Universities Council on Water Resources
Journal of Contemporary Water Research & Education
Issue 157, Pages 14-22, April 2016

Modeling Population Growth and Response to Harvest for River Otters in Illinois

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Abstract: Population modeling is an invaluable tool for predicting wildlife population dynamics and the effects of management. I created a state-space population model for unharvested river otters in the Illinois, Kaskaskia, and Wabash river basins in Illinois, and modeled future harvest at 5%, 10%, and 20% levels. River otter populations increased in the absence of harvest during 2000 - 2009 to 8,408 ± 1,934 individuals (λ = 1.11 ± 0.09). Harvest at 0%, 5%, 10%, and 20% levels resulted in continued population growth over time, with annual harvest numbers ranging from 446 - 1,786 in 2010 to 884 - 2,614 in 2014, depending on harvest scenario. I concluded that river otter populations in Illinois were thriving and capable of withstanding a regulated harvest.

Keywords: *harvest, Illinois, population modeling, river otter, trapping*

Population modeling is an invaluable tool for predicting wildlife population dynamics and the effects of management. Wildlife managers often require models that can integrate data from multiple sources that may not be available in successive years (Walters and Hilborn 1978; Nichols et al. 1992; Buckland et al. 2007). Such models also should have the capability to handle the inherent errors in data obtained from hunters and trappers that are regularly implemented into models (Clark and Bjornstad 2004; Buckland et al. 2007).

State-space modeling is a relatively novel modeling technique that allows for integration of multiple forms of models, errors, and data sets, which shows great promise for modeling wildlife populations (Buckland et al. 2004). Kalman (1960) originated the idea for the state-space model for use in engineering systems. State-space models have since been used in many applications including population modeling, survival analysis, and disease modeling (Tan and Xiang 1998; Buckland et al. 2004; Tan and Ke 2004).

State-space models are composed of two elements, the state process and the observation process (Borchers et al. 2002). These components allow for a fairly robust estimation of population parameters and an effective way to test for uncertainty. The state process is referred to as the hidden or "true" state model (Buckland et al. 2007). This model generally refers to population processes which can be represented by a population projection matrix and are not explicitly known (e.g., population abundance). This in turn can include sub-processes which may also be modeled as separate Leslie matrices which may include metapopulations or processes such as births and deaths. Habitat modeling and animal movements also can be included in the state process (Thomas et al. 2005).

Two primary methods used in state-space modeling are probability equations and matrix models (Buckland et al. 2004). Probability equations are more commonly used when there is a lack of substantial data for setting the prior distribution of the state variables (Tan and Ke 2004). Matrix models are used commonly when sufficient data to develop a prior distribution are present (Thomas et al. 2005). These methods also are used in combination with the observational process to infer state variables. One of the more common methods for this technique involves a simple time series analysis coupled with recorded observational data to establish a projected Leslie

matrix (Buckland et al. 2004). Within the Leslie matrix, projection state variables are allowed to possess intermediate states. This allows for a variable such as population abundance to have matrix intermediaries that may include births, aging, and survival.

The observation process (i.e., the second portion of the state-space model) seeks to model measurements or observations that can be projected onto the state process; these are generally known quantities obtained from surveys. The observation process can include many of the same aspects of the state process which can then affect the hidden matrices to provide an estimation of state values. The observation process also can include parameters for stochasticity, observational error, and maximum likelihood estimates (Wang 2007). The observational process can be used to determine posterior distributions which can be linearized, and through the use of Bayesian statistics or appropriate Kalman filters, differentiated through the state process (Wang 2007). These in turn can then be assessed through Monte Carlo Markov chain (MCMC) methods to estimate unknown parameters that may be lacking in the state process (Schaub et al. 2007).

Wildlife managers required updated models for river otter (*Lontra canadensis*) populations in Illinois. River otters were listed as a state endangered species in Illinois in 1989 (Bluett et al. 1999). As part of a comprehensive recovery plan developed by the Illinois Department of Natural Resources (IDNR), 346 wild otters were obtained from Louisiana and released in Illinois during January 1994 - March 1997. River otters were downlisted to state-threatened in 1999 following the initial success of the reintroduction program (Bluett et al. 1999). Research then indicated rapid population growth, reproduction, and excellent condition of Illinois river otters (Woolf and Nielsen 2001; Bluett et al. 2005). This research, in conjunction with data collected by the IDNR, resulted in river otters being delisted to non-game status in 2004 (Bluett et al. 2005). Growth in river otter populations in Illinois (similar to that observed in Missouri; Hamilton 1998) led to increased concern regarding potential negative impacts of river otters on native fish and wildlife resources, fish hatcheries, and private ponds (Serfass et al. 1990) as occurred in Missouri (Hamilton 1998).

