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Variation in metapopulation dynamics of a wetland mammal: The effect of hydrology

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Abstract. Key factors affecting metapopulation dynamics of animals include patch size, isolation, and patch quality. For wetland-associated species, hydrology can affect patch availability, connectivity, and potentially habitat quality; and therefore drive metapopulation dynamics. Wetlands occurring on natural river floodplains typically have more dynamic hydrology than anthropogenic wetlands. Our overall objective was to assess the multiyear spatial and temporal variation in occupancy and turnover rates of a semi-aquatic small mammal at two hydrologically distinct wetland complexes. We live-trapped marsh rice rats (*Oryzomys palustris*) for 3 yr and >50 000 trap nights at nine wetland patches on the Mississippi River floodplain and 14 patches at a reclaimed surface mine in southern Illinois. We used dynamic occupancy modeling to estimate initial occupancy, detection, colonization, and extinction rates at each complex. Catch per unit effort (rice rats captured/1000 trap nights) was markedly higher at the floodplain site (28.1) than the mining site (8.1). We found no evidence that temperature, rainfall, or trapping effort affected detection probability. Probability of initial occupancy was similar between sites and positively related to patch size. Patch colonization probability at both sites was related negatively to total rainfall 3 weeks prior to trapping, and varied across years differently at each site. We found interacting effects of site and rainfall on extinction probability: extinction increased with total rainfall 3 months prior to trapping but markedly more at the floodplain site than at the mining site. These site-specific patterns of colonization and extinction are consistent with the rice rat metapopulation in the floodplain exhibiting a habitat-tracking dynamic (occupancy dynamics driven by fluctuating quality), whereas the mineland complex behaved more as a classic metapopulation (stochastic colonization & extinction). Our study supports previous work demonstrating metapopulation dynamics in wetland systems being driven by changes in patch quality (via hydrology) rather than solely area and isolation.

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INTRODUCTION

A metapopulation is the term used to describe "a population of populations which go extinct locally and recolonize" (Levins 1970). Metapopulation ecology is concerned with the movement of animals between areas of discrete patches of suitable habitat that are large enough to support breeding populations and are surrounded by areas of unsuitable habitat or matrix (Hanski 1999). Classical metapopulations are represented by patches of equal size and strictly stochastic

extinction and colonization (Levins 1970). This framework has been expanded to include the influence of patch size, quality, and degree of isolation on colonization and extinction rates, but the actual colonization and extinction events are considered stochastic (Hanski 1998, Moilanen 1999). If suitability varies asynchronously among patches over time, however, then extinction and colonization events may actually represent habitat tracking: largely deterministic responses to a "shifting spatial mosaic of suitable environmental conditions" (Thomas 1994). Studies of key factors influencing metapopulation dynamics have focused on patch size and isolation. However, variation in patch quality also can influence these dynamics (Franken and Hik 2004, Schooley and Branch 2009, 2011). Ranius (2007) showed that incorporating temporally varying habitat quality could increase extinction risk in metapopulation models, leading to habitat tracking patterns instead of classic metapopulations. Habitat tracking patterns are seen when populations have a relatively low risk of stochastic extinction (i.e., as a result of demographic or environmental stochasticity) over the time scale over which habitat patches deteriorate or completely disappear. Hence, turnover rates and patterns should be markedly different between metapopulations that behave "classically" (Hanski 1998) and those characterized by "habitat tracking" (Thomas 1994).

Palustrine wetlands located on floodplains of major rivers are highly dynamic systems that can support unique faunal and floral assemblages of high species diversity and richness (Benke 2001). Flood regimes of rivers are important to many wetland organisms, which are adapted to extremes of inundation and drying (Junk and Wantzen 2006). These wetlands change seasonally and annually (Gosselink and Maltby 1990), with ephemeral wetlands forming in flood years and some wetlands drying up in drought years. They also vary in expanse and nutrient retention throughout the year (Fink and Mitsch 2007). Because of these spatio-temporal changes, patches can fluctuate between unsuitable and suitable habitat over the short and long-term for wetland-associated species, affecting patch availability and quality and, therefore, occupancy (Marsh and Trenham 2001, Fortuna et al. 2006, Roe and Georges 2008,

Cosentino et al. 2010). For example, deeper and more permanent water reduced occurrence and densities of many frog species (Van Buskirk 2005), whereas the probability of occurrence of mole salamanders (*Ambystoma talpoideum*) decreased with a decrease in rainfall), in part because breeding sites dried prematurely (Walls et al. 2013.

Many wetland-associated vertebrates persist in metapopulations because wetlands are often fragmented naturally or because of urban development, agricultural conversion, and mining activities (Gosselink and Maltby 1990, Batzer and Sharitz 2006). Examples include pond-breeding amphibians (Gibbs 1993, Alford and Richards 1999, but see Smith and Green 2005, Purrenhage et al. 2009) and small mammals living in patchy wetland environments (Lima et al. 1996), including round-tailed muskrats (*Neofiber alleni;* Schooley and Branch 2009), water voles (*Arvicola* spp.; Fedriani et al. 2002), and marsh rice rats (*Oryzomys palustris;* Forys and Dueser 1993, Kruchek 2004). The composition of the matrix is crucial in determining how successfully these species move between isolated wetlands (Baum et al. 2004, Haynes and Cronin 2004, Cooney et al. 2015*a*). During extreme flood events in river floodplains, local populations will be cut off from each other by large expanses of water. Local extinctions can occur, or displacement by floodwaters might force members of multiple populations together on dry ground. Conversely, palustrine wetlands associated with mining (Nawrot and Klimstra 1989) and other anthropogenic activities are likely to be more stable in number and expanse, but could have lower nutrient levels than wetlands associated with floodplains (Stolt et al. 2000). These stable wetland sites should still allow for movements among local populations (Forys and Dueser 1993), with the matrix less likely to become completely inundated during flood events than is the case with floodplain systems.

