T. 2006: Uses and requirements of ecological niche models and related distributional models. *Biodiv. Inform.* 3: 52–79.
- PETERSON A.T., PAPES M., SOBERÓN J. 2008: Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Model.* 213: 63–72.
- PHILLIPS S.J., ANDERSON R.P., SCHAPIRE R.E. 2006: Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190: 231–259.
- PHILLIPS S.J., DUDIK M. 2008: Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161–175.
- PHILLIPS S.J., DUDIK M., SCHAPIRE R.E. 2004: A maximum entropy approach to species distribution modeling. 21st Int. Conf. on Machine Learning, 4–8 July 2004. Banff, Alberta, Canada.
- ROBERTS N.M., CRIMMINS S.M. 2010: Bobcat populations status and management in North America: evidence of large-scale population increase. *J. Fish Wildl. Manage* 1: 167–174.
- ROBERTSON I.D., IRWIN P.J., LYMBERY A.J., THOMPSON R.C.A. 2000: The role of companion animals in the emergence of parasitic zoonoses. *Int. J. Parasitol.* 30: 1369–1377.
- ROYLE J.A., CHANDLER R.B., YACKULIC C., NICHOLS J.D. 2012: Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods Ecol. Evol.* 3: 545–554.
- SCHWEGMAN J.E. 1972: Comprehensive plan for the Illinois Nature Preserves System, Part II, the natural divisions of Illinois. Illinois Nature Preserves Commission, Rockford, Illinois, 32 pp.
- SCOTT M.E. 1988: The impact of infection and disease on animal populations: implications for conservation biology. *Conserv. Biol.* 2: 40–56.
- SHOCK B.C., MURPHY S.M., PATTON L.L., SHOCK P.M., OLFENBUTTEL C., BERINGER J., PRANGE S., GROVE D.M., PEEK M., BUTFILOSKI J.W., HUGHES D.W., LOCKHART J.M., BEVINS S.N., VANDEWOUDE S., CROOKS K.R., NETTLES V.F., BROWN H.M., PETERSON D.S., YABSLEY M.J. 2011: Distribution and prevalence of *Cytauxzoon felis* in bobcats (*Lynx rufus*), the natural reservoir, and other wild felids in thirteen states. *Vet. Parasitol.* 175: 325–330.
- SLATER H., MICHAEL E. 2010: Geostatistical mapping of malaria and lymphatic filariasis co-endemicity in Africa. *Am. J. Trop. Med. Hyg.* 83: 235–235.
- SPRENT J.F. 1956: The life history and development of *Toxocara cati* (Schränk 1788) in the domestic cat. *Parasitology* 46: 54–78.
- SWANEPOEL L.H., LINDSEY P., SOMERS M.J., VAN HOVEN W., DALERUM F. 2013: Extent and fragmentation of suitable leopard habitat in South Africa. *Anim. Conserv.* 16: 41–50.
- SWERCZEK T.W., NIELSEN S.W., HELMBOLDT C.F. 1971: Transmammary passage of *Toxocara cati* in the cat. *Am. J. Vet. Res.* 32: 89–92.
- SWETS J.A. 1988: Measuring the accuracy of diagnostic systems. *Science* 240: 1285–1293.
- SWETS J.A. 1992: The science of choosing the right decision threshold in high-stakes diagnostics. *Am. Psychol.* 47: 522–532.
- TELFORD C. 1926: Third report on a forest survey of Illinois. In: N.H.S. Bulletin (Ed.), Natural History Survey Bulletin, Illinois Natural History Survey, Urbana, Illinois, pp. 102.
- THOMPSON R.C.A., LYMBERY A.J., SMITH A. 2010: Parasites, emerging disease and wildlife conservation. *Int. J. Parasitol.* 40: 1163–1170.
- TSENG M. 2006: Interactions between the parasite's previous and current environment mediate the outcome of parasite infection. *Am. Nat.* 168: 565–571.
- WALTHER G.R., POST E., CONVEY P., MENZEL A., PARMESAN C., BEEBEE T.J.C., FROMENTIN J.M., HOEGH-GULDBERG O., BAIRLEIN F. 2002: Ecological responses to recent climate change. *Nature* 416: 389–395.
- WISZ M.S., HIJMANS R.J., LI J., PETERSON A.T., GRAHAM C.H., GUISAN A., GROUP N.P.S.D.W. 2008: Effects of sample size on the performance of species distribution models. *Divers. Distrib.* 14: 763–773.
- WOOLF A., NIELSEN C.K., WEBER T., GIBBS-KIENINGER T.J. 2002: Statewide modeling of bobcat, *Lynx rufus*, habitat in Illinois, USA. *Biol. Conserv.* 104: 191–198.

Received 3 February 2014

Accepted 5 June 2014