

AMPHIBIAN OCCUPANCY IN FLOOD-CREATED AND EXISTING WETLANDS OF THE LOWER MISSOURI RIVER ALLUVIAL VALLEY

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ABSTRACT

During the previous century, the wetland area in the lower Missouri River alluvial valley was reduced by 39% because of river channelization and bank stabilization projects. The Great Flood of 1993 reversed the trend of wetland loss by creating 466 new wetlands in the alluvial valley between Kansas City and St. Louis, Missouri. We estimated amphibian occupancy, detection probability and number of species exhibiting evidence of reproduction in eight flood-created and 16 pre-flood existing wetlands from 1996 through 1998. We also evaluated whether hydroperiod (the number of days any water was present in a wetland from 20 February through 31 August) and distance to river predicted those values. Detection probabilities for adult amphibian species were relatively constant across years and ranged from 0.013 [Great Plains toad (*Anaxyrus cognatus*)] to 0.280 [Woodhouse's toad (*Anaxyrus woodhousii woodhousii*)]. Occupancy of adult amphibians differed across years and was not correlated with habitat features. Estimated occupancy probabilities for amphibian species ranged from 0.126 [Plains spadefoot (*Spea bombifrons*)] to 0.896 [boreal chorus frog (*Pseudacris maculata*)]. Almost double the number of amphibian species showed evidence of reproduction in existing wetlands (wetlands created before the Great Flood of 1993) when compared with that in flood-created wetlands. Similarly, temporary wetlands had nearly double the number of amphibian species showing evidence of reproduction when compared with permanent wetlands. Finally, the highest number of species showed evidence of reproduction in wetlands with spring–summer hydroperiods between 135 and 140 days. All these relationships suggest that the invasion and persistence of predators in wetlands negatively influence amphibian reproduction. If the Missouri River is allowed to reconnect with the alluvial valley, more predators may be introduced into wetlands, leading to reduced amphibian occupancy and reproduction. However, this connection will not likely occur over the entire alluvial valley and, therefore, should not adversely impact amphibians that find refuge in higher-elevation, non-connected regions of the alluvial valley. Copyright © 2011 John Wiley & Sons, Ltd.

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INTRODUCTION

The lower 1180 km of the Missouri River and its alluvial valley have been greatly altered during the past century. Historically, the river was a wide braided channel that consumed its banks, deposited new sediment and unpredictably changed its channel (Hesse *et al.*, 1989; Galat *et al.*, 1996). The river inundated its floodplain, the portion of the alluvial valley next to the river, on average every 1.5 to 2 years (Hesse and Mestl, 1993), and the timing and duration of water on the floodplain were most influenced by the river. Although still occasionally influenced by the river, higher and more river-distant terraces [floodplains abandoned by the river (Leopold, 1994)] with marshes and shallow wetlands were inundated only by extreme flood events, and the timing and duration of water in these basins were driven by local precipitation and runoff from uplands.

Since the establishment of upstream reservoirs and the completion of the lower-river channelization and bank stabilization project, an estimated 41 000 ha of aquatic habitat has been lost through drainage, filling and conversion of the alluvial valley for agriculture (Hesse *et al.*, 1989). The transformation of the Missouri River has shortened its length in Missouri by 74 km and eliminated 50% of the water surface area (Funk and Robinson, 1974), and currently only 10% of the alluvial valley is periodically inundated by the river (Hesse *et al.*, 1989). At present, the alluvial valley is now highly developed for agriculture and is largely a terrestrial system rather than an aquatic system.

The Great Missouri River Flood of 1993, which had a peak flow in Booneville, Missouri, of $21\,240\text{ m}^3\text{ s}^{-1}$ and a return period of >100 years (Parrett *et al.*, 1993), somewhat reversed the trend of habitat loss by creating 466 new wetlands within the 296-km-long alluvial valley between Kansas City and St. Louis, Missouri (SAST, 1994; Galat *et al.*, 1997). These new wetlands were created as floodwaters broke through levees and scoured holes that were often 7 to 15 m deep (SAST, 1994; Galat *et al.*, 1997). As floodwaters receded,

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water remained in these new basins, and they were available for colonization and use by flora and fauna. Scientists in a multi-agency cooperative effort, called the Missouri River Post-flood Evaluation Project, joined forces to determine if these new wetlands contributed suitable habitat to various plant and animal groups existing in the river and alluvial valley (Galat *et al.*, 1998). Researchers examined limnological characteristics, plant communities and various animal communities (zooplankton, macroinvertebrates, fishes, amphibians, turtles and birds) at these new wetlands and compared them with plant and animal communities at wetlands that existed prior to the flood and remained after floodwaters receded.

Amphibians are important vertebrate components of wetland systems and can readily colonize new wetlands. Amphibians will appear around a new wetland within the first several years after its creation (Boomsma and Arntzen, 1985; Laan and Verboom, 1990; Arntzen and Teunis, 1993; Baker and Halliday, 1999). Amphibian reproduction may even occur at a new wetland within the first several years, but it takes time for the amphibian community to build in numbers and species richness to a level resembling that in natural wetlands (Monello and Wright, 1999). Amphibian use of a new wetland depends upon the species inhabiting nearby wetlands, the distance between the new wetland and existing wetlands, habitat surrounding the wetland and the physical and biological characteristics of the wetland, such as hydroperiod and the presence of fishes (Laan and Verboom, 1990; Baker and Halliday, 1999). Thus, monitoring amphibian presence around a variety of wetlands within the alluvial valley might aid in determining how flood events influence amphibian species abundance and richness.

Monitoring amphibians can lead to biased population estimates and inaccurate interpretations of habitat relationships when imperfect detection of the species is not considered (Bailey *et al.*, 2004; MacKenzie *et al.*, 2006). Occupancy modelling and probabilistic sampling are methods that help overcome this deficiency. Occupancy models have become popular because they do not assume that all individuals are detected, only require the investigator to determine the presence or absence of the species during repeated surveys, and can be robust predictors of the proportion of the study area occupied when appropriate predictor variables are considered (MacKenzie *et al.*, 2002, 2006; Crossland *et al.*, 2005).

Our first objective was to estimate the probability of detecting each amphibian species at both existing wetlands (i.e. wetlands present prior to the Great Flood of 1993) and wetlands created by the Great Flood of 1993 (hereby referred to as flood-created) in the lower Missouri River Valley from 1996 to 1998. Our second objective was to determine how specific wetland characteristics, including water dynamics (permanent versus temporary), wetland type (existing versus flood-created), distance to river and hydroperiod, influenced

the probability of occupancy for each adult amphibian species captured. Our final objective was to evaluate how wetland characteristics influenced amphibian reproduction by estimating the number of species that displayed evidence of reproduction within a wetland. Understanding how wetland and temporal characteristics influence occupancy, detection probability and the number of species showing evidence of reproduction will help characterize how flood events affect amphibian use of the Missouri River alluvial valley.