Marsh rice rats occurring in wetland complexes serve as a useful model species thought to persist in metapopulations (Kruchek 2004). They occupy fresh- and saltwater wetlands (Hamilton 1946, Wolfe 1982, Hofmann et al. 1990), as well as adjacent upland areas in the southeastern United States (Kruchek 2004). Their abilities to cross more than 300 m of water (Smith and

Vrieze 1979, Forys and Dueser 1993) and to move ~400 m daily (Cooney et al. 2015*b*) increase their dispersal potential, which in turn increases gene flow among distinct populations (Loxterman et al. 1998). Rice rats alter their movement in response to water fluctuations, including dispersal in search of water during dry seasons (Smith and Vrieze 1979) and the use of upland areas during floods (Kruchek 2004). However, little is known about their response to prolonged inundation (Abuzeineh et al. 2007) or drought conditions, or their consequent ability to colonize unoccupied habitat patches.

Our overall goal was to investigate the role of hydrology in metapopulation dynamics in a key wetland mammal. We studied metapopulation dynamics of rice rats at two hydrologically distinct wetland complexes (mineland and floodplain) over 3 yr to meet two objectives: (1) determine important landscape covariates influencing rice rat occupancy of patches within each wetland system, and (2) quantitate spatial and temporal variation in extinction and colonization rates of rice rats among local populations at these wetland complexes. We expected the metapopulation structure and dynamics of rice rats to be shaped by the hydrology of the system in which they occurred, specifically predicting lower turnover of patch occupancy (i.e., lower and less variable colonization and extinction rates) in mineland areas where hydrology is more stable. We expected that matrix composition surrounding wetland patches, inter-patch distance, and dominant vegetation type might influence persistence of rice rats at a patch. In addition, we predicted that colonization and extinction rates of rice rats in floodplain areas would vary dramatically among seasons and over years in response to flood pulses of the river, whereas these rates at mining-associated wetlands should remain more stable. For example, colonization rates of rice rats might be higher in riverine floodplain wetlands during periods between flood events, when there is enough dry land to facilitate movement among multiple wetland patches.

Methods

Study area

We trapped marsh rice rats at two wetland complexes (hereafter referred to as "sites") in

southern Illinois: a reclaimed surface mine located in Jackson County and a wetland complex located in the floodplain of the Mississippi River in Alexander County (Fig. 1). The reclaimed mining site was at Illinois Department of Natural Resources CONSOL Energy – Burning Star 5 Wildlife area (37°52′32.95″ N; 89°12′30.47″ W). Mining occurred here mostly after 1978, when reclamation of at least part of the mined areas became required by federal law. The mining site covered approximately 3400 ha, which included approximately 1600 ha of cropland, 800 ha of forest, 400 ha of grassland, and 560 ha of lakes and wetlands. Common trees included oaks (*Quercus* spp.), maples (*Acer* spp.), and hickories (*Carya* spp.); and grassland included cattails (*Typha* spp.), common reed (*Phragmites* spp.), tall fescue (*Festuca* spp.), switchgrass (*Panicum virgatum*), and big bluestem (*Andropogon gerardii*). Corn (*Zea mays)*, soybeans (*Glycine* max), sorghum (*Sorghum* spp.), and wheat (*Triticum* spp.) made up the most common crop species. Six percent of the total area (204 ha) was composed of deep and shallow water impoundments or wetlands (Delahunt 2011). Most impoundments and wetlands were surrounded by dense stands of common reed and cattails. Although the mining site is located in the Big Muddy River watershed, few of the wetlands are natural and most water bodies are permanent. Average annual precipitation for this region is 1160 mm, with a third of precipitation concentrated in spring. Average minimum winter temperature is −3.5°C and average maximum summer temperature is 31°C (www.stateclimate.org, 2014). At the mining site, we chose to sample 14 of 21 available wetlands. We selected wetlands to encompass a range of least ephemeral to most ephemeral water bodies.

