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Original Article

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ABSTRACT The river otter (*Lontra canadensis*) was extirpated from Nebraska, USA, in the early 1900s and reintroduced starting in 1986. Information is needed regarding the distribution of river otters in Nebraska before decisions can be made regarding its conservation status. Understanding distribution of a species is critically important for effective management. We investigated river otter distribution in Nebraska with occupancy modeling and maximum entropy (Maxent) modeling using 190 otter sign observations on Nebraska's navigable rivers and 380 historical otter records from November 1977 to April 2014. Both methods identified the Platte River, Elkhorn River, central and eastern Niobrara River, and southern Loup River system as core areas within the distribution of otters in Nebraska. The Maxent model provided more liberal estimates of site occupancy and identified some smaller rivers as being within the distribution of otters in Nebraska, which were not identified using occupancy modeling. We recommend that multiple data sets and analysis methods be used to estimate species distribution because this allows for the broadest geographical coverage and decreases the likelihood of overlooking areas with fewer animal records. If further reintroduction efforts or translocation efforts are to take place in the future, we recommend focusing on areas with high modeled occupancy but few historical and survey records. © 2018 The Wildlife Society.

KEY WORDS *Lontra canadensis*, maximum entropy, Nebraska, occupancy, river otter, species distribution.

The North American river otter (*Lontra canadensis*; hereafter, otter) was once a common mammal in Nebraska, USA, ranging throughout all of the state's major rivers, particularly in the Missouri and Platte rivers (Swenk 1908, Jones 1964). By the early 1900s, unregulated fur-trapping and changes in land-use practices had eliminated otters from Nebraska's rivers (Melquist and Dronkert 1987). In the late 1800s through the early 1900s, reports of otters were very infrequent. Single records on the Big Blue River in 1897 (Swenk 1918) and in Seward County, Nebraska, in 1916 (Jones 1964) were among the last to occur for nearly 50 years when 2 specimens were reported from the Missouri River near Council Bluffs, Iowa, USA, and Beaver City, Nebraska, in the late 1960s and early 1970s (Hoffman and Genoways 2005).

In 1986, the Nebraska Game and Parks Commission (NGPC) began releasing otters back into Nebraska rivers; by 1991, NGPC had released 159 otters at 7 sites throughout the state (Bischof 2003; Fig. 1). With the reintroductions, the otter was listed as a Tier 1 at-risk species in Nebraska (Bischof 2003, Wilson 2012). Early efforts to monitor reintroduced otters were limited primarily to winter bridge surveys by NGPC (Bischof 2002), incidental take reported to NGPC, and research along the Big Bend of the Platte River between Overton and Chapman, Nebraska (Williams 2011, Wilson 2012). Early indications were that otters were spreading throughout the state, establishing home ranges, occurring locally at high densities, and experiencing low mortality rates (Raesly 2001, Bischof 2003, Gorman et al. 2006, Williams 2011, Wilson 2012). However, statewide distribution of otters in Nebraska since reintroductions took place remains uncertain. This information is vital for future management of the species. The NGPC prepared a distribution estimate for otters in 2014, which took into account expert opinion and potential habitat (Fig. 1). This estimate included the central and eastern Niobrara, Platte, and Elkhorn rivers as well as the southern Loup River system and isolated sections of the Missouri, Republican, Little Blue, Big Blue, and Little Nemaha rivers. To date, there has been no effort to model statewide distribution based on available or collected location data or to systematically survey Nebraska rivers for otters.

Estimating statewide species distribution presents a unique set of challenges (MacKenzie and Royle 2005, Hernandez et al. 2006). To provide the most unbiased estimate, the data set must provide very broad geographical coverage. The ability to obtain such data is limited by funding, time, available labor, land accessibility, and conditions within the study area. Furthermore, multiple data sets may exist, and it