METHODS

Study area

We examined amphibian communities at 24 wetlands in the lower Missouri River alluvial valley from Sandy Hook to Missouri City, Missouri [approximately 38°47'30"N and 92°24'30"W to 39°16'N and 94°15'W; river km 254 to 550 (Figure 1)]. The average bank-full width of the Missouri River in this reach was 345 m (Elliot *et al.*, 2009), with an average flow range of 1000 m³ s⁻¹ in December and January to 2700 m³ s⁻¹ in April and May (Galat and Lipkin, 2000). We used simple random sampling, without replacement, to select the 24 wetlands from a list of wetlands observed in aerial surveys conducted immediately following the flood of 1993. Study wetlands were spaced 0.5–37 km apart and were equally distributed among six wetland categories: (i) flood-created, connected to the river; (ii) flood-created, not connected to the river; (iii) remnant; (iv) wooded slough; (v) agricultural temporary; and (vi) non-agricultural temporary. Sixteen of the 24 wetlands were existing wetlands, and the remaining eight were flood-created wetlands, formed by river flow through breaks in interior and adjacent levees in the alluvial valley (Galat *et al.*, 1997). During our study, all the flood-created wetlands were considered permanent wetlands, whereas existing wetlands consisted of both temporary and permanent wetlands.

Prior to the Great Flood of 1993, the landscape in the alluvial valley was comprised of approximately the following proportion of land uses: 75% in agriculture, 10% in forest, 13% in water (the river and wetlands) and 2% in early successional habitat such as sand and grass (based on the 1978 information for a representative portion of the alluvial valley in central Missouri). By 2000, state and federal agencies had purchased or enrolled approximately 35 458 ha of the flood-impacted land into federal programmes for fish and wildlife habitat (D. Galat, University of Missouri, Columbia, MO and M. Lastrup, United States Geological Survey-Biological Resources Division, Columbia, MO, pers. comm.).

Field methods

Adult capture. We captured amphibians using terrestrial drift fences and funnel traps (Gibbons and Semlitsch, 1982) to

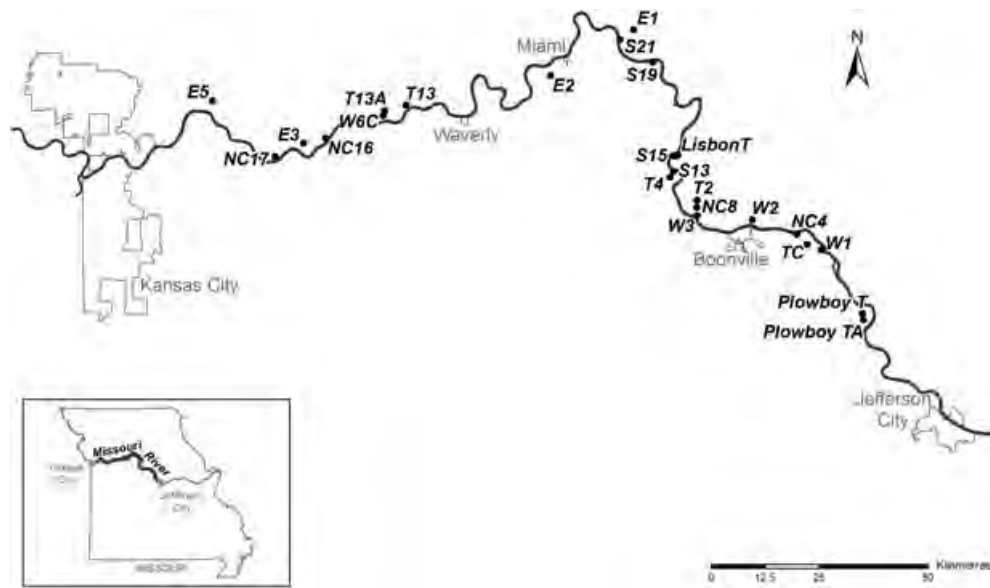


Figure 1. Location of wetlands along the Missouri River used to study occupancy of amphibian species in the alluvial valley from 1996 to 1998. Black dots represent study wetlands.

determine the occupancy (proportion of study sites occupied by each amphibian species) and detection probability (probability that each amphibian species will be detected, if present) of all adult amphibian species captured at study wetlands. Most study wetlands were too large (>0.5 ha) to encircle with drift fences, so we trapped adult amphibians at random locations around the perimeter of a wetland using 7.5-m-long, 60-cm-tall aluminium drift fences buried approximately 10 cm in the ground. We placed two double-ended funnel traps on either side of the fence mid-sections and placed two single-ended funnel traps at the ends of each fence. Each fence with its four funnel traps was defined as a trap. We sampled every study wetland with at least four traps. Study wetlands greater than 20 ha in water surface area received additional traps at a rate of one trap per 5 ha of surface area. We erected traps approximately 4.6 m landward from and parallel to the wetland edge. Trap location at a wetland remained the same during 1996 through 1998, although occasional flooding sometimes forced us to move fences approximately 4.6 m from the wetland edge.

We sampled adult amphibian communities from 19 February through 31 May 1996, from 18 February through 30 May 1997 and from 5 February through 22 May 1998. We checked traps, identified and classified amphibians as adult or juvenile and released amphibians within 2 m of the trap at a wetland approximately every 2 to 4 days, depending on travel conditions, amphibian activity and flooding.

Larvae capture. We sampled larval amphibian communities during mid-May through June of each year to determine whether the wetland exhibited evidence of amphibian reproduction. If a wetland contained water during this period,

we sampled for larval amphibians at the wetland for two consecutive nights through the use of funnel traps suspended from drift fences within wetlands. We constructed funnel traps (modified from Richter, 1995) from plastic 2-l beverage containers and suspended two funnel traps from each side of a 5 m × 0.9 m section of drift fence made from silt fencing material (Enge, 1997) staked in ≤1-m-deep water. On each fence side, we suspended one funnel trap 20 cm from the wetland substrate and suspended the other funnel trap 75 cm from the substrate or 10 cm from the wetland surface if the water was <75 cm deep. We did this to account for any vertical migrations amphibian larvae might make during a 24-h period (Anderson and Graham, 1967). We sampled wetlands in a random order with the same number of traps (i.e. a drift fence with four funnel traps) as were used for adult amphibian sampling. We emptied larvae from traps each day and identified each to species, if possible.