The floodplain site was at the Middle Mississippi River Wetland Field Station. This 560-ha site was managed by Southern Illinois University Carbondale (SIUC) and located on the eastern side of the Mississippi River, 4 km ESE of Cape Girardeau, Missouri (37°17′2.08″ N; 89°28′6.37″ W), 66 km SW of the mining site. It consisted of various managed natural wetlands in the Mississippi River floodplain within Cape Bend State Fish and Wildlife Area. Because this wetland complex was located on the Mississippi River floodplain,
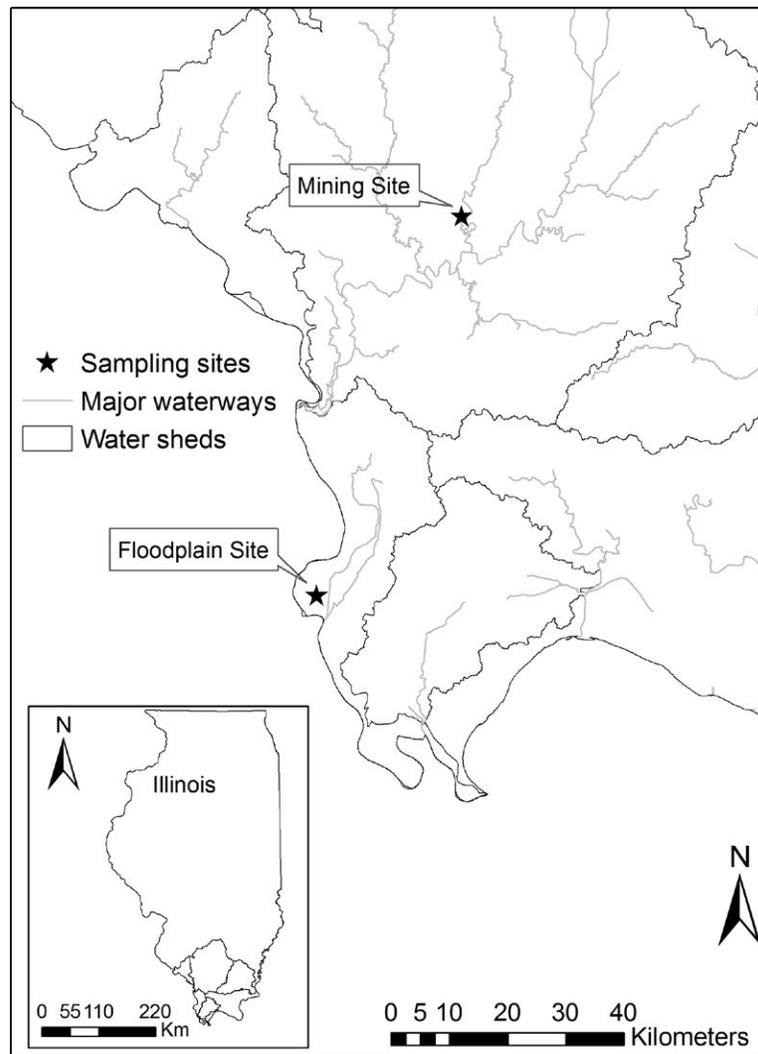
Fig. 1. Location of two sampling sites (floodplain site and mining site) in southern Illinois, 2011–2013.

occasional inundation occurred and the hydrology of the associated wetlands was driven by the flood pulses of the river. Grass species composition was similar to the mining site, but one major difference between the two sites was that *Phragmites* and *Typha* spp. were not present at any of the floodplain wetland patches. Mean annual precipitation is 1100 mm, mean minimum winter temperature is −3°C, and mean maximum summer temperature is 31°C (www.stateclimate.org, 2014). We sampled all nine wetland patches (as defined by the National Wetlands Inventory; US Fish and Wildlife Service 2011) that were present in our floodplain study area.

Data collection and analysis
Trapping and handling

We deployed transects of 30–100 Sherman live traps (8 cm × 9 cm × 23 cm, H.B. Sherman Traps Inc., Tallahassee, Florida, USA) adjacent to water at nine wetland patches at the floodplain site and 14 wetland patches at the mining site. Nearest neighbor distances varied between 0.04 and 0.98 km at both sites, with an average inter-patch distance of 0.25 km at the mining site and 0.29 km at the floodplain site. The number of traps in each transect depended on wetland patch size. Traps were baited with bird seed and cotton balls were placed in each trap

during cold nights to provide nesting material. Traps were deployed for 3–4 consecutive nights at each wetland patch every 8 weeks during March–November 2011–2013, for a total of four trapping sessions per year (spring [mid-March to mid-May], early summer [mid-May to mid-July], late summer [mid-July to mid-September], and fall [mid-September to mid-November]). Due to logistical constraints, the mining site only had two trapping sessions during 2011 (late summer and fall). Unlike round-tailed muskrats that build noticeable lodges indicative of presence (Schooley and Branch 2009), rice rats on our sites did not build structures that are easy to detect visually.

Captured rice rats were anesthetized with Isoflurane to reduce stress on the animals during handling. Each animal was marked using passive integrated transponder (PIT) tags (Biomark, Boise, Idaho, USA) in the interscapular region. All individuals were scanned for PIT tag number, weighed, measured (as an estimate of age; Negus et al. 1961), fur-clipped, sexed, and released at the capture site. This work was done in accordance with stipulations set forth by the SIUC Institutional Animal Care and Use Committee (IACUC; Protocol 10-009).

Habitat and survey covariates

We measured landscape covariates to model occupancy probability. Using the 2006 National land cover layer in ArcMap 10.2 (ESRI, Redlands, California, USA), we calculated percentage of land cover (upland grass, agriculture, upland forest, emergent wetland vegetation, and developed area) contained within a 100-m buffer surrounding each patch by counting the number of 30- × 30-m pixels for each cover type present. This buffer distance is the approximate radius of circle of 3.5 ha, which is the estimate of home-range size (kernel estimator) for rice rats provided by Cooney et al. (2015*b*) for the mining site. In addition to the land cover variables, we included the area encompassed within the 100-m buffer around each patch to provide a surrogate for patch size of the wetland. Using aerial photos, we also calculated the distance to the nearest wetland (from water edge to water edge). To account for variation in hydrology among patches, each patch was ranked from most ephemeral (1) to most permanent (4). These ranks were based on observations made over a 3-yr period for each wetland patch. Finally, because rice rats occupy habitat that is dominated by dense emergent herbaceous vegetation such as common reed (*Phragmites australis*; Eubanks et al. 2011), cattails (*Typha* spp; Hofmann et al. 1990), and salt marsh grass (*Spartina alterniflora*; Hamilton 1946), we classified each patch based on the presence of *Phragmites* (none, 25%, 50%, and completely) and ranked each patch for the presence or absence of all other emergent macrophytes (excluding *Phragmites*).

