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Relating Yellow Rail (*Coturnicops noveboracensis*) Occupancy to Habitat and Landscape Features in the Context of Fire

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Abstract.—The Yellow Rail (Coturnicops noveboracensis) is a focal species of concern associated with shallowly flooded emergent wetlands, most commonly sedge (Carex spp.) meadows. Their populations are believed to be limited by loss or degradation of wetland habitat due to drainage, altered hydrology, and fire suppression, factors that have often resulted in encroachment of shrubs into sedge meadows and change in vegetative cover. Nocturnal call-playback surveys for Yellow Rails were conducted over 3 years at Seney National Wildlife Refuge in the Upper Peninsula of Michigan. Effects of habitat structure and landscape variables on the probability of use by Yellow Rails were assessed at two scales, representing a range of home range sizes, using generalized linear mixed models. At the 163-m (8-ha) scale, year with quadratic models of maximum and mean water depths best explained the data. At the 300-m (28-ha) scale, the best model contained year and time since last fire (≤ 1, 2-5, and > 10 years). The probability of use by Yellow Rails was 0.285 ± 0.132 (SE) for points burned 2-5 years ago, 0.253 ± 0.097 for points burned ≤ 1 year ago, and 0.028 ± 0.019 for points burned > 10 years ago. Habitat differences relative to fire history and comparisons between sites with and without Yellow Rails indicated that Yellow Rails used areas with the deepest litter and highest ground cover, and relatively low shrub cover and heights, as well as landscapes having greater sedge-grass cover and less lowland woody or upland cover types. Burning every 2-5 years appears to provide the litter, ground-level cover, and woody conditions attractive to Yellow Rails. Managers seeking to restore and sustain these wetland systems would benefit from further investigations into how flooding and fire create habitat conditions attractive to breeding Yellow Rails. Received 30 July 2012, accepted 30 January 2013.

Key words.—Coturnicops noveboracensis, habitat management, prescribed burning, sedge meadow, Yellow Rail. Waterbirds 36(2): 199-213, 2013

Breeding Yellow Rails (Coturnicops noveboracensis) are widely distributed across the eastern two-thirds of Canada and the northern United States, but their breeding areas are often disjunct and imperfectly known (Bookhout 1995; Committee on the Status of Endangered Wildlife in Canada 2001). Knowledge of the species' ecology is limited because of their secretive and nocturnal nature. However, there is clear evidence of contraction of their distribution along the southern edge of their breeding range and declining abundance in other areas. The contraction of their range and dependence on vulnerable wetland habitats led to Yellow Rails being designated as a focal species of concern in Canada (Committee on the Status of Endangered Wildlife in Canada 2001) and a Migratory Nongame Bird of Special Management Concern (U.S. Fish and Wildlife Service 2008).

Breeding Yellow Rails are generally found in the drier portions (0-12 cm water) of fresh to brackish wetlands, most often in sedge meadows or fens dominated by fine sedges (*Carex* spp.), grasses, and rushes and that re-

main shallowly flooded or saturated through the summer and have a mat of senescent vegetation (Bookhout 1995). Loss of Yellow Rails from historical areas has largely been attributed to loss or degradation of their preferred habitats, most often from drainage and conversion to croplands, pastures, or drier hay lands (Bookhout 1995; Committee on the Status of Endangered Wildlife in Canada 2001; Goldade et al. 2002). Habitat losses also have been attributed to impoundment of natural wetlands to increase water levels for waterfowl management (Committee on the Status of Endangered Wildlife in Canada 2001). A less recognized threat is habitat degradation due to the absence of periodic disturbance and resulting encroachment of shrubs. Without periodic disturbance such as burning or grazing, wetland productivity is reduced; the senescent litter mat can become decadent, limiting vegetative emergence and productivity; and woody vegetation can become established or more dominant (Curtis 1959; Jean and Bouchard 1991; Middleton 1999, 2002). Woody encroachment often increases where seasonal

flooding has been reduced by drainage or drought (Curtis 1959; Jahn and Hunt 1964; Warren et al. 2007). Periodic fire is an important disturbance event in wetlands that recycles nutrients, removes decadent growth and litter, rejuvenates plant growth, and top-kills woody vegetation, suppressing its growth and dominance (e.g., Johnson and Knapp 1995; Warners 1997; Kost and de Steven 2000). Fire has been actively suppressed in many northern ecosystems since the early 1900s as areas became settled (Jean and Bouchard 1991; Pyne 2004). Today, use of prescribed fire to manage sedge meadows is often difficult due to limited resources, logistical challenges, and limited knowledge of effective application.