Analytical methods for adult amphibians

Detection histories. We classified each wetland, with all associated traps within the wetland, as a sample site ($n = 24$) and used trap visit observations to construct species-specific detection histories for adult amphibians at each wetland, each year. We considered each survey year to be a unique 'season', thereby, allowing the possibility of amphibian immigration or emigration to or from wetlands among years. However, we assumed that amphibians were not present at sample wetlands throughout sample seasons (February–May) because of species-specific amphibian behaviour (e.g. breeding). Thus, we created a unique sample season each year for each amphibian species based solely upon the time the species of

interest was present or could be present at the wetland. We used the length of time between the first and last date a species was detected to define a sample season. Further, if there was not sufficient time between the first and last detections (<10 days), we used the published breeding season (Johnson, 2000) for the species as the sample season (Table I). Using this technique to determine sample season length ensured that the wetland was occupied by the species of interest throughout the entire season, which is an important assumption when estimating occupancy (MacKenzie *et al.*, 2002, 2006). On average, sample seasons lasted approximately 2 months ($\bar{x} = 67.7$ days, $SE = 4.12$).

The number of surveys completed at a wetland within a season varied considerably (2–56 surveys). Some wetlands were flooded during some years and, therefore, could not be surveyed as often. Because this large range of surveys might cause problems when estimating occupancy and detection probabilities, we limited the number of survey events for a species to a maximum of 25 per wetland per season. If a wetland was surveyed more than 25 times, we systematically removed observations throughout the season until only 25 equally distributed surveys remained. By removing surveys systematically, we effectively reduced the survey range without diminishing our ability to evaluate spatial or temporal variables on occupancy and detection probability.

Model development. Typically, when conducting a multi-year occupancy study, dynamic parameters such as colonization and local extinction probabilities may be estimated for each site, using the multi-season model design (MacKenzie *et al.*, 2003, 2006). However, because of the low

number of wetlands we sampled, we did not have enough power to estimate colonization and local extinction parameters with adequate precision. As a result, we used the single-season model to calculate occupancy and detection probabilities each year for each species, making it possible to detect trends in occupancy and detection probability without having to also estimate colonization and local extinction probabilities.

It is necessary to model spatial and temporal heterogeneity in occupancy and detection probability to obtain unbiased estimates for each (MacKenzie *et al.*, 2006). As a result, we developed a suite of models for amphibian occupancy and detection probability based on published literature and evaluated them using an information-theoretic approach (Burnham and Anderson, 2002). We used a two-stage approach in our model selection procedures (e.g. Franklin *et al.*, 2000; Washburn *et al.*, 2004). In the first stage, we compared models that evaluated the influence of date and wetland characteristics on detection probability (p), while holding occupancy probability (Ψ) constant [i.e. $\Psi(\cdot)p$ (*covariate*)]. In the second stage, we modelled the influence of wetland characteristics on occupancy probability simultaneously with the most supported detection probability model from stage 1 [i.e. $\Psi(\text{covariate})p(\text{best})$; Bailey *et al.*, 2004; Olson *et al.*, 2005; MacKenzie *et al.*, 2006; Kroll *et al.*, 2007]. By incorporating a two-stage design, we reduced our candidate model set while still evaluating a sufficient set of covariates that might have caused heterogeneity in occupancy and detection probability.

Detection models. To model detection probability of each species, we evaluated a constant detection model and

Table I. Dates of sample seasons used for an occupancy modelling analysis of 12 adult amphibian species in the Missouri River alluvial basin from 1996 to 1998

Species	Season		
	1996	1997	1998
ACCR	26 Feb.–31 May	20 Feb.–31 May	23 Feb.–22 May
AMTE	1 April–31 May	20 Feb.–23 April	26 Feb.–22 May
ANAM	15 April–31 May	21 March–31 May	2 April–22 May
ANCO	1 April–31 May	1 May–31 May	16 April–22 May
ANWO	18 April–31 May	7 March–31 May	30 March–22 May
HYCH	4 April–31 May	31 March–31 May	1 April–22 May
PSCR	23 Feb.–15 May	28 Feb.–8 May	27 March–22 April
PSMA	27 Feb.–31 May	21 Feb.–31 May	18 Feb.–22 May
LIBL	26 Feb.–31 May	21 Feb.–31 May	16 Feb.–22 May
LICA	28 Feb.–1 May	25 March–31 May	16 March–22 May
LISP	26 Feb.–31 May	6 March–31 May	26 Feb.–22 May
SPBO	1 May–31 May	23 April–31 May	31 March–22 May

ACCR, *Acris crepitans*; AMTE, *Ambystoma texanum*; ANAM, *Anaxyrus americanus americanus*; ANCO, *Anaxyrus cognatus*; ANWO, *Anaxyrus woodhousii woodhousii*; HYCH, *Hyla chrysoseclis*–*Hyla versicolor* complex; PSMA, *Pseudacris maculata*; PSCR, *Pseudacris crucifer*; LIBL, *Lithobates blairi*; LICA, *Lithobates catesbeiana*; LISP, *Lithobates spenocephalus*; SPBO, *Spea bombifrons*.

models with added covariates (date and wetland type) that we hypothesized would influence detection probability. Preliminary examination of our data suggested that the association of date with detection probability might be non-linear because some species might be more active during the peak of the breeding season, making them easier to capture. As a result, we compared support for linear, quadratic, pseudothreshold (hereby referred to as asymptotic) and exponential forms (Franklin *et al.*, 2000) for date using Akaike's information criterion adjusted for small sample size (AIC_c ; Burnham and Anderson, 2002) before evaluating other models. We retained the form with the lowest AIC_c value for each species, each year. We then used the most supported form when evaluating detection probability models.

Site covariates, such as wetland type, might influence the ability to detect amphibian species because species that are more abundant within a site are typically easier to detect (Royle and Nichols, 2003; MacKenzie *et al.*, 2006). Consequently, we evaluated whether detection probability differed between existing and flood-created wetlands and between temporary and permanent wetlands. Further, we evaluated whether these wetland types had an additive effect with date on detection probability.

Occupancy models. Numerous site attributes could influence the probability that adult amphibian species occupy a wetland. Thus, we evaluated one constant occupancy model and 12 models including site covariates for all species, while incorporating the most supported detection probability model (see Model development). We chose four site covariates that we believed would have the strongest influence on occupancy probability: distance to river, hydroperiod, existing versus flood-created wetland and temporary versus permanent wetland. Distance to river represented the shortest straight-line distance in kilometre between the Missouri River and the study wetland. We defined wetland hydroperiod as the number of days any amount of water was in a wetland from 20 February through 31 August (a 194-day period) that year because all the amphibians that might breed in the Missouri River alluvial valley do so during this portion of the calendar year (Johnson, 2000). Existing and flood-created wetlands represented wetlands that were present before the 1993 flood and wetlands that were created by the 1993 flood, respectively. Temporary wetlands only held water for part of the year, whereas permanent wetlands always held water. Again, we compared support for linear, quadratic, asymptotic and exponential structural forms for continuous parameters and retained the most supported form for each parameter in the occupancy models.