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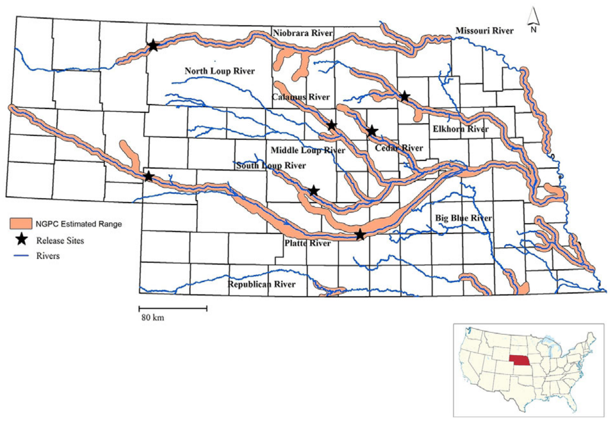

Figure 1. In 2014, the Nebraska Game and Parks Commission (NGPC), Nebraska, USA, estimated river otter distribution in Nebraska, USA, considering reports of river otters as well as nearby potential habitat. Potential habitat consisted of lakes and sandpit lakes nearby to the river channel.

may be appropriate to analyze each with different techniques. The consideration of multiple data sets and analysis methods may allow for greater representation of the study area and direct comparisons of results among methods. Two commonly used methods that exist for the estimation of species distribution are occupancy modeling and maximum entropy modeling.

Occupancy modeling techniques were developed by MacKenzie et al. (2002) and allow for estimation of site occupancy (psi) while accounting for imperfect detection rates (p). This method takes advantage of repeated site visits to generate detection histories so patterns in site occupancy may be examined in areas where animals were observed as well as areas where animals were not observed. Occupancy modeling assumes that site occupancy and detection likelihoods are constant between visits, all observations are independent, and no false detections occur (MacKenzie et al. 2002, Powell and Gale 2015). By conducting multiple surveys of each site, a detection probability may be estimated. Incorporating covariate data then allows for the consideration of site attributes, site detection history, and detection probability in determining the likelihood that any given site is occupied (MacKenzie et al. 2002, Powell and Gale 2015).

Maximum-entropy modeling is a method of estimating potential habitat and species distribution that has become widely used in recent years because of its effectiveness, availability of the intuitive Maxent software (https://biodiversityinformatics.amnh.org/open_source/maxent/) that interfaces well with ArcGIS software (Environmental Systems Research Institute, Inc., Redlands, CA; Merow et al. 2013), and because it offers a means of analyzing presence-only data, which are common and relatively easy to obtain (Phillips et al. 2004). In a Maxent analysis, models of the distribution of a species over the study area are created. These models represent probability distributions that account for relationships found among the available presence data and environmental characteristics data subject to a key constraint, which is that the mean value of any environmental characteristic predicted by the model should be close to the mean value observed in the data (Phillips et al. 2006). Of these probability distributions, the distribution with maximum entropy, or the most uniform distribution, is selected (Jaynes 1957, Phillips et al. 2006). This method also assumes that occurrence records are the product of random sampling and differences in site-specific covariates do not influence detection rates at those sites (Yackulic et al. 2013, Fourcade et al. 2014).

We used both presence–absence occupancy modeling and presence-only Maxent modeling to 1) explore 2 methods of estimating otter distribution using different available data sets, and 2) identify areas of increased otter occupancy in Nebraska.

STUDY AREA

We focused our survey and modeling efforts on the navigable rivers of Nebraska, in particular the Platte, Niobrara, Elkhorn, Loup, Republican, Big Blue, and Missouri rivers; however, we also considered some smaller rivers, the Big Nemaha, Little Nemaha, Little Blue, Dismal, and Cedar rivers. We chose these rivers because they allowed for relatively easy navigation and survey by kayak, and included the rivers chosen as reintroduction points during otter reintroduction efforts.

Rivers in Nebraska flowed primarily through the Western High Plains, Nebraska Sand Hills, Western Corn Belt Plains, and Central Great Plains ecoregions (Chapman et al. 2001). The dominant land cover was cultivated crops along the Missouri, Big Blue, Little Blue, Big Nemaha, Little Nemaha, central and eastern Platte, and southern Elkhorn rivers. The dominant land cover was perennial vegetation along the Niobrara, western Platte, and northern Republican rivers as well as throughout the Loup River system including the Dismal and Cedar rivers. Land cover varied between cultivated and perennial vegetation along the Republican River. Most of Nebraska's rivers exhibited a great deal of seasonal fluctuation in water level as winter snow melt and spring rains inundated rivers and decreasing seasonal precipitation and increasing agricultural irrigation demands lowered summer and autumn water levels.