Temporal covariates used as predictors in modeling colonization and extinction rates included year (2011, 2012, and 2013), session (spring, early summer, late summer, and fall), previous rainfall (short- and long-term), and Mississippi River stage. Because of temporal and spatial variation in size and depth of the wetland patches (depths ranging from 10 cm to 1.5 m), a small change in depth could have great effect on a shallow patch but little effect on a deeper patch. Therefore, we did not use water depth as a covariate. Instead, we used rainfall as a proxy for water depth, calculating total rainfall over 1 week, 3 weeks, 1 month, and 3 months before each trapping session (http://www.wunderground.com/history). Finally, we calculated the weekly average stage of the Mississippi River at Cape Girardeau directly adjacent to the floodplain site (http://www.waterwatch.usgs.gov).

Analysis

We used the occupancy modeling package "unmarked" (Fiske and Chandler 2011) in program R version 2.15.2 (R Development Core Team 2014), which accounts for imperfect detection (p), to develop dynamic occupancy models (MacKenzie et al. 2003). The purpose of this modeling was to assess if initial occupancy (Ψ) was influenced by patch-specific covariates and to assess how environmental factors influenced colonization (γ) and extinction (ε) probabilities. Each patch was classified based on whether rice rats were detected or not for each secondary sampling period (3–4 consecutive nights per trapping session) during each primary sampling period (4 trapping sessions/year).

Table 1. Summary statistics for rice rats captured during each year of trapping (2011–2013) at two sites in southern Illinois.

| | | | | | Capture success | |
Year	Site	No. trap nights	No. individual rice rats	% Males	Rice rats/1000 trap nights	SE
2011	Floodplain	6477	26	53	4.0	3.3
	Mining	3661	26	64	7.1	7.5
2012	Floodplain	11 101	363	65	32.7	8.6
	Mining	9865	120	50	12.2	5.3
2013	Floodplain	10 343	396	64	38.3	7.4
	Mining	10 343	47	67	4.5	5.3

We started the modeling process by finding the model that best described detection probability (p), by holding Ψ, γ, and ε constant. Potential effects on detection included minimum daily temperature and total daily rainfall (because cold or wet weather could influence whether an animal is moving around or not), as well as the amount of effort (number of traps set and available per night). We used Akaike's Information Criterion (AIC) to compare and rank candidate models (Anderson 2008), and used the most-supported model for detection as the basis for modeling initial occupancy, colonization and extinction. We created a set of 17 initial occupancy models. This model set consisted of single covariate models, additive and interactive models including dominant land cover types, patch size, nearest neighbor distances, presence of emergent vegetation, and ephemerality as covariates. The most-supported occupancy model was the basis for comparing 13 colonization and 13 extinction models using temporal covariates (session, year, rainfall, and river level). To investigate whether occupancy and turnover differed between the two wetland complexes, we included site as a factor in model sets for initial occupancy, colonization, and extinction. Covariates were tested for collinearity. If any covariates were found to be highly correlated ($|r| > 0.6$), one was dropped from the analyses.

We also developed a set of linear regression models to test whether trap success [rice rats captured/1000 trap nights (as a measure of relative abundance; Kelt 1996)] varied by site or year, or an interaction between site and year. These models also were assessed by using the model with the lowest AIC as the model that best described the data.

RESULTS

Site overview

We captured 785 individual rice rats in 27 921 trap nights (28.1 rice rats/1000 trap nights) on the floodplain during 12 trapping sessions at nine wetland patches. At the mining site, we captured 193 individual rice rats in 23 869 trap nights (8.1 rice rats/1000 trap nights) during 10 trapping sessions at 14 wetland patches. At both sites, males composed >50% of captured individuals (Table 1; Fig. 2). Both complexes experienced flood conditions in 2011 and severe drought in 2012, as did much of the Midwestern United States (Fig. 3). Rainfall was highest in 2011 at both sites, which together with snow melt in northern parts of the country led to flooding of the Mississippi River at Cape Girardeau and coupled inundation of the floodplain site. At least four wetland patches at each site dried up completely in 2012. The last year of trapping (2013) started with above-average rainfall, but ended with below-average (near-drought) conditions (Fig. 3). Over the 3-yr period we detected rice rats in 13 of 14 patches at the mining site and in all nine patches at the floodplain site. Recapture success was low at both sites. At the mining site, 18 rats were recaptured a second time in a different trapping sessions; whereas at the floodplain only eight rice rats were recaptured in a second session. The model that best described trap success (rice rats/1000 trap nights) included an interaction between year and site (Table 2). Trap success was similar at both sites in 2011, but success was greater at the floodplain than at the mining site during 2012 and 2013 (Table 1).
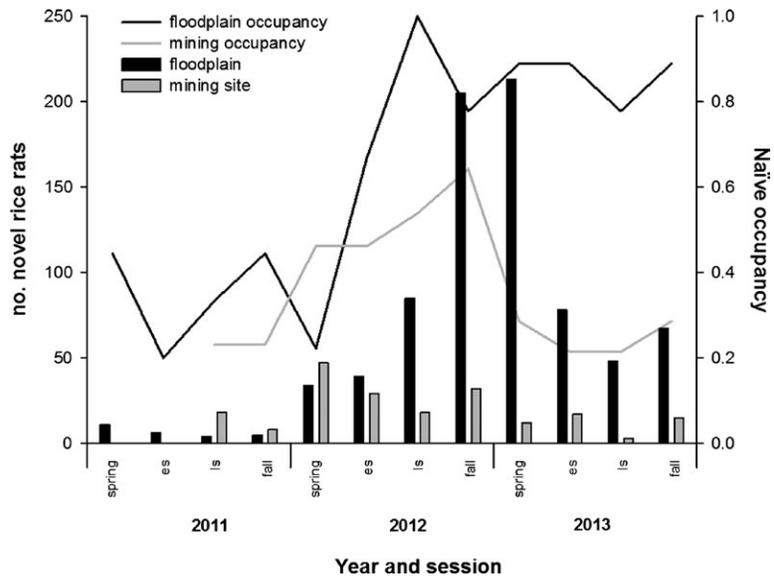
Fig. 2.   Total number of novel captures (bars) by season and naïve occupancy (lines) at floodplain and mining sites during 3 yr of sampling in southern Illinois. Each year had four trapping sessions 8 weeks apart: one trapping session in spring, one early summer session (es), one late summer session (ls) and, one session in fall.
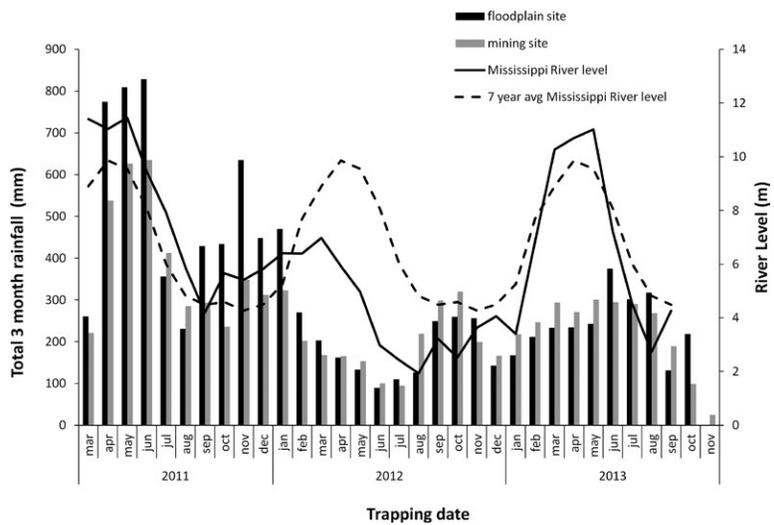