Occupancy and detection probability estimation methods. We calculated occupancy and detection probabilities for each amphibian species, each year, in program PRESENCE

(MacKenzie *et al.*, 2006) by using the single-season method where the likelihood (L) can be written as

$$L(\Psi, p | X_1, \dots, X_N) = \prod_{i=1}^N \Pr X_i \quad (1)$$

where Ψ is the occupancy probability, p is the detection probability and X_N are the detection histories for number (N) of surveyed sites. We used the most supported model for each species, each year, to estimate occupancy and detection probabilities. If there were not sufficient data for program PRESENCE to converge upon an occupancy probability estimate, we only reported the 'naïve' occupancy probability estimate, which is the estimate of occupancy probability without accounting for imperfect detection (MacKenzie *et al.*, 2006).

We based our model rankings on ΔAIC_c and Akaike weights (Burnham and Anderson, 2002) for each model. We calculated odds ratios and 95% confidence intervals for parameter estimates to assess the strength of each parameter's relationship with occupancy and detection probability. We did not consider parameters influential if they had 95% odds ratio confidence intervals that included 1. Because AIC_c rankings are relative conditional on the models in the candidate set, we validated the models to determine their predictive ability. We applied the Pearson chi-squared statistic to our global model for each species and performed 10 000 parametric bootstraps to obtain a \hat{c} value (MacKenzie and Bailey, 2004). We assumed that models with \hat{c} values of ~ 1 were adequate descriptors of the data whereas models with $\hat{c} > 1$ suggested that there was more variation in the observed data than expected by the model (Burnham and Anderson, 2002).

Analytical methods for juvenile and larval amphibians

We did not use occupancy modelling to estimate occupancy and detection probabilities of larval/juvenile amphibians because we could not determine exactly when individuals hatched, making it more difficult to meet the occupancy closure assumption (MacKenzie *et al.*, 2002). As a result, rather than creating larval detection histories, we determined which wetlands exhibited evidence of reproduction for each species from the larval surveys and drift fence sampling each year. We considered there to be evidence of reproduction if larvae or juveniles of a particular species were captured at a wetland during the sampling year. We identified juveniles by size (snout-vent length and total length) and considered juveniles as evidence of reproduction because some amphibian species reproduce earlier than others (Johnson, 2000) and would have already metamorphosed before the end of drift fence sampling. Using these data, we counted the number of amphibian species that exhibited evidence of reproduction within the wetland at least once from 1996 to

1998 and used this count as the response variable in our analysis.

We assumed that many of the wetland characteristics influencing the occupancy probability of adult amphibians would also affect the number of species showing evidence of reproduction. Thus, we used the same variables from the occupancy models (distance to river, hydroperiod, existing versus flood-created wetland and temporary versus permanent wetland) in our analysis. We assumed that there might be non-linear relationships between the continuous variables and the number of species reproducing; therefore, we compared support for linear, quadratic, asymptotic and exponential structural forms, retained the structural form with the lowest AIC_c value and incorporated the structural form into the models when evaluating our model set. We compared a constant model against five other models that assumed that the number of species reproducing was a function of wetland characteristics. We evaluated the four covariates in separate single-parameter models and evaluated a global model, which included all covariates.

We used Poisson regression and fit models using PROC GENMOD in SAS (SAS Institute, 2006, Cary, NC, USA) because Poisson regression is appropriate for count data. We ranked the candidate models using AIC_c values and Akaike weights provided in the SAS output. To test for overdispersion, we calculated \hat{c} for the global model. We assumed that a \hat{c} value of ~ 1 suggested that the global model was an adequate descriptor of the data, whereas a $\hat{c} > 1$ suggested that there was more variation in the observed data than expected by the global model (Burnham and Anderson, 2002). Additionally, we assumed that \hat{c} values > 1 represented poor fit of the data, therefore requiring a quasi-likelihood form of AIC_c ($QAIC_c$) (Burnham and Anderson, 1998) and an inflation of parameter standard errors (McCullagh and Nelder, 1989).

We addressed model selection uncertainty by calculating model-averaged estimates of the coefficients for models in the 90% Akaike weight confidence set (Burnham and Anderson, 2002). We estimated model-averaged parameter estimates ($\hat{\beta}_j$) by model-averaging across only the models in which the predictor variable x_j appeared using

$$\hat{\beta}_j = \frac{\sum_{i=1}^R w_i I_j g_i \hat{\beta}_{j,i}}{\sum_{i=1}^R w_i I_j g_i} \quad (2)$$

where $I_j(g_i) = 1$ if the predictor variable x_j is in model g_i and 0 otherwise, w_i is the Akaike weight of the model and $\hat{\beta}_{j,i}$ is the estimate for parameter j in model i (Burnham and Anderson, 2002). After model averaging, we calculated Wald's 95% confidence limits for each of the parameters to determine which parameters had substantial influences on the number of species showing evidence of reproduction in a wetland. We did not consider parameters influential if they had

95% confidence intervals that included 0. Finally, to examine the effects of the parameters in the model-averaged model, we plotted the fitted relationship of each parameter, while keeping the other parameters constant at their mean values.

RESULTS

Adult amphibians

We captured 13 adult amphibian species around wetland perimeters from 1996 to 1998: Northern cricket frog (*Acris crepitans*), small-mouthed salamander (*Ambystoma texanum*), tiger salamander (*Ambystoma tigrinum*), Eastern American toad (*Anaxyrus americanus americanus*), Great Plains toad (*Anaxyrus cognatus*), Woodhouse's toad (*Anaxyrus woodhousii woodhousii*), grey tree frog (*Hyla chrysoscelis*–*Hyla versicolor* complex), spring peeper (*Pseudacris crucifer*), boreal chorus frog (*Pseudacris maculata*), Plains leopard frog (*Lithobates blairi*), bullfrog (*Lithobates catesbeiana*), Southern leopard frog (*Lithobates sphenoccephalus*) and Plains spadefoot (*Spea bombifrons*). *A. tigrinum* was only captured once in one wetland (existing temporary); therefore, we did not evaluate this species any further.

Detection probability. The most supported detection probability models for adult amphibian species were year and species dependent (Table II). Many of the most supported models for individual amphibian species suggested that detection probability was influenced by date or wetland type. The existing versus flood-created parameter influenced the probability of detecting seven species between 1996 and 1998 (Table II). Existing wetlands had a negative influence on detection probability for three species [*A. crepitans* (1996), *A. woodhousii woodhousii* (1997–1998) and *L. blairi* (1996)] and a positive influence for the remaining four species [*L. catesbeiana* (1998), *L. sphenoccephalus* (1997), *H. chrysoscelis*–*H. versicolor* complex (1998) and *P. maculata* (1997)]. The temporary versus permanent parameter influenced the probability of detecting five species during the 3-year study (Table II). Temporary wetlands had a positive influence on detecting three species [*P. crucifer* (1998), *P. maculata* (1998) and *L. blairi* (1998)] and a negative influence on detecting two species [*A. texanum* (1996) and *L. catesbeiana* (1997)]. Date had a quadratic influence on detecting three species [*A. woodhousii woodhousii* (1996–1997), *P. crucifer* (1998) and *P. maculata* (1996–1998)] and a positive influence on detecting four species [*A. crepitans* (1996), *A. americanus americanus* (1997), *A. woodhousii woodhousii* (1998) and *H. chrysoscelis*–*H. versicolor* complex (1997)] (Table II). The only species whose detection was not influenced by any parameters, any year of the study, were *A. cognatus* and *S. bombifrons* (Table II).