METHODS

Data Collection

We collected presence–absence otter sign data to be used in occupancy analyses from July to September 2014 and July to October 2015. We conducted double-observer surveys by kayak and typically began and ended at bridges or public access areas. In order to maximize survey coverage, we surveyed 5–25 km of river per day and began the next survey 5–25 km downstream from the end point of the previous survey. We instructed surveyors to stay only within distant view of one another while paddling to ensure that observations recorded were independent between observers. While paddling, each observer made note of any sign of river otter and beaver (*Castor canadensis*) encountered on an exposed substrate and recorded Universal Transverse Mercator coordinates. Sign typically consisted of tracks, scats, or animal sightings.

We obtained presence-only data for Maxent analyses from NGPC. These records included 5 November 1977 through 23 April 2014. Data consisted of geographic coordinates for the record, date the record was made, whether or not a carcass was collected in association with the record, and, in the case of a visual record, how many individuals were observed. Records were primarily of otters incidentally trapped and reported by fur trappers, otters struck by vehicles, and otter sightings with photographic evidence. A total of 380 observations were collected; of these records, 352 had the necessary geographic coordinate data associated with them for analysis.

To create discrete sampling units with which to associate otter records and covariate data, we *a priori* constructed a grid of 6- × 6-km grid cells using ArcMap10.2.2 (Environmental Systems Research Institute, Inc.) covering Nebraska. We extracted all grid cells ($n = 1{,}192$) that contained focal survey rivers such that each extracted grid cell constituted one sampling unit along those rivers. We chose the 6- × 6-km resolution because this represents a 36-km^2 area, which is a conservative estimate of home range size for river otters on the Platte River of Nebraska (Wilson 2012).

Covariates were defined *a priori* and covariate data collected *post hoc* for each sampling unit. Survey-specific covariates included the numbers of days since the last rainfall >2 cm, and the survey period, such that periods 1–3 corresponded to July–September 2014 and periods 4–7 corresponded to July–October 2015. Site-specific covariates included the distance to the nearest otter release site (km), amount of non–river-channel wetland area (m^2), long-term median flow rate of the river (m^3/s water), an estimate of beaver occupancy, dominant vegetation land cover, and a binary variable describing whether or not the river had gone dry in the past 5 years. There was a large range of values among continuous variables, so values for these covariates were standardized by calculating z-scores. We populated each sampling unit with detection data in surveyed units and covariate data in all units.

We considered the time since the last rainfall >2 cm as a survey-specific covariate to determine if recent rainfall affected an observer's ability to detect otter sign, perhaps by eroding tracks and degrading scats on exposed substrate. We included the survey period covariate to examine factors that could affect seasonal variability in detection and variability in detection within the 2 field seasons, such as temperature and water level.

We included the distance to a release site covariate to investigate how otters had dispersed from reintroduction points and whether or not sufficient time had elapsed since reintroduction for the otters to disperse to all habitable areas. The distance to the nearest release site was measured from the center of a given sampling unit in a straight line to the nearest release site. This method assumed that river otters are able to travel over land in addition to along waterways (Melquist and Hornocker 1983).

We considered wetland area as a covariate because it represented habitat outside of the main river channel that an otter would use while traveling over land (Tranl and Chapman 2007). We derived wetland area data from a wetland layer made available through the U.S. Department of Agriculture (USDA), Natural Resources Conservation Service (NRCS) Geospatial Data Gateway. We selected only wetlands >0.2 ha in size to avoid including seasonal and very small wetlands. We removed river channels from the layer so that only wetland area beyond the river channel would be considered. In the event that a reservoir occurred along the river, we did not include the area covered by the reservoir because we were interested in considering wetland areas beyond the contiguous river body that could be used while traveling and foraging over land.