Fig. 3.   Graph of total precipitation for the 3-month period preceding each trapping session (left *y*-axis) and stage of Mississippi River at Cape Girardeau, Missouri (right *y*-axis) by trapping date, 2011–2013. The broken line (right *y*-axis) shows the average monthly river level for the Mississippi River over the past 7 yr.

Occupancy and seasonal turnover

The most supported model of detection probability was the null model, which indicates no compelling evidence that rain, temperature, or trapping effort influenced the detectability of rice rats at either site (Table 3). Initial occupancy was best predicted by the total area within a 100-m buffer surrounding the wetland patch, a measure of patch size ($\beta_{buffer\ area} = 0.95$, SE = 0.49; Table 4); site was not included in the most-supported model. Although wide confidence intervals weaken predictions, our top

Table 2. Ranking of models describing trap success, based on the lowest Akaike's Information Criterion number (Δ AIC) at the floodplain and mining sites in southern Illinois over 3 yr (2011–2013) with the number of parameters (K).

Model rank	Covariates	Δ AIC	K
1	Year*Site	0.00	4
2	Site	2.7	2
3	Year + Site	5.93	3
4	NULL	10.58	1
5	Year	12.10	2

Table 3. Top five detection (p) models for rice rats at two wetland sites in southern Illinois (2011–2013), based on the lowest Akaike's Information Criterion number (Δ AIC).

Model rank	Covariates	Δ AIC	K	w	LL
1	NULL	0.00	7	0.98	−342.10
2	$\Psi(.)$, $\gamma(.)$, $\varepsilon(.)$, p(effort)	7.83	5	0.02	−348.01
3	$\Psi(.)$, $\gamma(.)$, $\varepsilon(.)$, p(rain)	42.38	5	0.00	−365.29
4	$\Psi(.)$, $\gamma(.)$, $\varepsilon(.)$, p(site)	62.37	4	0.00	−376.28
5	$\Psi(.)$, $\gamma(.)$, $\varepsilon(.)$, p(site*effort)	63.61	5	0.00	−375.90

Note: Detection covariates included site (floodplain or mining), effort (the number of traps per night), daily minimum temperature, and daily total rainfall. Occupancy (Ψ), colonization (γ), extinction (ε) estimates were held constant. K = number of estimable parameters. LL is the log likelihood, w is the AIC weight.

Table 4. Top five occupancy models (Ψ) for rice rats at two wetland sites in southern Illinois (2011–2013), based on the lowest Akaike's Information Criterion number (Δ AIC), after accounting for detection from the best detection model; Colonization (γ), extinction (ε) estimates were held constant.

Model rank	Covariates	Δ AIC	K	w	LL
1	Ψ(buffer area), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	0.00	5	0.37	−371.45
2	Ψ(site), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	6.68	5	0.03	−374.80
3	Ψ(%wetland), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	8.94	5	0.01	−375.92
4	Ψ(%grass*site), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	8.97	7	0.01	−373.94
5	Ψ(%crop), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	9.17	5	0.01	−376.04

Note: K = number of estimable parameters, LL is the log likelihood, w is the AIC weight.

SE = 0.62) and 2013 (β_{2013} = −2.05, SE = 0.90) at the mining site.

The probability of an occupied patch going extinct was positively related to the total 3-month rain prior to trapping (Table 6) but showed a steeper trend at the floodplain site (Fig. 7). Extinction probability at the mining site was lower when 3-month precipitation was <300 mm and increased gradually with increasing rainfall, whereas extinction probability at the floodplain site increased rapidly once 3-month rainfall exceeded 300 mm.

Discussion

Extremes in precipitation during the 3-yr study allowed for deeper insight into the mechanisms of metapopulation dynamics than we might have observed with conditions closer to normal. Contrary to our expectation, we did not see lower occupancy or turnover (i.e., overall colonization and extinction rates) of rice rats at patches in our site with more stable hydrology. However, we found differences in turnover patterns between the two sites, with particularly variable extinction rates at the floodplain site. Dynamic occupancy modeling provided evidence that metapopulations at the mining site follow a classic metapopulation model (Hanski 1999) where suitable patches are colonized and populations go extinct at a steady rate. In

model indicated that occupancy probability increased above 0.5 when area inside the 100-m buffer exceeded 5 ha. Except for spring 2012, naïve occupancy at the floodplain site was always greater than at the mining site (Figs. 4 and 5).