Research was necessary to monitor population growth for river otters given that population models currently in place for the assessment and management of river otter populations in Illinois were outdated and require incorporation of new data (Woolf and Nielsen 2001). Furthermore, there was potential opportunity for a well-regulated river otter harvest in Illinois (Woolf and Nielsen 2001), and updated information on the biology of this species was necessary to support harvest management while providing a method of monitoring population status. My objective in this study was to use state-space models to forecast population growth in river otters and determine response to varying harvest levels.

Methods

I used state-space modeling to develop a population model for river otters in the Illinois, Kaskaskia, and Wabash river basins in Illinois, where river otters were reintroduced during 1994-97 (Buckland et al. 2004; Moore and Read 2008; Yamamura et al. 2008). My goal was to provide a population estimate for 2009 based on collected data and then project population growth into the future given selected harvest scenarios. I used a Bayesian uncertainty analysis to estimate survival and growth rate from age-at-death data (Moore and Read 2008) following animal necropsy. Population growth was modeled starting with estimates provided in 2001 (Woolf and Nielsen 2001) to the present time (i.e., 2009); I then modeled population growth and response to harvest five years into the future (i.e., until 2014). All models were density-independent.

Empirical Data

To inform model construction, I used empirical data collected from river otter necropsies and previous river otter modeling efforts (Hamilton 1998; Woolf and Nielsen 2001; Bluett et al. 2005). Age data were from necropsies performed on 332 river otters (199 M, 133 F) collected mostly as road kills or incidental harvest in Illinois during 1996 - 2008. The sex of all specimens was determined and the uterine tract examined

in females to quantify fecundity rates based on placental scarring and presence of embryos. However, due to insufficient fecundity data due to poor resolution of placental scars, rates were based on those in previous models (Hamilton 1998; Woolf and Nielsen 2001; Bluett et al. 2005). The age of all specimens was determined through inspection of cementum annuli from lower canine teeth (Crowe 1972).

Model Structure

My global model consisted of two sub-models with the first sub-model consisting of a Bayesian uncertainty analysis (Moore and Read 2008), called as such given there are several different combinations of demographic parameters that may lead to the same overall growth rate (Moore and Read 2008). The uncertainty analysis was used to estimate survival rates and population growth. The second sub-model of the global model consisted of a state-space model (Kalman 1960). The state-space model was used to estimate current abundance and incorporate varying harvest strategies.

Modeling Current Population Abundance and Growth Rate

The first sub-model I developed was used to determine an overall population growth rate based on likely survival and fecundity rates for river otters. Fecundity rates were based on a joint estimate using rates provided by Hamilton (1998) and the more conservative Woolf and Nielsen (2001; Table 1). For survival rates, I used a competing risk model where mortality was age-based and dependent on three combined hazard equations, one each for juvenile, adult, and senescing animals, respectively (Siler 1979; Skalski et al. 2005; Moore and Read 2008). I used the age-at-death data from necropsies to determine these parameters for the hazard equations. Upon estimating survival parameters, I combined survival estimates with fecundity estimates within the Euler equation (Moore and Read 2008) to determine the population growth rate. I also included a conservative error term allowing my estimates to vary by 10%.

I began with the population estimate for river otters in 2001 (N=1,830; Woolf and Nielsen 2001) and then projected population growth forward to 2009 using a state-space model. The original model started only with the 346 river otters released in the Illinois, Kaskaskia, and Wabash river basins in Illinois during 1994-97 (Woolf and Nielsen 2001). The population growth rate was modeled in the state process using a Lefkovitch matrix model (Lefkovitch 1965, Caswell 2001), while stochasticity was modeled in the observation process. I modeled stochasticity in the observation process to allow for individual variation between years and for simplicity when harvest effects were incorporated thereafter.

Table 1. Breeding parameters used to determine fecundity in a model of river otter population growth in Illinois.