We considered the river flow-rate covariate because size of a river may have implications for how much forage is available within the river; otters select rivers with larger and deeper pools and open-water sections (Tranl and Chapman 2007, Wilson 2012). The U.S. Geological Survey (USGS) National Water Information System (NWIS) flow meters established throughout Nebraska provided information for long-term median flow rates. There were a relatively limited number of these meters; therefore, it was necessary to extrapolate flow-rate values in many sampling units that did not contain flow meters. We accomplished this using linear regression where the dependent variable was the flow rate and the independent variable was the distance from the nearest flow meter.

We considered beaver occupancy as a covariate because of the frequent use of beaver lodges by river otters (Melquist and Hornocker 1983, Swimley et al. 1999). Naïve occupancy, or the proportion of sites where beaver sign was found during surveys, was used during the model selection process; but, because these data were not available for unsurveyed sampling units, it was necessary to estimate beaver occupancy in these areas (Tables S1 and S2, available online at www.onlinelibrary.wiley.com).

We derived and simplified vegetation land-cover data from land cover raster sets (2011) available through USDA, NRCS Geospatial Data Gateway. We simplified data to consist of the 2 dominant vegetation cover types. We assigned each sampling unit a cover-type value based on the dominant cover type within the unit. "Cultivated crops" and "perennial vegetation" land covers dominated the study area, and all other land covers along the focal rivers existed in only a very small number of sampling units. In the event that some other uncommon land cover was dominant in a sampling unit, the surrounding vegetation cover was chosen.

The final covariate was an estimate of whether or not the river in a given sampling unit was likely to have gone dry in the past 5 years, which in most cases would have occurred during the 2012 drought (Mallya et al. 2013). It is possible that if the river had gone dry, resident otters may have left the area and not yet returned. We derived the information for this covariate from the USGS NWIS flow meters and considered areas to have gone dry if their flow rate during the previous 5 years dropped as low as 0.56 m^3/s of water for a period of 1 month. This flow rate represents an estimate for long-term median flow rates in the headwaters of smaller Nebraska rivers that typically are dry during summer and autumn.

Occupancy Analysis

We compared a null detection model in which detection rates did not vary between observers with a detection model in which each of our 5 observers had different detection rates, or observer-specific detection rates. Survey-specific covariates were then considered in detection models where observers had detection rates that did not vary or were affected by survey period, recent rainfalls, and a combination of these. Lastly, we considered detection models where each observer had different detection rates and were affected by survey period, recent rainfalls, and a combination of these.

The best detection model was incorporated into models exploring effects of site-specific covariates. We considered 6 single-covariate and 4 multiple-covariates site-occupancy models. Multiple covariate models included "basic needs" model, "incomplete dispersal" model, "available water" model, and a global model. The "basic needs" model included flow-rate and beaver occupancy covariates and assumed otter occupancy depended primarily upon the availability of den sites and available foraging waters. The "incomplete dispersal" model included the release distance, flow rate, and beaver occupancy covariates and assumed that otter occupancy depended primarily upon availability of den sites and suitable foraging water, but otters were also more closely associated with reintroduction sites than would be expected in a fully dispersed population. The "available water" model included the flow rate, wetland area, and 5-year dry-history covariates and assumed that otter occupancy depended on a range of factors that described the amount and nature of the water present in a sampling unit. The global model included all 6 covariates. We conducted occupancy analyses using PRESENCE and data were analyzed as a simple single-season model where we treated data from the 2 field seasons as a single season (Program PRESENCE Version 8.8, www.mbr-pwrc.usgs.gov, accessed 27 Apr 2015).

We used Akaike's Information Criterion (AIC) to determine relative fit of competing models. We developed models in stepwise fashion. We first analyzed detection models of survey-specific covariates using global site-specific covariates. We then used the strongest detection model while assessing occupancy models incorporating the site-specific covariates. These models sought to identify relationships between site characteristics in the 324 sites that were surveyed and detection histories generated within each site. We then used the best model to estimate the probability of occupancy in the 824 sampling units that were not surveyed based on covariate values in those units. We then imported resultant occupancy estimates from the best model into the appropriate sampling units in ArcGIS to display results.