There were 12 apparent colonization events and nine apparent extinction events at the floodplain, whereas colonization balanced extinctions at the mining site (17 and 16 events, respectively). The best model of colonization probability (γ) included a site*year interaction and a negative relationship with total rainfall 3 weeks before trapping (Table 5; Fig. 6). After accounting for rainfall, colonization probabilities increased from 2011 (β_{2011} = −1.08, SE = 0.77) to 2013 (β_{2013} = 2.50, SE = 1.60) in the floodplain, whereas they were low in 2011 (β_{2011} = −0.85,
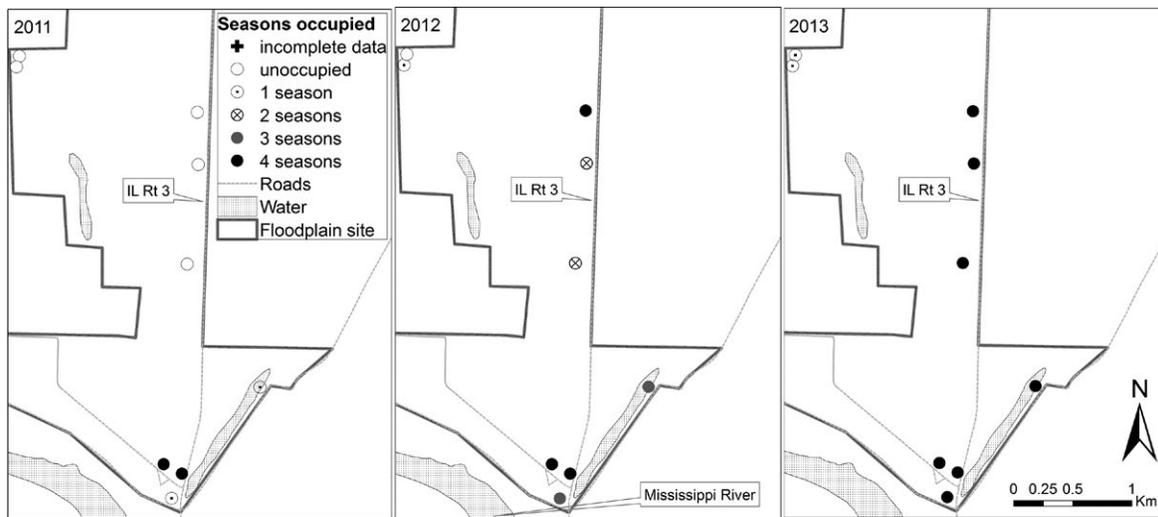
Fig. 4. Naïve occupancy for each year (2011–2013) indicated by the number of sessions per year that rice rats (*Oryzomys palustris*) were captured at a wetland patch at the floodplain site in Alexander County, Illinois. Because of flooding in 2011, most patches were trapped for a maximum of three seasons.
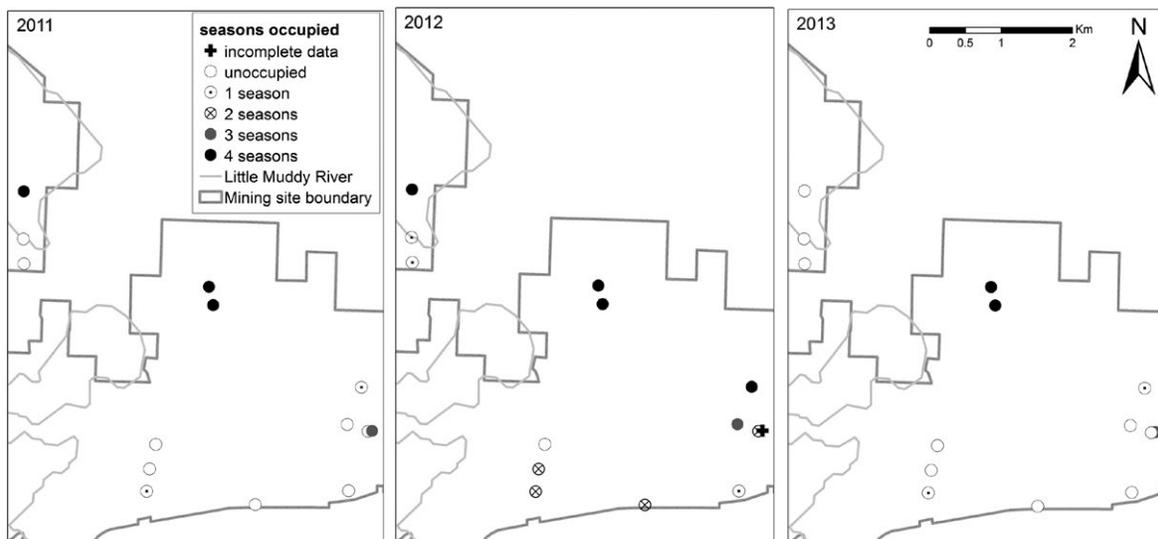

Fig. 5. Naïve occupancy for each year (2011–2013) indicated by the number of sessions per year that rice rats (*Oryzomys palustris*) were captured at a wetland patch at the mining site, Jackson County, Illinois. During 2011, patches at the mining site were only trapped for a maximum of two seasons. Incomplete data indicate patches that were not trapped for any of the seasons during a particular year.

contrast, metapopulation behavior at the floodplain was suggestive of a habitat-tracking dynamic, with populations colonizing suitable patches as they become available and retreat as flooding or drought occurs (Thomas 1994).