Parameter	-------- Breeding Probabilities --------		
	Hamilton (1998)	**Woolf and Nielsen (2001)**	**Average Probability**
Yearling	0.350	---	0.350
Adult	0.700	---	0.700
Female Young	1.750	0.875	1.313

Modeling Population Response to Harvest

My goal in modeling river otter response to harvest was to be conservative, as to not affect considerable declines in river otter numbers if my assumptions were inaccurate. I modeled harvest as an additive source of mortality (i.e., as a direct reduction in survival rates) and assumed harvest affected all stage-classes equally. I modeled annual harvest rates of 0% (i.e., assuming no harvest whatsoever and maintaining current growth levels), 5%, 10%, and 20%. I assumed that regulated harvest would replace incidental take (i.e., from beaver trappers who once accidentally killed river otters but would now be able to harvest them) in a compensatory manner (i.e., I did not include any additional parameters for accidental or illegal take). Population growth and response to harvest was projected five years into the future, until 2014, in one-year increments beginning with

the year 2009. I again used a state-space model similar to that used for estimating population abundance in 2009, this time including an equation in the observation process representing yearly additive harvest mortality.

Model Assumptions

My population model must be understood within the confines of a few important assumptions that I was unable to measure. The Lefkovitch model has the assumptions of a stable and stationary population with no measurement error in stage-classification (Skalski et al. 2005). The Lefkovitch model also assumes that all carcasses have the same probability of harvest and that the sample is representative of mortality within the species due to the use of pooled data (Skalski et al. 2005). The model further assumes that it is both appropriate to classify the population by stage-class and that there is no within-class variability (Caswell 2001).

Model Solutions

I used Bayesian analysis and MCMC to solve both subsections of these models (Moore and Read 2008, Yamamura et al. 2008). The MCMC analysis was carried out using the program WinBUGS (Lunn et al. 2000). Bayesian analysis requires the use of prior distributions for parameters (Tables 2 and 3). Each model was run using three separate Markov chains and convergence was determined using the Gelman-Rubin statistic (Gelman and Rubin 1996, Spiegelhalter et al. 1999). I also examined autocorrelation within my chains; convergence and autocorrelation analysis was conducted using the R package BOA (Smith 2007).

Results and Discussion

The Bayesian uncertainty analysis indicated a growing river otter population in the absence of harvest during 2000 - 2009 ($\lambda = 1.11 \pm 0.09$, SE throughout). Using the survival estimates provided by the uncertainty analysis and the joint fecundity estimate, the state-space model projected a river otter population abundance of 8,408 ± 1,934 in Fall 2009 (Figure 1). The 90% credible interval (similar to confidence interval) increased to roughly 21% of the mean value by 2009 (Figure 1) due to increased model uncertainty over time.

Table 2. Prior distributions for the Bayesian uncertainty analysis used to determine survival and population growth rate for river otters in Illinois.

Parameter	Distribution (Values)	Description
a_1	uniform (0, 3) [a]	juvenile mortality
a_2	uniform (0, 3) [a]	adult mortality
a_3	uniform (0, 3) [a]	senescent mortality
b_1	uniform (0, 5) [a]	decrease in juvenile mortality
b_3	uniform (0, 5) [a]	increase in adult mortality
f_1	beta (1, 0.27) x 0.88	fertility of yearling individuals
f_2	beta (1, 0.25) x 1.855	fertility of adult individuals
l_{nat}	uniform (0, 0.01)	survivorship to oldest age represented in the data

[a] Place-holder values for which data were not initially available due to modeling technique.

Table 3. Prior distributions for the state-space model used to estimate river otter abundance in Illinois.

Parameter	Distribution (Values)	Description
s_j	uniform (0.84, 0.91)	survival of juvenile animals
s_y	uniform (0.76, 0.83)	survival of yearling animals
s_a	uniform (0.73, 0.81)	survival of adult animals
f_j	uniform (0, 0)	fecundity of juvenile animals
f_y	uniform (0.4, 0.9)	fecundity of yearling animals
f_a	uniform (2.0, 2.6)	fecundity of adult animals

Harvest estimates were based on the mean population abundance value provided by the state-space model for the year 2009. The model continued to predict an increase in river otter abundance in the absence of harvest through 2014 to 23,599 animals (a 281% increase over 2009 levels). Harvest levels at 5% and 10% still resulted in population growth of river otters by 2014 (Figure 2). At the 5% and 10% harvest rates, river otter population abundance was 18,852 (a 224% increase over 2009) and 15,331 (a 182% increase over 2009), respectively. Population growth was nearly zero with the 20% harvest scenario, but not negative despite the 11% annual growth calculated during 2000-2009 (Figure 2). This is likely because of the slight J-shape in the population growth curve (an artifact of the particular modeling process used) exhibited during 2009-2014 (Figure 1). Annual harvest numbers ranged from 446-1,786 in 2010 to 884-2,614 in 2014 (Table 4).