Maxent Analysis

We created a model using Maxent (Program Maxent Version 3.3.3k; www.cs.princeton.edu/~schapire/maxent, accessed 5 Jun 2015), that incorporated the 6 site-specific covariates and presence-only otter records in a model of otter distribution. To avoid oversampling bias, we considered only 1 otter record/sampling unit in the data set (Fourcade et al. 2014). This removal left 170 records in the data set. We converted the environmental variable polygon-shapefiles to raster files in ArcMap10.2.2 and then from raster to ASCII files to import into Maxent.

We analyzed these data with 10,000 background samples, a regularization multiplier of 1, a random test percentage of 10, and a random seed for each replicate run. The geographic extent of the combined extracted sampling units defined the "bounding box" from which background samples were taken. The replicate run type was cross-validation, and 10 replicates were tested (Merow et al. 2013). The default prevalence was 0.16, which is an estimate of occurrence probability obtained through the previously described occupancy modeling efforts. The output format was "logistic," which is the format recommended for estimating relative occupancy (Merow et al. 2013). We ran a jackknife test of variable importance to examine the relative effect of each environmental variable.

We evaluated the fit of the Maxent model using the average test area under the curve (AUC) in the receiver operating characteristic plot (Phillips et al. 2006, Baldwin 2009). We conducted an analysis of variable contribution with the model, which provided an estimate of the percentage contribution of each variable to the final Maxent models. The jackknife analysis provided similar information on variable importance, but provided additional information about the strength of a model where each variable was the sole variable in the model as well as a model where each variable was left out.

Comparing Methods

We compared occupancy estimates produced by the Maxent model with the estimates produced using presence–absence occupancy-modeling techniques in Program PRESENCE. Estimates of spatial correspondence were made by subtracting the presence–absence occupancy modeling estimates from the presence-only Maxent occupancy estimates.

RESULTS

Sign Surveys

We surveyed approximately 1,630 km of river by kayak and sampled in 324 of the 1,192 sampling units. We detected otter sign on the Niobrara, Elkhorn, Platte, Loup, and Cedar rivers during kayak surveys. We made 190 observations, with records occurring in 52 of 324 surveyed sampling units, which equates to a naïve occupancy rate of 16%. On the Niobrara River, we detected otter sign from Cody, Nebraska east to Lynch. Otter sign on the Elkhorn was concentrated between O'Neill and Meadow Grove, but was found as far south as Scribner. On the Platte River, we detected otter sign primarily on the North Platte River west of the reservoir at Ogallala and along the Big Bend of the Platte River between Overton and Chapman. We found otter sign sporadically and infrequently in the Loup River

Table 1. Detection model comparisons and model weights for an occupancy analysis of river otters in Nebraska, USA. Data for these analyses were collected July to September 2014 and July to October 2015.

Model	AIC[a]	ΔAIC[b]	w[c]	−2log(L)[d]	K[e]
psi(Global), p(Observer, Rain, Period)	356.05	0.00	0.9983	312.05	22
psi(Global), p(Observer, Period)	369.44	13.39	0.0012	335.44	17
psi(Global), p(Rain)	373.29	17.24	0.0002	355.29	9
psi(Global), p(Rain, Period)	373.61	17.56	0.0002	353.61	10
psi(Global), p(Observer, Rain)	373.84	17.79	0.0001	339.84	17
psi(Global), p(.)	382.35	26.3	0.0000	366.35	8
psi(Global), p(Period)	383.55	27.5	0.0000	365.55	9
psi(Global), p(Observer)	384.64	28.59	0.0000	360.64	12

[a] AIC = Akaike's Information Criterion.
[b] ΔAIC = change in AIC.
[c] w = AIC wt.
[d] −2log(L) = −2 times the logarithm of the likelihood.
[e] K = no. of parameters.

system with records occurring near Loup City on the Middle Loup, Cotesfield and Elba on the North Loup, and southwest of Dannebrog on the Loup River. We made one observation on the Cedar River of an animal spotted swimming across the river channel southeast of Cedar Rapids.

Occupancy Analysis

The highest ranked detection model included different detection rates by observer and effects from both survey period and recent heavy rainfall (AIC wt = 0.99; Table 1). The highest ranked site-occupancy model was the "incomplete dispersal" model, which considered otter occupancy to be a function of the distance from the survey site to a release site, presence of beaver in the area, and long-term median flow rate of the river (AIC wt = 0.91). The only other model with >5% of the AIC weight was the global model, which accounted for the effects of all 6 site-specific covariates (AIC wt = 0.09; Table 2). Beta estimates for the covariates in the highest ranked model suggested a strong positive effect of beaver occupancy on otter occupancy, a strong negative effect of the distance from the nearest release site on otter occupancy, and a weak negative effect of the river flow rate on otter occupancy (Table 3).