Initial occupancy of patches by rice rats in our study was more related to patch size than to composition of the matrix (i.e., none of the measured landscape variables appeared to affect occupancy), despite the important role

matrix characteristics play in animal dispersal (Baum et al. 2004, Haynes and Cronin 2004). Increased occupancy with increased patch size is a common observation (Van Dorp and Opdam 1987, Day and Possingham 1995, Roy Nielsen et al. 2008, Schooley and Branch 2009, Cosentino et al. 2010, Cotner and Schooley 2011), as larger patches can support greater absolute population

sizes that are less susceptible to stochastic extinction. Rice rats are specialists of wetland habitats (Wolfe 1982, Loxterman et al. 1998), so increases in the size of wetland patches and consequently resources should have a positive effect on rice rat abundance and occurrence.

Habitat quality often has a stronger independent effect on occupancy than habitat area (Fleishman et al. 2002), and recent work with mammals in wetland environments has strengthened inference about this conclusion (Schooley and Branch 2009, Glorvigen et al. 2013). Fluctuating hydrology leads to temporal resource pulses (Holt 2008), which in turn can affect population sizes and colonization dynamics. The flood-pulse concept (Junk et al. 1989) suggests that floodplain wetlands are more productive and have greater species diversity than river channels or man-made impoundments, mainly because of associated nutrient inputs from the flood pulses of the river. On this basis, we expected that floodplain habitat should provide higher quality for a wetland species such as the rice rat. Although we could not effectively quantitate habitat quality, we speculate that higher relative abundance observed at the dynamic floodplain site in the last 2 yr reflected differences in habitat quality between the two wetland complexes. For round-tailed muskrats, habitat quality was predicted

Table 5. Top five colonization (γ) models, using the best model from detection (NULL) and occupancy (buffer-area), at the floodplain and mining sites in southern Illinois over 3 yr (2011–2013); extinction estimates (ε) were held constant in this step.

Model rank	Covariates	Δ AIC	K	w	LL
1	Ψ(buffer area), γ (site × year + 3-week rain), ε(.), p(.)	0.00	11	0.61	−356.17
2	Ψ(buffer area), γ (site*year), ε(.), p(.)	1.44	10	0.30	−357.89
3	Ψ(buffer area), γ (site), ε(.), p(.)	5.17	7	0.05	−362.75
4	Ψ(buffer area), γ (site + year), ε(.), p(.)	5.70	8	0.04	−369.02
5	Ψ(buffer area), γ (3-week rain + site), ε(.), p(.)	9.21	7	0.00	−364.77

Note: K = number of estimable parameters, LL is the log likelihood, w is the AIC weight.
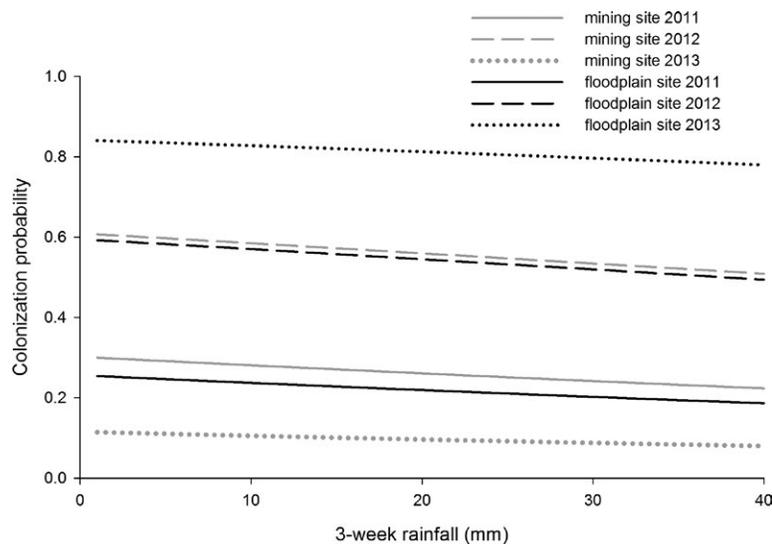

Fig. 6. Estimated probability of a patch being colonized by rice rats (*Oryzomys palustris*) based on the total rainfall recorded for 3 weeks prior to trapping at two wetland complexes in southern Illinois over a 3-yr period (2011–2013).

by percent cover of a preferred food and nesting material (Schooley and Branch 2009); in root voles (*Micotus oeconomus*), habitat quality was best assessed by percent cover of food-producing shrubs on each patch (Glorvigen et al. 2013). Our

Table 6. Top five models (lowest Δ AIC) describing initial occupancy (Ψ), colonization (γ), extinction (ε) and detection (p) at the floodplain and mining sites in southern Illinois over 3 yr (2011–2013) with the number of parameters (K), w as the AIC weights, and LL the log likelihood.

Model rank	Covariates	Δ AIC	K	w	LL
1	Ψ(buffer area), γ(Site*Year + 3-week rain), ε(Site*3-month rain), p(.)	0.00	14	0.53	−347.73
2	Ψ(buffer area), γ(Site*Year + 3-week rain), ε(Site + 3-month rain), p(.)	0.60	13	0.39	−349.03
3	Ψ(buffer area), γ(Site*Year + 3-week rain), ε(year*3-month rain), p(.)	5.53	16	0.03	−348.49
4	Ψ(buffer area), γ(Site*Year + 3-week rain), ε(1_week_rain), p(.)	5.71	12	0.03	−352.58
5	Ψ(buffer area), γ(Site*Year + 3-week rain), ε(Season), p(.)	8.69	12	0.01	−354.07

cover index of emergent macrophytes was not a useful covariate for any measure of occupancy dynamics. We posit that measuring food abundance would improve occupancy modeling, although the catholic diet of marsh rice rats (Wolfe 1982, Kruchek 2004) handicaps this assessment.