Although some authors have described or discussed fire relative to Yellow Rails (Stenzel 1982; Niemi and Probst 1990), few studies have directly examined the effects of fire on Yellow Rail habitat during wintering (Mizell 1999; Given 2005) or breeding seasons (Burkman 1993). In an experimental study using burned and unburned plots, Burkman (1993) found breeding Yellow Rails responded positively to burned habitat. Yellow Rails used burned plots that had lower percentages of shrubs and higher percentages of woollyfruit sedge (Carex lasiocarpa), a fine-leaved sedge, than control plots. That study, however, was limited by small sample sizes and a short time frame (1-2 years after burning). Yellow Rails may be deterred from using areas that have not been burned in many years due to encroachment of woody vegetation and reduced wetland productivity. Areas with a large proportion or many patches of upland or lowland woody habitat may impede territorial patrolling by males and transmission of their calls and provide more habitat for avian predators. Studies at Seney National Wildlife Refuge (NWR) noted shrub cover of < 20% in their study areas (Stenzel 1982; Burkman 1993), but Yellow Rail studies elsewhere indicate only trace levels or no mention of shrub cover (Gibbs et al. 1991; Popper and Stern 2000; Robert et al. 2000, 2004). The timeframe and thresholds at which shrub cover or structure become attractive or a deterrent to Yellow Rail use remain unclear, and likely interact with other structural features affected by fire such as litter and graminoid density.

The study was conducted at Seney NWR, one of the best known breeding areas for Yellow Rails in the United States (Bookhout 1995) and the site of previous studies on the species (Walkinshaw 1939; Bart et al. 1984; Bookhout and Stenzel 1987; Burkman 1993). Our goal was to provide better information on the use of fire as a habitat management tool for Yellow Rails. Our objective was to evaluate effects of habitat and landscape variables on probability of use by Yellow Rails in the context of fire. Based on earlier studies (Bookhout and Stenzel 1987; Hanowski and Niemi 1988; Burkman 1993; Popper and Stern 2000), we hypothesized that the occurrence of Yellow Rails is: 1) limited by water depths greater than about 15 cm, 2) positively related to percent cover of fine-leaved graminoids, 3) positively related to the thickness of the senescent litter mat, 4) negatively affected by woody vegetation and vertical cover, and 5) negatively related to more complex landscapes or those with a higher proportion of woody or upland cover. Finally, we hypothesized that recency of fire would affect occurrence of Yellow Rails through its effects on vegetative cover and structure.

METHODS

Study Area

Seney NWR (46° 15' N, 86° 04' W) is located in Schoolcraft County on the eastern Upper Peninsula of Michigan (Fig. 1). The refuge's extensive peatlands consist of sedge meadows, shrub thickets, and patterned bogs, interspersed with sand ridges and knolls (U.S. Fish and Wildlife Service 2009). The sedge meadows have a diverse community of sedges, grasses, rushes, forbs, Sphagnum spp. and other mosses, and low shrubs, with scattered, sparse patches of cattail (Typha spp.) in some areas. Speckled alder (Alnus incana), bog birch (Betula pumila), and leatherleaf (Chamaedaphne calyculata) are the most common shrub species in sedge meadows and shrub thickets. The primary land cover types of non-forested lowlands in the refuge are scrub/shrub lowland (27%), sedge-bluejoint grass (Carex spp./Calamagrostis canadensis; 10%), Sphagnum spp./leatherleaf (4%), and mixed emergents/grasses/forbs (3%) (U.S. Geological Survey 1992, National Land Cover Dataset