In addition to predicting occupancy in all areas where otter sign was found, occupancy estimates of 10–25% were predicted throughout much of the southern Loup River system. A lower occupancy estimate of 5–10% was predicted intermittently throughout the central and eastern Niobrara River, the central Elkhorn River, the southern Loup River system, the South Platte River, and the Republican River near the Harlan County Lake (Fig. 2).

Maxent Analysis

The Maxent model had an AUC value of 0.69 (SD = 0.062). Variable contributions were greatest for the distance to release site and river flow-rate variables (permutation importance = 41.8%, 31.4%). The amount of wetland area and beaver presence had permutation importance levels of 10.1% and 10.4%, respectively, and the 5 year dry-history of the river and dominant vegetation land cover had permutation importance levels of 0.2% and 6.2%.

None of the models with single environmental variables omitted produced any gain over the model with all 6 variables, suggesting each variable provided at least some measure of nonredundant information. The variable that provided the greatest gain when used in isolation was the river flow rate, which suggests that this was the most

Table 2. Site-occupancy model comparisons and model weights for an occupancy analysis of river otters in Nebraska, USA. Data for these analyses were collected July to September 2014 and July to October 2015.

Model	AIC[a]	ΔAIC[b]	w[c]	−2log(L)[d]	K[e]
psi(IncompleteDispersal), p(Detection)	351.51	0.00	0.9050	313.51	19
psi(Global), p(Detection)	356.05	4.54	0.0935	312.05	22
psi(BasicNeeds), p(Detection)	365.12	13.61	0.0010	329.12	18
psi(Beaver), p(Detection)	367.28	15.77	0.0003	333.28	17
psi(ReleaseDistance), p(Detection)	404.68	53.17	0.0000	370.68	17
psi(FlowRate), p(Detection)	416.21	64.7	0.0000	382.21	17
psi(DryHistory), p(Detection)	417.31	65.8	0.0000	383.31	17
psi(AvailableWater), p(Detection)	418.46	66.95	0.0000	380.46	19
psi(WetlandArea), p(Detection)	419.25	67.74	0.0000	385.25	17
psi(LandCover), p(Detection)	419.68	68.17	0.0000	385.68	17

[a] AIC = Akaike's Information Criterion.
[b] ΔAIC = change in AIC.
[c] w = AIC wt.
[d] −2log(L) = −2 times the logarithm of the likelihood.
[e] K = no. of parameters.

Table 3. Beta estimates for the covariates of the highest ranked occupancy model from an occupancy analysis of river otters in Nebraska, USA. Data for these analyses were collected July to September 2014 and July to October 2015.

K[a]	Estimate	SE
psi[b]	−70.615	0.679
psi, ReleaseDistance	−85.496	2.676
psi, FlowRate	−0.642	0.683
psi, Beaver	36.540	1.028
p[c](1)	0.718	0.640
p(2)	3.696	1.892
p(3)	2.085	1.225
p(4)	8.582	3.445
p(5)	254.980	1.464
p(1), Rain	−0.174	0.050
p(2), Rain	0.291	0.242
p(3), Rain	−0.107	0.088
p(4), Rain	−0.227	0.119
p(5), Rain	1.288	1.496
p(1), Period	0.253	0.191
p(2), Period	−2.198	1.128
p(3), Period	−1.005	0.583
p(4), Period	−1.489	0.597
p(5), Period	−64.170	0.364

[a] *K* = no. of parameters.
[b] psi = occupancy probability.
[c] p = detection probability.

informative variable. The distance to a release site variable decreased the model gain the most when omitted, so we concluded that this variable provided the most information that was not accounted for by other variables.