Colonization and extinction dynamics of rice rats at the floodplain sites were consistent with a habitat-tracking metapopulation (Thomas 1994). Thomas (1994) argued that occupancy tracks habitat suitability in many metapopulations, with extinctions following shifts to unsuitable conditions and colonizations trailing the return of suitable habitat within the dispersal range of remnant populations. For metapopulations in wetland habitats, extinction rates are often influenced directly by wetland hydroperiod. For example, high precipitation over the long-term coupled to high water levels can lead to local extinctions when patches flood and animals either drown or are forced to leave (Glorvigen et al. 2013). Colonization probability also can decrease if the matrix becomes too wet for rice rats to disperse successfully. At the floodplain site in 2011, deep (up to 2 m) inundation occurred for several months and multiple rice rat populations went extinct. As the site dried and dense vegetation returned to the site, the colonization rate increased in 2012–2013. During the same period at the mining site, only brief periods of flash flooding occurred, mainly due to more variable topography and greater
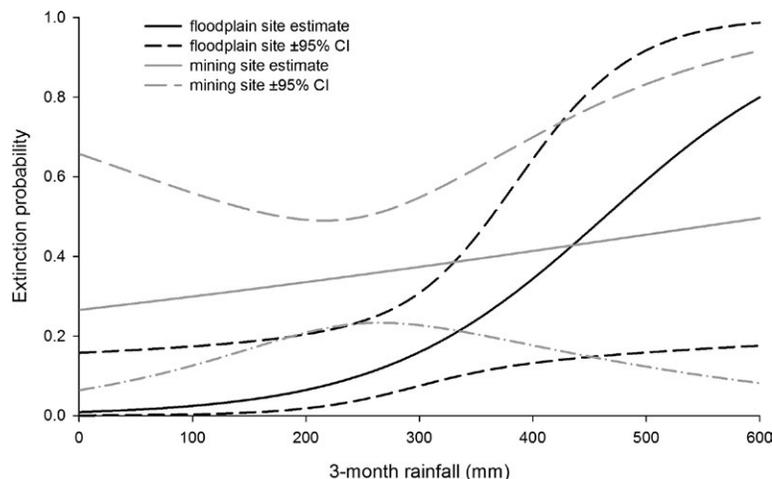

Fig. 7. Estimated probability (±95% CI) of a patch going extinct, given that it was occupied, based on the total rainfall 3 months prior to trapping at the floodplain and mining wetland complexes in southern Illinois, 2011–2013.

distance from a major river. The only previous work studying responses of rice rats to long-term (6 months) inundation documented persistence of a rice rat population on a single trapping grid (Abuzeineh et al. 2007). However, inundation at this site was only 12–18 cm. Rice rats in Everglades tree islands were restricted to upland hammocks during the wet season, when the matrix was flooded (Smith and Vrieze 1979). Overall, metapopulation dynamics at the floodplain site supported Thomas's (1994) assertion that extinction is sometimes the results of the environment becoming unsuitable and remaining unsuitable for a long period after extinction, hence not providing available patches for recolonization.

Contrary to our expectations, hydrology of the Mississippi River (river levels) did not appear to affect extinction and colonization rates. We assumed that the floodplain site would be more influenced by regional weather (precipitation upstream and elsewhere in the river basin that affects river levels; Kunkel et al. 1994) than the mining site. Yet, the apparent effects of river hydrology on turnover rates were inconsistent. A combination of high regional rainfall and snowmelt in 2011 led to flooding of the Mississippi River and the aforementioned deepwater (up to 2 m) trapped on the east side of the levee at the floodplain site for months. Consequently, extinction rates were high at the floodplain site. High rainfall in upstream regions in 2013 again led to high river levels, but river hydrology was decoupled from the floodplain site because the levee and low local rainfall conditions kept the floodplain site dry. Hence, extinction rates were more closely linked to local rainfall, which served to be a better indicator of water dynamics in the matrix and at each site.

Dynamics of the mining site metapopulation were more indicative of a classic metapopulation (Hanski 1999). Metapopulations characterized by low patch occupancy and low population density in occupied patches will be less resilient to disturbances (Opdam and Wascher 2004). Our findings were consistent with this prediction at the mining site, where rice rat abundance and occupancy were low before the severe drought, and these numbers declined even further post-drought in 2013. In addition, modeled extinction rates for the mining site were higher than at the floodplain site when 3-month rainfall was <400 mm, which occurs >70% of the time in the region (Fig. 3). These findings are interesting because there was more permanent water at the mining site than on the floodplain. We had expected rice rats at the mining site to easily disperse to other wet patches when ephemeral water dried up (Cosentino et al. 2010). However, many of the water bodies at the mining site were surrounded by forest, grassland, or agriculture rather than by emergent wetland vegetation. As Eubanks et al. (2011) demonstrated, such upland vegetation types are unlikely to promote rice rat occurrence or dispersal (but see Cooney et al. 2015a). Therefore, disappearance of ephemeral wetland patches because of drought could have led to extinction of multiple local populations, and potentially reduced trap success and patch occupancy in 2013 at the mining site. At the floodplain site, however, the drought had less of an effect (perhaps because of the much higher relative abundance) on colonization. Similar to Fleishman et al. (2002), we show that there are systems in which turnover rates are not best predicted by area and isolation; for wetland systems, hydrology can be an important driver of metapopulation dynamics.

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