The state-space model indicated that river otter populations will continue to grow in Illinois, and that they can certainly withstand modest harvest levels. I believe the current estimate of 8,408 river otters is likely conservative because I originally began modeling in 1996 with only reintroduced individuals (Woolf and Nielsen 2001). Immigrants have likely entered Illinois from nearby states (i.e., Missouri and Kentucky) that had growing river otter populations prior to Illinois otter reintroductions, and remnant otters likely were present in portions of Illinois before reintroductions in the mid-1990s.

Otter population growth was estimated to be 11% during 2000 - 2009, which is less than the 25% growth rate modeled during 1996 - 2001 (Woolf and Nielsen 2001). This disparity may be explained by slight density-dependent influences (which I could not truly assess due to relatively low annual sample sizes of necropsied animals) and/or considerable differences in modeling techniques. Woolf and Nielsen (2001) used simpler models that lacked the rigor of the state-space modeling framework (Moore and Read 2008, Yamamura et al. 2008), and growth rates of >25% were also noted in river otters in Missouri (Hamilton 1998) based on similar data sources and accounting-based models. Conversely, Iowa river otter populations were thought to be growing at a 7% annual rate, with a statewide population of 7,000 animals (Iowa DNR 2016), results that are more similar to those found in this study. Regardless, Illinois river otter populations are growing and could support a harvest season, which would provide recreational benefits to trappers while possibly reducing river otter damage to native wildlife populations. This is

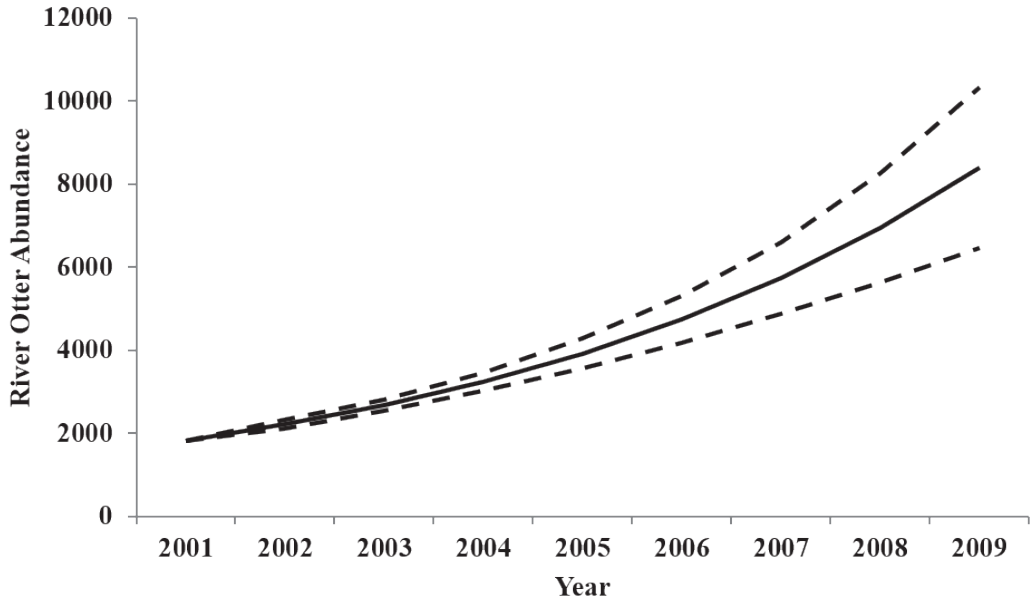


Figure 1. Projected population growth of river otters in Illinois during 2000 - 2009, including the 90% credible interval.