This model identified the majority of the Platte River from Ogallala east to the convergence with the Missouri River, the northern half of the Elkhorn River, the southern Loup River system, and sections in both the western and eastern Niobrara River as areas with occupancy estimates between 0.1 and 0.5 (Fig. 3). The greatest concentration of sampling units with occupancy estimates >0.25 occurred on the central Platte River.

Comparison of Methods

Of the 1,192 sampling units, 717 had less than a 0.1 difference in occupancy estimates between methods (Fig. 4).

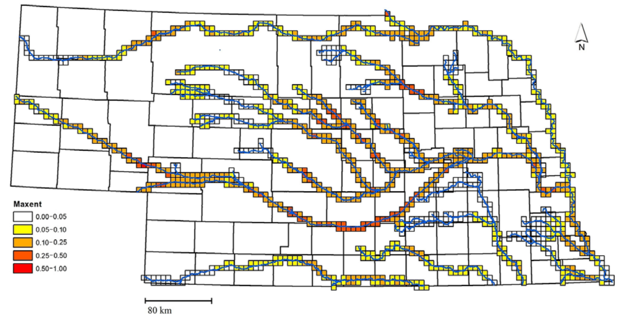

Figure 3. A maximum entropy analysis examining patterns in river otter occupancy in Nebraska, USA, suggested that the areas most likely occupied by river otters are along the Platte River, northern Elkhorn River, southern Loup River system, and sections of the western and eastern Niobrara River. Data for this analysis were collected July–September 2014 and July–October 2015.

The Maxent method of occupancy estimation tended to produce more liberal estimates. There were 421 sampling units with positive spatial correspondence values >0.1. Only 54 sampling units had negative spatial correspondence values; in only one of these was the greater presence–absence occupancy estimate not influenced by a "1" value, which reflected a known occurrence using that method.

DISCUSSION

Our data and modeling results are largely consistent with historical descriptions of otter distribution in the state prior to their extirpation and distribution estimates produced by NGPC. This suggests that a detailed knowledge of a species' historical range in addition to a longstanding monitoring program, even one so simple as collection of incidental trapping accounts, may be a useful tool in estimating species distribution, particularly when limited resources do not allow for more extensive survey efforts. Similarities between our occupancy and Maxent range estimates and historical range estimates suggest that otters in the state have repopulated much of their original distribution since reintroductions began.

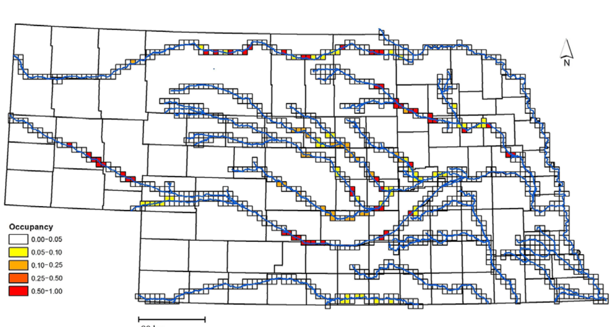

Figure 2. River otter occupancy estimates of 10–25% occurred throughout the southern Loup River system, Nebraska, USA. Occupancy estimates of 5–10% were common throughout the state, primarily on the Platte, Niobrara, Elkhorn, and eastern Republican rivers as well as the southern Loup River system. Data for this analysis were collected July–September 2014 and July–October 2015.

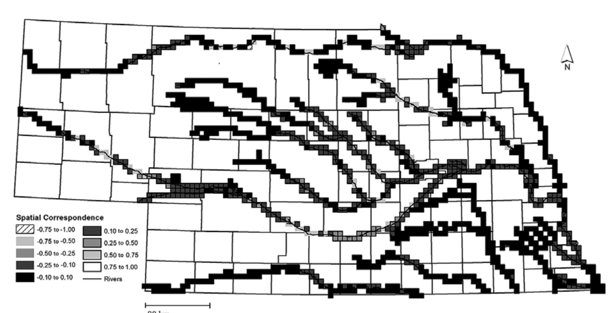

Figure 4. The areas of Nebraska, USA, identified by occupancy modeling and maximum entropy modeling efforts as areas more likely to have resident river otters were consistent, but occupancy modeling in Program PRESENCE produced more conservative estimates than did Maxent modeling. This resulted in much greater coverage and far fewer occupancy estimates of zero. Data for these analyses were collected July–September 2014 and July–October 2015.