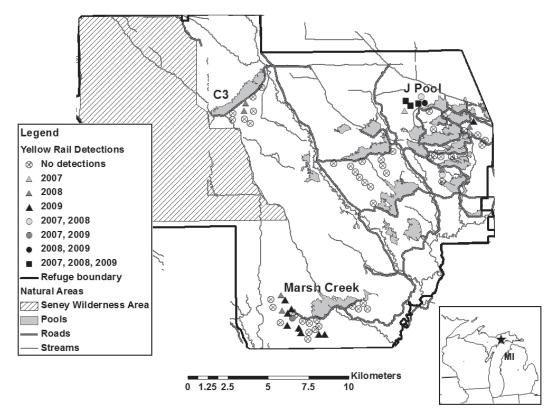


Figure 1. The location of survey points and detections of Yellow Rails (*Coturnicops noveboracensis*) at Seney National Wildlife Refuge, Michigan, during 2007-2009.

[NLCD], based on interpretation of 2004 color-infrared aerial images). Wetland hydrology is affected by natural flow patterns, which move northwest to southeast, and water management of man-made pools, constructed in the 1930s. Sedge meadows are usually shallowly flooded in the spring and remain saturated into the fall. Soils are generally mucks and peat 1-3 m in depth, overlaid on sand. Natural and modified drainages drain the area to the southeast into the Manistique River. A more detailed description of the refuge landscape and habitats is provided in U.S. Fish and Wildlife Service (2009).

Annual weather data for the area were obtained from the National Climate Data Center (2009). Precipitation varied from moderate drought during much of 2006 and 2007 to moderately wet in 2008 and average precipitation in 2009. Annual and seasonal differences in spring runoff and rain were reflected in wetland water depths. Mean water depths at survey points during the first Yellow Rail survey were 2.7 cm in 2007 (range 0-14 cm), 8.4 cm in 2008 (range 1-20 cm), and 9.1 cm in 2009 (range 0-23 cm). Water depths declined to 0 in most areas in 2007, held steady through 2008, and declined in the third survey in 2009. By the time habitat data were collected in late June-early July each year, mean water depths had declined to 0.3 cm in 2007, 3.2 cm in 2008, and 2.4 cm in 2009.

Yellow Rail Surveys

Survey points were selected so that points: 1) were distributed across all major wet-meadow regions of the refuge, 2) were stratified across a range of lowland land cover types that might attract Yellow Rails, 3) included areas that had historically held Yellow Rails (Stenzel 1982; Bart et al. 1984; Burkman 1993; Seney NWR, unpubl. data), 4) could be reasonably accessed on foot (< 2 km from road), and 5) were \geq 400 m apart and \geq 100 m away from a road. Points meeting these criteria were located using ArcGIS (Environmental Systems Research Institute 2007) and the refuge's land-cover data. In the field, selected points were located using a global positioning system (GPS) receiver and marked using tall poplar (Populus spp.) poles with reflective tape and flagging. Of the 68 points selected for surveys (Fig. 1), 21% were located in sedge-bluejoint grass, > 90% cover; 13% sedge-bluejoint grass, 25-60% cover; 9% sedge-bluejoint grass, 60-90% cover; 32% low shrub, 25-60% cover; 9% low shrub, 60-90% cover; 15% mixed emergents/grasses/forbs, > 90% cover; and 1% mixed marsh/emergent, 60-90% cover. Other points initially selected using GIS were found to be incorrectly classified or deeply flooded (> 40 cm) in 2007 and were dropped.

Surveys were conducted on 64-68 points each year (2007-2009), with 90% of points surveyed all 3 years.