Detection probability estimates were low (Table III) and fairly constant across years for all species (Figure 2). The

Table II. Most supported occupancy (Ψ) and detection probability (p) models for 12 adult amphibian species in the Missouri River alluvial valley from 1996 to 1998

Species	Season		
	1996	1997	1998
ACCR	$\Psi(.)$ $p(\text{existing wetland}^a + \mathbf{T_date}^a)$	$\Psi(.)$ $p(.)$	$\Psi(.)$ $p(.)$
AMTE	$\Psi(.)$ $p(\text{temporary wetland}^a + \mathbf{T_date})$	$\Psi(.)$ $p(\text{existing wetland} + \mathbf{T_date})$	$\Psi(\text{temporary wetland})$ $p(\mathbf{L_date})$
ANAM	$\Psi(--)$ $p(\mathbf{L_date})$	$\Psi(.)$ $p(\mathbf{L_date}^a)^b$	$\Psi(.)$ $p(.)$
ANCO	$\Psi(--)$ $p(.)$	$\Psi(--)$ $p(.)$	$\Psi(--)$ $p(.)$
ANWO	$\Psi(--)$ $p(\text{existing wetland} + \mathbf{Q_date}^a)$	$\Psi(.)$ $p(\text{existing wetland}^a + \mathbf{Q_date}^a)^b$	$\Psi(.)$ $p(\text{existing wetland}^a + \mathbf{T_date}^a)^b$
HYCH	$\Psi(\text{existing wetland} + \mathbf{E_distance to river})$ $p(\text{temporary wetland})$	$\Psi(\text{temporary wetland} + \mathbf{T_distance to river})$ $p(\mathbf{L_date}^a)$	$\Psi(.)$ $p(\text{existing wetland}^a)$
PSCR	No data –	$\Psi(\mathbf{E_hydroperiod})$ $p(.)$	$\Psi(\mathbf{T_hydroperiod})$ $p(\text{temporary wetland}^a + \mathbf{Q_date}^a)$
PSMA	$\Psi(\text{existing wetland})$ $p(\text{existing wetland} + \mathbf{Q_date}^a)$	$\Psi(.)$ $p(\text{existing wetland}^a + \mathbf{Q_date}^a)^b$	$\Psi(\mathbf{L_distance to river})$ $p(\text{temporary wetland}^a + \mathbf{Q_date}^a)$
LIBL	$\Psi(\mathbf{T_hydroperiod})$ $p(\text{existing wetland}^a + \mathbf{L_date})$	$\Psi(.)$ $p(\text{existing wetland})^b$	$\Psi(.)$ $p(\text{temporary wetland}^a)$
LICA	$\Psi(\mathbf{E_distance to river})$ $p(\text{temporary wetland})$	$\Psi(\mathbf{T_distance to river})$ $p(\text{temporary wetland}^a + \mathbf{E_date})$	$\Psi(\mathbf{T_hydroperiod}^a)$ $p(\text{existing wetland}^a)$
LISP	$\Psi(.)$ $p(\text{temporary wetland} + \mathbf{Q_date})^b$	$\Psi(.)$ $p(\text{existing wetland}^a)$	$\Psi(\mathbf{Q_hydroperiod})$ $p(.)$
SPBO	$\Psi(--)$ $p(.)$	$\Psi(.)$ $p(.)$	$\Psi(.)$ $p(.)$

Dots (.) represent a constant occupancy or detection probability model, whereas dashes (–) represent models where occupancy or detection probability estimates could not be calculated. Each continuous occupancy and detection probability parameter included in the models are in their most supported structural form [linear ($\mathbf{L_}$), quadratic ($\mathbf{Q_}$), asymptotic ($\mathbf{T_}$), exponential ($\mathbf{E_}$)], determined from single-parameter information-theoretic analyses.

ACCR, *Acris crepitans*; AMTE, *Ambystoma texanum*; ANAM, *Anaxyrus americanus americanus*; ANCO, *Anaxyrus cognatus*; ANWO, *Anaxyrus woodhousii woodhousii*; HYCH, *Hyla chrysoscelis–Hyla versicolor* complex; PSMA, *Pseudacris maculata*; PSCR, *Pseudacris crucifer*; LIBL, *Lithobates blairi*; LICA, *Lithobates catesbeiana*; LISP, *Lithobates sphenoccephalus*; SPBO, *Spea bombifrons*.

^aOccupancy or detection probability parameters that had 95% odds ratio confidence intervals that did not eclipse 1.

^bYears when \hat{c} for the global model was >1.

most easily detected species was *A. woodhousii woodhousii* with an average detection probability across years of $\bar{p} = 0.280$, $SE = 0.014$. The most difficult species to detect was *A. cognatus* with an average detection probability across years of $\bar{p} = 0.013$, $SE = 0.009$. Species in the family Hylidae (*A. crepitans*, *H. chrysoscelis–H. versicolor* complex, *P. crucifer* and *P. maculata*) had the highest probability of being detected with an average detection probability of $\bar{p} = 0.165$, $SE = 0.012$. Species in the family Bufonidae (*A. americanus americanus*, *A. cognatus* and *A. woodhousii woodhousii*) and Ranidae (*L. blairi*, *L. catesbeiana* and *L. sphenoccephalus*) had similar average detection probabilities of $\bar{p} = 0.124$, $SE = 0.007$ and $\bar{p} = 0.125$, $SE = 0.008$, respectively. The average detection probability across all species, all years, was $\bar{p} = 0.125$, $SE = 0.005$.

Occupancy probability. The most supported occupancy models for adult amphibian species were also year and

species dependent (Table II). Only one species had occupancy parameters included in the most supported model with 95% odds ratio confidence intervals that did not include 1. The occupancy probability of *L. catesbeiana* was influenced by hydroperiod in a positive pseudothreshold form in 1998 (Table II).