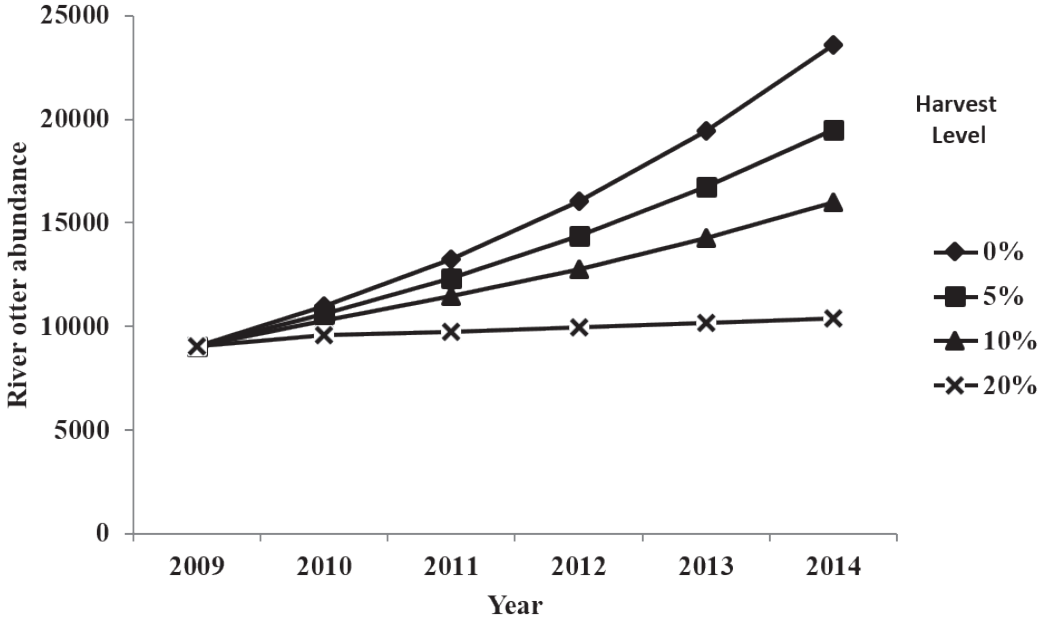


Figure 2. Simulated harvest levels based on population growth projections for river otters in Illinois during 2009 - 2014.

Table 4. Forecasted mean river otter harvest levels in Illinois, 2010 - 2014.

Harvest Rate	---------- Number of River Otters Harvested / Year ----------				
	2010	**2011**	**2012**	**2013**	**2014**
5%	440	513	588	667	751
10%	881	999	1117	1236	1355
20%	1762	1903	2028	2132	2220

especially important given that river otters are top carnivores in aquatic ecosystems with relatively few natural predators in Illinois.

I modeled several harvest levels, assuming the goal of harvesting river otters to maintain zero percent or greater population growth. Harvest rates of 15 to 20% are common in river otter populations (Erb 2009), and my scenarios indicated that even a 20% harvest rate did not result in population declines. However, with slower population growth, Iowa allowed harvest rates of only 6% (Iowa DNR 2016).

Population models represent abstractions of reality, and although my models were based on relatively sound empirical data (with the exception of somewhat low annual sample sizes), these results must be interpreted with some caution. One of my assumptions was that density-independence was not acting on river otters, although slower growth during 2001 - 2009 relative to 1996 - 2001 (Woolf and Nielsen 2001) may indicate some density dependence. Although no empirical data were available to test the assumption of density-independence explicitly, I believe this analysis was appropriately conservative to ensure against overharvest, especially given that the starting estimate in 1996 was likely biased low. Thus, during the study period (i.e., 2000 - 2009) I believed it appropriate to model river population growth in the absence of density-dependence, and was not compelled to do so five years further into the future when incorporating harvest. This resulted in a 281% increase in river otter populations to 23,599 in the absence of harvest, which may be an overestimate of population growth potential, given that density-dependence may begin operating as populations grow further.

Management and Policy Implications

River otter populations continue to grow in Illinois, and as suggested previously (Woolf and Nielsen 2001), can sustain a regulated harvest. Harvest should occur close to the months of November-February (i.e., in conjunction with the beaver season when river otters are currently incidentally trapped) and employ bag and possession limits until the quota is filled, as in Iowa (Iowa DNR 2016) and Minnesota (Minnesota DNR 2009). These recommendations were ultimately employed by the IDNR, and as a result, a trapping season was enacted in Illinois in 2012 with a five otter/trapper limit. Data from harvested otters will be used to increase annual sample sizes, which will allow for the further testing and revision of the model presented in this study. Specifically, I will attempt to test for density dependence and differences in age- and sex-specific parameters used in the model.

Acknowledgements

I thank the Illinois Department of Natural Resources for funding this research via the Federal Aid in Wildlife Restoration Program (Project W-135-R). Further logistical support was provided by B. Bluett, J. Melko, trappers and biologists who provided river otter carcasses, and the Cooperative Wildlife Research Laboratory at Southern Illinois University. Two anonymous reviewers provided valuable revisions to the original draft of this manuscript.

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