Call-playback methods were used to conduct surveys, following standard marsh-bird monitoring procedures (Conway and Nadeau 2006; Conway 2011) modified for Yellow Rails. Each survey period consisted of 10 1-min blocks, with 5 min of passive listening, 3 calling sequences (30 sec of Yellow Rail clicking calls followed by 30 sec for listening), and 2 min of passive listening. The broadcast recording was obtained from the Marsh Bird Population Assessment and Monitoring Project (U.S. Geological Survey 2006) and played using a compactdisc player set on the ground and set at full volume (80-90 db). Surveys were conducted during full darkness (between 23:00 and 05:00) and repeated at each point three times each year, ≥ 10 days apart, starting in early May and ending in mid- to late June. Surveys were not conducted if ambient noise from precipitation, wind, or frog calls interfered with an observer's ability to detect calling birds. For safety, two observers jointly conducted each survey. Comparison of detection abilities between observers indicated that detections differed by $\leq 3\%$.

At each survey point, observers recorded time, weather (wind, ambient temperature, cloud cover, moon stage and visibility), and water depth (cm; averaged from 4-6 measures around the survey point). Observers recorded all secretive marsh birds detected (Conway 2011), with a primary focus on Yellow Rails. If a Yellow Rail was heard, observers estimated direction and distance to the calling bird. Observers also determined direction and distance from other locations between survey points to better estimate actual location through triangulation and, when possible, by walking to within about 20 m of the calling bird to verify its location, as evidenced by call volume and angle of approach.

Habitat Data and Land Cover Composition

Habitat data at each surveyed point were collected each year in June and early July. Subsampling points were located in the four cardinal directions 25 m from the central point to avoid the trampled area around the survey pole. At each subsample point, vegetative cover was determined using a modified point-intercept method (Elzinga et al. 1998) along a 2-m transect; percent cover was estimated for open area (no vegetation or litter), mosses, fine sedges (leaf blades < 3 mm wide), coarse sedges (leaf blades ≥ 3 mm wide), broadleaf cattail (Typha latifolia), grasses, forbs, shrubs, other woody vegetation, and other vegetation (e.g., ferns, Equisetum spp.). Litter depth (cm) and graminoid height (cm) were also measured along the 2-m transect. A 2-m tall cover board was divided into six 33-cm strata and used to determine vertical obstruction readings (VOR; Nudds 1977). Observers estimated the proportion of each stratum that was covered (obstructed) from four cardinal directions and 2 m away. VOR data were averaged for each point for the lowest stratum (ground-level VOR) as well the entire 2-m cover board (total VOR). Data on shrub cover, height, and patchiness were collected along a separate 5-m transect at each subsample point. Length and height of each distinct shrub patch (i.e., < 10-cm gap in shrub cover) were measured along

the 5-m transects to calculate percent shrub cover, shrub height (dm), and number of shrub patches. For analysis, means of these measures were calculated for each point.

Land cover around each survey point was determined for two scales, 163-m (8.3-ha) and 300-m (28.2ha) radius, respectively, using ArcGIS (Environmental Systems Research Institute 2009). These two scales were selected to represent a range of wetland and home range sizes reported for Yellow Rail males (Stenzel 1982; Goldade et al. 2002). The land-cover data layer was developed for the refuge based on photo-interpretation of 2004 color-infrared photographs; minimum mapping unit was 0.8 ha (U.S. Fish and Wildlife Service 2009). The land-cover classes described dominant plant taxa and cover density (e.g., sedge/bluejoint grass, 25-60% cover; speckled alder, > 90% cover). To simplify the large number of forest classes, all classes of trees were combined into lowland woody cover or upland trees (Table 1). Upland trees were primarily pines (Pinus spp.) on sand islands and renamed upland habitat. While unlikely to be used by Yellow Rails, such treed islands alter water flow through the sedge meadows, creating small pockets of ponded water above them, as well as affecting sound transmission of bird calls.