Estimated occupancy probabilities of adult amphibian species differed by year. Average occupancy probabilities across all species increased from 1996 to 1997, reached a peak in 1997 and declined slightly into 1998 (Figure 2). Individually, seven species exhibited a peak in estimated occupancy probabilities in 1997 (*A. crepitans*, *A. texanum*, *A. americanus americanus*, *A. woodhousii woodhousii*, *P. maculata*, *L. blairi* and *L. catesbeiana*), three species exhibited an increase in occupancy probability across years (*H. chrysoscelis–H. versicolor* complex, *P. crucifer* and *S. bombifrons*) and one species showed a decrease in estimated occupancy probability across years (*L. sphenoccephalus*) (Table III). Only naïve estimates of occupancy could be

Table III. Occupancy (Ψ) and detection probability (p) estimates and associated standard errors (SE) for 12 adult amphibian species in the Missouri River alluvial valley from 1996 to 1998

Species	Season			
	1996	1997	1998	Average ^a
ACCR [Ψ (SE)]	0.519 (0.139)	0.848 (0.121)	0.400 (0.107)	0.589 (0.071)
ACCR [p (SE)]	0.081 (0.023)	0.098 (0.018)	0.120 (0.025)	0.100 (0.013)
AMTE [Ψ (SE)]	0.260 (0.122)	0.593 (0.206)	0.250 (0.106)	0.368 (0.087)
AMTE [p (SE)]	0.107 (0.041)	0.087 (0.029)	0.079 (0.031)	0.091 (0.020)
ANAM [Ψ (SE)]	0.500 ^b	0.930 (0.112)	0.389 (0.170)	0.606 (0.102)
ANAM [p (SE)]	0.073 (0.0161)	0.102 (0.019)	0.058 (0.026)	0.078 (0.012)
ANCO [Ψ (SE)]	0.125 ^b	0.083 ^b	0.167 ^b	0.127 (0.026)
ANCO [p (SE)]	0.020 (0.011)	0.0084 (0.006)	0.012 (0.024)	0.013 (0.009)
ANWO [Ψ (SE)]	0.792 ^b	0.896 (0.069)	0.839 (0.077)	0.842 (0.052)
ANWO [p (SE)]	0.353 (0.031)	0.193 (0.020)	0.294 (0.023)	0.280 (0.014)
HYCH [Ψ (SE)]	0.446 (0.172)	0.638 (0.125)	0.800 (0.143)	0.628 (0.085)
HYCH [p (SE)]	0.119 (0.035)	0.130 (0.024)	0.094 (0.022)	0.114 (0.016)
PSCR [Ψ (SE)]	0.000 ^b	0.158 (0.088)	0.255 (0.124)	0.138 (0.076)
PSCR [p (SE)]	No data	0.113 (0.044)	0.290 (0.075)	0.201 (0.043)
PSMA [Ψ (SE)]	0.862 (0.130)	0.956 (0.049)	0.869 (0.104)	0.896 (0.058)
PSMA [p (SE)]	0.150 (0.021)	0.348 (0.023)	0.235 (0.021)	0.244 (0.012)
LIBL [Ψ (SE)]	0.509 (0.111)	0.935 (0.057)	0.793 (0.100)	0.746 (0.053)
LIBL [p (SE)]	0.174 (0.026)	0.192 (0.019)	0.135 (0.019)	0.167 (0.012)
LICA [Ψ (SE)]	0.294 (0.139)	0.487 (0.154)	0.394 (0.123)	0.392 (0.080)
LICA [p (SE)]	0.087 (0.038)	0.120 (0.033)	0.142 (0.029)	0.116 (0.019)
LISP [Ψ (SE)]	0.945 (0.156)	0.628 (0.116)	0.352 (0.120)	0.642 (0.076)
LISP [p (SE)]	0.070 (0.016)	0.126 (0.023)	0.077 (0.025)	0.091 (0.012)
SPBO [Ψ (SE)]	0.083 ^b	0.175 (0.166)	0.371 (0.354)	0.209 (0.195)
SPBO [p (SE)]	0.013 (0.009)	0.055 (0.051)	0.022 (0.021)	0.03 (0.019)

ACCR, *Acris crepitans*; AMTE, *Ambystoma texanum*; ANAM, *Anaxyrus americanus americanus*; ANCO, *Anaxyrus cognatus*; ANWO, *Anaxyrus woodhousii woodhousii*; HYCH, *Hyla chrysoscelis*–*Hyla versicolor* complex; PSMA, *Pseudacris maculata*; PSCR, *Pseudacris crucifer*; LIBL, *Lithobates blairi*; LICA, *Lithobates catesbeiana*; LISP, *Lithobates spinocephalus*; SPBO, *Spea bombifrons*.

^aAverage occupancy or detection probability estimate across all years.

^bNaïve occupancy probability estimate.

calculated for *A. cognatus*; therefore, we did not make robust interpretations of this trend. The species with the highest occupancy probability was *P. maculata* with an average probability across years of $\bar{\Psi} = 0.896$, $SE = 0.058$. The species with the lowest estimated occupancy probability was *A. cognatus* with an average naïve occupancy probability across years of $\bar{\Psi} = 0.127$, $SE = 0.026$ (Table III). Occupancy probabilities for the family Hylidae, Bufonidae and Ranidae were all similar, with estimates of $\bar{\Psi} = 0.562$, $SE = 0.037$; $\bar{\Psi} = 0.525$, $SE = 0.038$; and $\bar{\Psi} = 0.593$, $SE = 0.041$, respectively.

Juvenile/larval amphibians

We captured 13 species of either juvenile or larval amphibians within the 24 wetlands we surveyed between 1996 and 1998. Twelve of these species were the same as the adult species we captured, whereas one species, Eastern narrow-mouthed toad (*Gastrophryne carolinensis*), was new. The number of amphibian species displaying evidence of reproduction varied across years with nearly twice the

number of amphibians/wetland showing evidence of reproduction in 1997 (2.29) and 1998 (2.33) than in 1996 (1.21). Existing wetlands averaged 4.81 amphibian species showing evidence of reproduction per wetland, whereas flood-created wetlands only averaged 2.50. Also, temporary wetlands had an average of 5.08 amphibian species displaying evidence of reproduction per wetland, whereas permanent wetlands only averaged 3.00. The most supported model from our model selection procedures corroborated our raw data, indicating that the type of wetland had the highest influence on the number of species exhibiting evidence of reproduction (Table IV). Our model predicted that existing wetlands had almost double the estimated number of amphibian species reproducing than flood-created wetlands, and temporary wetlands had approximately 1.7 times more species reproducing than permanent wetlands (Figure 3).