Survey records and modeling efforts indicate that otters are found throughout the Niobrara River from Cody, Nebraska east to the Missouri River, throughout the Elkhorn and Platte rivers, and in the southern Loup River system. Our survey records indicate that the Niobrara River in Keya Peha County has resident otters, but this is an area not well-supported by historical records. This may be due to the remote nature of the area presenting fewer opportunities for humans to contact and report otters, or otters may have only recently moved into the area. Modeling results suggest that otter occupancy on the Republican River is elevated around the Harlan County Lake, but surveys in this area failed to detect any otter presence. The Maxent model suggested elevated occupancy on the southern Big Nemaha and Little Nemaha rivers. Surveys on the Big Nemaha River did not yield any otter records; the Little Nemaha had insufficient water flow for kayak surveys. There have been increasing reports of otters in the Little Nemaha, with 10 new records made from 2001 to 2014. The Missouri River is well-supported as being within the historical distribution of river otters in Nebraska (Swenk 1908), but very little of the river was able to be surveyed by kayak, and the NGPC data set contained few records from the Missouri.

Detection rates were variable among observers. Average detection rates by observer were 0.56, 0.59, 0.38, 0.43, and 0.36. An Oklahoma, USA, study using bridges as survey locations found variable detections rates of 30–50% and 7–17% during high otter abundance and low otter abundance years, respectively (Shackelford and Whitaker 1997). A Missouri, USA, study showed 68% and 40% detection rates at random and bridge sites respectively (Crimmins et al. 2009). MacKenzie and Royle (2005) recommends surveying sites $\geq$3 times when detection probability is $>$0.5, but this is emphasized for studies where surveys are not done on the same day. With detection rates above or near 50% and all surveys being conducted on the same day, the 2–3 observers used per site were adequate.

The variable that contributed most to the fit of the highest ranked occupancy model as well as the Maxent model was the distance to a release site. It may be that otters have not yet fully dispersed across Nebraska so that they tend to be closely linked to release areas or it may be that the original release sites were ideally located to begin with such that a fully dispersed population would have localized around those sites regardless. Monitoring efforts were limited in the decade following otter reintroductions, so it is difficult to examine patterns of dispersal in the early reintroduction population.

River flow rate was also an important factor in otter occupancy estimates. This factor was strongly supported by the highest ranked occupancy model, and contributed 31.4% of the model fit in the Maxent model. This is in agreement with the assertion that river otters tend to use larger, open-water areas (Tranl and Chapman 2007, Wilson 2012). The highest ranked occupancy model strongly supported beaver presence as a contributor to otter occupancy. This factor was of secondary importance to the fit of the Maxent model. Otters are known to frequently use beaver dens as their own (Melquist and Hornocker 1983, Swimley et al. 1999), so it is reasonable that otters would be found more often in areas with local beaver populations.

The variability in occupancy estimates between methods suggests it is worthwhile to consider multiple data sets and analysis methods. This may better account for variable coverage in data sets and differences in estimates between methods. For example, inclusion of historical records on the Little Nemaha River resulted in its inclusion in Maxent distribution estimates. This area was not in the distribution estimate produced by presence–absence occupancy modeling because the river had inadequate river flow to be surveyed.

MANAGEMENT IMPLICATIONS

We identified the Niobrara, Platte, and Elkhorn rivers and the southern Loup River system as core areas within otter distribution in Nebraska, and continued monitoring and management efforts should be focused on these areas. We recommend beginning monitoring efforts immediately after reintroductions in future projects so that the initial spread of animals from release sites is better understood.

Though both methods of analysis identified many of the same areas as areas of elevated occupancy, estimates varied between methods. When making species distribution estimates, we recommend making use of multiple data sets and analysis techniques when possible. This practice ensures the broadest coverage within data sets, reflects the breadth of current knowledge, and decreases the likelihood of overlooking less-represented areas that may not be identified by all methods of estimating distribution.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site. This supporting material details the use of occupancy analysis to estimate beaver occupancy in Nebraska. Beaver occupancy estimates were used as a covariate in otter occupancy analyses.