Fire Histories

Seney NWR has a well-documented history of wildfires and prescribed fires dating back to the 1976 Seney fire, which burned most of the western half of the refuge (Anderson 1982). An active prescribed burning program was initiated in 2000, which broadly targets wetlands across the non-wilderness areas of the refuge using large-scale (100s of hectares) fires. Refuge records were used to determine the number of years since the area around each point had last burned relative to the Yellow Rail surveys in this study. Fire histories were categorized as burned within the previous year (≤ 1 year), 2-5 years ago, or > 10 years ago. Fires occurring since 1985 burned most survey points west of J Pool (summer 2006), south of C3 Pool (May 2008), and south of Marsh Creek (July 2008), all historically important Yellow Rail areas (Fig. 1). Those fires were light to moderate in severity; 74% of the Yellow Rail survey points were burned in July or August, the remaining in May.

Data Analysis

We were able to estimate and often verify distances from the survey point to calling Yellow Rails and determine their actual location by triangulation from multiple locations or walking up to within about 20 m of calling males. Several Yellow Rails detected were > 400 m away. However, at such long distances the habitat data collected around a survey point likely could not adequately represent habitat within the area actually used by the calling male. Therefore, the data set was reduced to those Yellow Rails we estimated, or knew, to be within either 163 m or 300 m of the survey point to match GIS data, and the model analyses run separately for each distance. This resulted in the exclusion of three detections that were ≥ 350 m from the survey

Table 1. Descriptions of variables included in logistic regression models for Yellow Rail occupancy at Seney National Wildlife Refuge, Michigan, 2007-2009. Year was included in all candidate models.

		Model Scale	
Variable	Description	163-m	300-m
Year	Survey year	X	X
MaxWtrDep	Max water depth (cm), quadratic, measured during Yellow Rail surveys	X	X
MeanWtrDep	Mean water depth (cm), quadratic, measured during Yellow Rail surveys	X	X
MOpen	Mean percent open cover, quadratic	X	
MFGram	Mean percent cover fine sedges and grasses	X	
MGramHt	Mean graminoid height (cm)	X	
MLitDep	Mean litter depth (cm)	X	
VOR_Total	Mean vertical visibility reading (%), all strata combined (2 m)	X	
VOR_MeanS1	Mean vertical visibility reading (%), ground level (lowest 33-cm stratum)	X	
Shrub-specific measu	ures (2007 and 2009 only)		
PctCover	Mean percent shrub cover	X	
NNPatch	Mean number of shrub patches	X	
Ht_Mean	Mean shrub height (cm)	X	
Landscape composit	tion metrics (GIS)		
LC_SBG LC_LS	Percent cover of sedge/bluejoint grass [SBG-B + SBG+C + SBG-D] Percent of lowland shrub	X	X
	[LS-B+LS-C]	X	X
LC_UPL	Percent cover of upland	X	X
LC_Woody	Percent cover of lowland woody cover [LS-D + LT-B + LT-C + LT-D]	X	X
LC_PatchR	Patch richness (number of types) as measure of habitat diversity	X	X
LC_EdgeDens	Edge density (linear distance of edge per unit area of landscape [m/ha]);		
-	a measure of habitat complexity	X	X
FireHistory	Category of time since last burned	X	X

point. We assumed that a survey point was within a Yellow Rail territory if they were estimated to be within 300 m and responding to the broadcast call, and that habitat measures at that point were representative of that part of the individual's territory.

To examine the effects of the habitat variables, fire history, and landscape variables on the probability of use by Yellow Rails, we attempted to use habitat occupancy models (MacKenzie et al. 2006). Such models account for the differences in the probability of detection, which is often a concern for secretive species. However, many of the models attempted had convergence issues or problems with the variance-covariance matrix that caused unreliable estimates of the parameter standard errors. We suspect these problems were due to low estimates of occupancy that converged near zero for some points, even though the estimated detection probabilities were ≥ 0.69. Therefore, we instead used a traditional approach, logistic regression models, to evaluate factors affecting occurrence of Yellow Rails. Logistic regression models assume that the probability of detection is near one or is constant across all points, surveys, and years (MacKenzie 2006). To examine the validity of this assumption, we estimated detection probabilities for each year and survey separately, using single-season habitat occupancy models (MacKenzie et al. 2006). The detection history for each point consisted of the 10 min of sampling summarized into three listening periods: 5 min pre-playback, 3 min of call playback, and 2 min post-playback. Two models were computed for each year and survey – one with the detection probability modeled as a constant and one with the detection probability modeled as a function of listening period.