There was some model uncertainty among our candidate model set. The hydroperiod and distance to river models were both within the 90% Akaike weight confidence set (Table IV). Hydroperiod had a quadratic relationship with

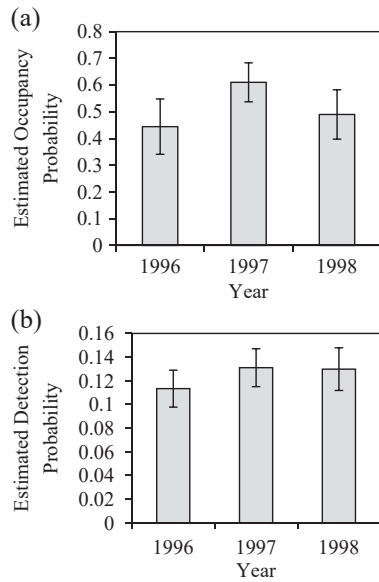


Figure 2. Estimates of average occupancy (a) and detection probability (b) across 12 species of amphibians captured from 1996 through 1998 in the Missouri River alluvial valley. Error bars represent the upper and lower 95% confidence limits.

the number of species showing evidence of reproduction, peaking between 135 and 140 days (Figure 3). Distance to river had a positive asymptotic relationship with the number of species exhibiting reproduction, meaning there was a positive relationship between the distance to river and the number of species reproducing until a threshold was reached (approximately 3 km) and the relationship began to level off (Figure 3). However, the distance to river relationship was less important because Wald's 95% confidence intervals included 0.

DISCUSSION

The occupancy probabilities of adult amphibians in the Missouri River alluvial valley between 1996 and 1998 were relatively high but were not strongly influenced by wetland characteristics. Only three species (*A. cognatus*, *P. crucifer* and *S. bombifrons*) had average occupancy probability estimates across years of less than 25%, and none of the species with low occupancy probability estimates were in decline, suggesting that their risk of extirpation was low. These results, and the lack of evidence for any wetland selection preference by adults, imply that amphibians might be opportunistic as adults in this region. Few studies have demonstrated that adult amphibians are opportunistic in regard to wetland selection after flood events. Maltchik *et al.* (2008) found that amphibians in Brazil were homogeneously distributed throughout the floodplain after flood events, which implies that there was no apparent selection between

existing and flood-created wetlands within the floodplain. Conversely, other studies observed that wetland characteristics, such as size (Petranka *et al.*, 2003), connectivity (Cunningham *et al.*, 2007) and adjacent terrestrial vegetative attributes (Baldwin *et al.*, 2006), influenced amphibian distribution and richness. Because of our limited data, we were not able to model similar variables, so we cannot conclude whether these variables affected the probability of adult amphibian occupancy in the alluvial valley. Even though only one species displayed a significant relationship between wetland characteristics and occupancy in the alluvial valley, many of the most supported occupancy models from our analysis showed that some wetland characteristics might have impacts on amphibian occupancy.

Occupancy probabilities of adult amphibians were not affected by wetland characteristics within seasons in the Missouri River alluvial valley; however, occupancy probabilities fluctuated from year to year, suggesting that annual changes in weather patterns might impact the probability of adult amphibians occupying wetlands. Occupancy probability estimates for the majority of adult amphibian species either increased continuously from 1996 through 1998 or increased from 1996 to 1997 and then declined slightly into 1998. Annual differences in weather patterns could cause this trend because variation in the amount and timing of precipitation can influence the presence and ability of adult amphibians to produce metamorphs (Pechmann *et al.*, 1991; Semlitsch *et al.*, 1996; Semlitsch, 2000). Between February and March, the amount of precipitation in Booneville, Missouri, was 4.1 cm lower than the normal precipitation of 12.2 cm (calculated as the prevailing amount of precipitation over the previous 30 years) in 1996 (NOAA, 1996) but 6.9 and 14.2 cm higher than normal in 1997 and 1998, respectively (NOAA, 1997, 1998). Furthermore, only 65% of basins in the alluvial valley contained water by 1 March 1996, whereas 92% contained water by 1 March 1997 and 1998 (R. B. Renken, Missouri Department of Conservation, Columbia, Missouri, pers. comm.). February and March are the months when many amphibian species begin breeding (Johnson, 2000). Thus, the amount of precipitation and proportion of wetlands containing water during these months likely led to the differences in adult amphibian occupancy probabilities during our study. Additionally, the timing of precipitation in February and March might have caused the decline in amphibian occupancy probabilities from 1997 to 1998. Large movements of amphibians in Maine (Vasconcelos and Calhoun, 2004) and Massachusetts (Timm *et al.*, 2007) were, in part, triggered by precipitation events. In 1997, periods of heavy precipitation occurred in the middle of February in the Missouri River alluvial valley, whereas heavy precipitation did not occur until late March in 1998 (USGS, 2009). The earlier influx of precipitation in 1997 might have caused more amphibians to immigrate into wetlands in the alluvial basin,

Table IV. Model selection results for estimating the number of amphibians showing evidence of reproduction in the Missouri River alluvial valley between 1996 and 1998

Model	<i>K</i>	-2 log likelihood	<i>QAIC_c</i>	$\Delta QAIC_c$	Weight
Existing wetland	2	99.988	90.768	0.000	0.420
Temporary wetland	2	101.139	91.760	0.992	0.256
Q _Hydroperiod	3	99.434	92.919	2.151	0.143
T _Distance to river	2	103.720	93.985	3.217	0.084
Constant	1	107.656	94.988	4.220	0.051
Global	5	94.952	95.189	4.421	0.046

Hydroperiod and distance to river are modelled in their most supported structural forms, quadratic (**Q**) and asymptotic (**T**), respectively. *K* represents the number of parameters in the model, *QAIC_c* represents Akaike’s information criterion adjusted for small sample size and overdispersed count data, $\Delta QAIC_c$ is the difference in *QAIC_c* value from the top model, and weight is the Akaike weight of the model.

which would explain why occupancy probabilities for some species were higher during that year.

Evaluating the diversity and propagation of amphibian species in the Missouri River alluvial valley is an important complement to adult occupancy probability estimation because amphibian larvae are more sensitive to wetland conditions than adults. Further, amphibian success at the population level is determined by larvae metamorphosing, leaving the wetland and becoming part of the adult population (Semlitsch, 2005). In the Missouri River alluvial valley, the type of wetland and hydroperiod of wetlands affected the number of amphibian species reproducing. Predatory fish and other invertebrates are more likely to be present in permanent wetlands and wetlands that are often inundated by flooding (Semlitsch, 2000). This heightened

risk of predation could be a reason why existing wetlands and temporary wetlands had almost double the number of amphibian species showing evidence of reproduction compared with flood-created and permanent wetlands. Amphibian larvae are also susceptible to desiccation if wetlands dry too early. Wetlands with hydroperiods that are too short are insufficient because the larvae do not have enough time to metamorphose, whereas wetlands with hydroperiods that are too long are more likely to harbour predatory fish and invertebrates (Duellman and Trueb, 1986; Semlitsch, 2000). It is for these reasons that we believe we observed the highest number of species showing evidence of reproduction in wetlands with spring–summer hydroperiod lengths of 135–140 days and in years where there were large amounts of precipitation in February and