Logistic regression models with repeated measures (Allison 1999) were used to examine the effects of the habitat variables, fire history, and landscape variables on the probability of use by Yellow Rails. Data within each year were combined across surveys, and a survey point was considered used in a given year if a Yellow Rail was heard from that point at least once that year (i.e., was present at least for one of the surveys). Survey point was the experimental unit; year was the repeated measure and included in every model to account for year effects. Sixteen candidate models were considered for analysis at the 163-m scale and 10 candidate models for analysis at the 300-m scale (Table 1). Because of limited number of detections, models included only year and a single additional variable, as well as a model with just year. For detections within 163 m, models included water depths (as measured during Yellow Rail surveys), point-based habitat data, and landscape metrics. For detections within 300 m, candidate models only included landscape-scale metrics and water depths. Water depth did not markedly vary spatially at either scale because of the flat topography of the wetlands and, therefore, they were retained in the candidate models for the 300-

m scale. Mean and maximum water depth (calculated from the three surveys each year) and percent open appeared to have curvilinear relationships, so a quadratic model was included for each of these variables. Because shrub variables were only available in two of the three years, the 163-m analysis was first conducted without these variables and then the shrub variables were added to the best model, one at a time, using just the available 2007 and 2009 data, to see if they would improve the model. Candidate models were evaluated using Akaike's Information Criterion for small samples (AIC_c; Burnham and Anderson 2002). The generalized linear mixed model procedure (PROC GLIMMIX) in SAS was used to conduct analyses (SAS Institute, Inc. 2010).

The effects of time since last fire on habitat variables were assessed using linear mixed models with repeated measures (Littell et al. 1996). As above, survey point was the experimental unit and year was the repeated measure and included in each model to account for year effects. Habitat variables considered in this analysis were percent cover of open, moss, fine sedge, coarse sedge, cattail, forbs, grass, low shrub, tall shrub, woody, and other vegetation; litter depth; graminoid height; ground-level and total VOR; shrub height; percent shrub cover; number of shrub patches; and shrub patch size. We were interested in differences among fire histories not only of mean values but also of variability, minimum, and maximum values. Only 2007 and 2009 data were used for examining the effects of fire history on shrub variables. Least squares means were computed for each fire history, and differences of least squares means were examined if the main effect of fire history was significant (at a significance level of 0.05).

RESULTS

Within the 300-m detection range, we recorded Yellow Rails at eight survey points in 2007, 13 points in 2008, and 15 points in

2009. In 2007, most Yellow Rails were found on the west side of I Pool (Fig. 1). With improved wetland conditions in 2008 and 2009, Yellow Rails were found across a wider range of areas. Sixty-eight percent of positive detections occurred during the first survey period; only one (in 2008) occurred during the third survey. The probability of detecting a Yellow Rail varied among years and surveys, but was quite high (range 0.69-0.96) and averaged 0.81 for the 163-m distance and 0.83 for the 300-m distance. The probability of detecting a Yellow Rail at a point during at least one of the three surveys within a year ranged from 0.93 to 0.98.

Depth of spring flooding was an important factor explaining occurrence of Yellow Rails. If a calling Yellow Rail was estimated to be within 163 m of a survey point, the quadratic models with maximum water depth and mean water depth were the most plausible models (Table 2). Adding the three shrub variables to the best model (maximum water depth) for the 2007 and 2009 data did not improve the model. The probability of use increased with maximum water depth up to about 10.5 cm and then decreased with increasing water depth (Fig. 2). Maximum water depths recorded at sites where Yellow Rails were present averaged 9.9 ± 0.6 cm (SE) (n = 25, range 4-16 cm) compared to $7.6 \pm$ 0.5 cm (n = 172; range 0-26 cm) where no Yellow Rails were detected. Water depths recorded at incidental locations of Yellow

Table 2. Results of logistic regression analysis with repeated measures (year) to examine the effects of the habitat variables, fire history, and landscape composition on the probability of use by Yellow Rails at Seney National Wildlife Refuge, Michigan, 2007-2009. Analyses were run for Yellow Rails detected within 163 and 300 m of the survey point. Reported are the top scores of Akaike's Information Criteria adjusted for small sample size (AIC_c), Δ AICc up to 5.0, and Akaike weights (w_i) up to 0.05 for models composed of linear, additive combinations of year plus a single habitat or landscape variable.