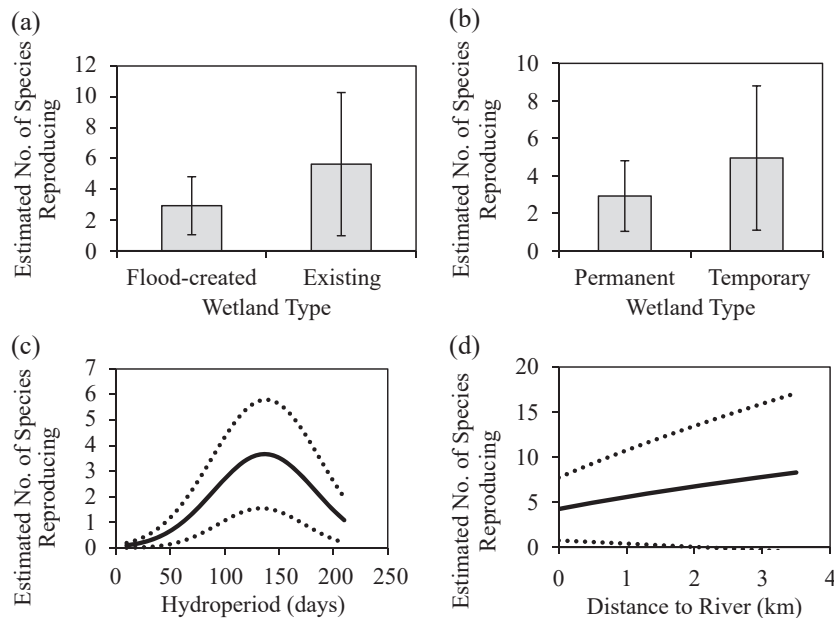


Figure 3. Influence of existing and flood-created wetlands (a), temporary and permanent wetlands (b), hydroperiod (c) and distance to the Missouri river (d) on the estimated number of amphibian species exhibiting evidence of reproduction in the Missouri River alluvial valley between 1996 and 1998. Dashed lines and error bars represent the upper and lower 95% confidence limits.

March. Our results suggest that, although the occupancy probability of adult amphibians might not be influenced by wetland characteristics, more species of amphibians are reproductively successful under specific wetlands conditions. Semlitsch (2000) provides a number of ways to manage for amphibians, which include maintaining wetlands with a diverse array of hydroperiods, protection of wetlands from invasion by fish predators, protection of terrestrial buffer zones and others. Managers should consider our results and these suggestions when managing wetlands and river flow in the alluvial valley.

The probability of detecting amphibian species in the Missouri River alluvial valley was quite low, which demonstrates the importance of accounting for imperfect detection when estimating occupancy probabilities. Accounting for imperfect detection when monitoring a species is essential for obtaining accurate occupancy probability estimates, especially when the species is cryptic or logistic issues prevent the investigator from sampling the entire site (MacKenzie *et al.*, 2002; Bailey *et al.*, 2004). Many of the amphibian species we observed had cryptic behaviours. For instance, *S. bombifrons* buries itself underground and comes out to breed only after warm rains. It breeds, lays eggs and then leaves the wetland, all within a few days (Johnson, 2000). As a result, this species was very difficult to capture, which explains why its detection probability was so low. Overall, the detection probabilities for most of the amphibian species we surveyed were lower than those documented in other occupancy studies on amphibians (e.g. Bailey *et al.*, 2004; Muths *et al.*, 2005). Detection probabilities were likely lower because we only used one survey method: drift fences with funnel traps. Mitchell *et al.* (1993) found that drift fences with pitfall traps (Gibbons and Semlitsch, 1982) were the most effective method to capture a variety of amphibian species; however, because amphibians have a wide variety of sizes and behaviours, they found that multiple capture methods should be employed. Another cause for the low detection probabilities we observed was our trapping capabilities. Drift fences were not large enough to completely encircle wetlands. Therefore, wide gaps were present for amphibian species to pass through undetected. Even though detection probabilities were low for most of the amphibian species we captured, we still had a high probability of detecting most species at least once throughout the sampling season because we completed up to 25 surveys for each site. The average probability of detecting an amphibian species during one survey at a wetland was 12.5%, but the probability of detecting the species at least once during the 25 surveys was 96.4%. MacKenzie *et al.* (2006) suggested surveying sites until the probability of detecting the species at least once during the season is above 85%. Because we reached this benchmark, we have confidence that we effectively surveyed the wetlands in the alluvial valley.

To further study occupancy probability trends for amphibians in the Missouri River alluvial valley, one should set management objectives that address the trade-off between the number of sites surveyed and the number of repeat surveys at each site. Capture and survey methods that maximize amphibian detection probabilities should be employed, which will optimize efficiency and productivity when monitoring. In general, we believe that drift fences and funnel traps were an effective trapping method. However, we agree with Mitchell *et al.* (1993) that multiple capture methods should be utilized in the future to increase the probability of detecting a variety of different amphibian species, given the variable influence of spatial and temporal factors on detection probability. Using the average detection probability across species and year from our study, we found that at least 15 surveys should be completed at each site in the future to reach the benchmark described by MacKenzie *et al.* (2006). However, if detection probabilities are increased for amphibian species, then fewer surveys will be necessary to reach this benchmark, which will allow managers to allocate more effort towards sampling a greater number of sites. Sampling more sites will increase the precision of occupancy estimates and will provide more inference on the factors influencing amphibian occupancy in the Missouri River alluvial valley.

Since the 1993 flood, there has been a great deal of discussion about restoring sections of the Missouri River alluvial valley and the river's hydrograph to a more natural condition to benefit fish and wildlife resources of the Missouri River basin (Galat *et al.*, 1996, 1998). However, conflicts arise when discussing amphibian breeding habitat needs and the habitat needs of native riverine fish, such as *Ictiobus* spp. and *Hiodon alosoides*, which would benefit from reconnecting the river and floodplain. Given our results, if the Missouri River was allowed to reconnect with the floodplain on a one-in-two-year or one-in-three-year basis and the river's hydrograph was allowed to fluctuate at levels and around dates resembling historical conditions, it would appear that the amphibian community might be greatly impacted because of the consistent invasion of predatory fishes in permanent wetlands. However, we suggest that the restoration of the historical hydrograph and reconnection of the river and alluvial valley would not adversely impact amphibian reproductive efforts because the historical flooding probably did not always cover the entire alluvial valley, just as the Great Flood of 1993 did not cover the entire alluvial valley (SAST, 1994). In large river systems, floods that cover distant terraces occur once in several decades (Poff *et al.*, 1997). Thus, fishless temporary wetlands and wetlands with a variety of hydroperiods will be annually available to breeding amphibians somewhere in the alluvial valley, given sufficient precipitation during February and March. As a result, we believe there will be adequate wetlands available

for a diversity of breeding amphibians in the alluvial valley if the river is once again allowed to reconnect with the floodplain and rise to magnitudes and durations resembling historical peaks.

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