Variable	n	No. Presences	K	AIC _c	ΔAIC_{c}	$w_{\rm i}$
Detections within 163 m	197	25				
Year MaxWtrDep MaxWtrDep ²			6	131.301	0.000	0.553
Year MeanWtrDep MeanWtrDep ²			6	131.731	0.430	0.446
Detections within 300 m	197	36				
Year Fire history			7	165.331	0.000	0.662
Year MaxWtrDep MaxWtrDep ²			6	168.121	2.790	0.164
Year MeanWtrDep MeanWtrDep ²			6	169.371	4.040	0.088
Year LC_Woody			5	170.042	4.710	0.063

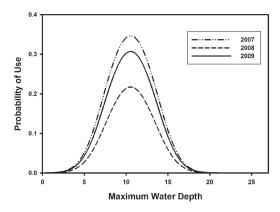


Figure 2. Probability of Yellow Rail occurrence within 163 m of survey points relative to maximum water depth at Seney National Wildlife Refuge, Michigan, during 2007-2009. Probabilities are the results of running the data through the best approximating model (occurrence: YEAR + MaxWtrDep + MaxWtrDep²) and generating a separate line for each year. Probability of occurrence decreases as depths become very deep and very shallow.

Rails (n = 6; range 5-12 cm) corresponded with survey results. Comparison of habitat measures relative to Yellow Rail presence suggested that Yellow Rails occurred in areas with greater percent open area, lower shrub cover and shrub heights, and fewer shrub patches. Examination of box plots indicated that 75% of Yellow Rail detections occurred in areas with $\leq 8\%$ shrub cover, shrub heights ≤ 6 dm, and < six shrub patches/5 m, all lower than data for non-detection sites (Fig. 3).

If a calling Yellow Rail was estimated to be within 300 m of a survey point, the best model was fire history, followed by the quadratic model with maximum water depth (Table 2). The probability of use was highest for points burned 2-5 years ago (0.285 ± 0.132), followed closely by points burned \leq 1 year ago (0.253 \pm 0.097), and lowest for points burned > 10 years ago (0.028 ± 0.019). Proportionately more Yellow Rail detections occurred on areas burned 2 years ago compared to proportional distribution of fire history of the survey points (Fig. 4). Fifteen detections occurred within 1 year of burning: two occurred within 3 weeks of an early May burn, seven occurred in the spring following mid-summer burns, and six occurred 1 year after a spring burn. Comparison of landscape metrics relative to Yellow Rail presence suggested Yellow Rails tended to occupy areas with greater sedge-bluejoint grass cover, less upland cover, less lowland woody cover, and less patch richness. Examination of box plots indicated that 75% of Yellow Rail detections occurred in areas with < 5% of the landscape in lowland woody cover, < 9% in upland cover, and patch richness of seven, all lower than data for non-detection sites (Fig. 3).

To understand how fire history affected habitat variables, we compared habitat variables across fire history categories. Fire history affected litter depth mean, variability (SE), and maximum values; variability in graminoid height; mean ground-level VOR; and minimum total VOR (Table 3). Generally, sites that had been burned 2-5 years ago had deeper and more variable litter depths, and greater ground-level VOR compared to areas with more recent burns or areas that had not been burned for at least 10 years. Differences for marginally significant (P = 0.050-0.090) variables suggested that percent cover of fine sedges was lowest in most recently burned areas, maximum ground-level VOR was highest 2-5 years after burning, and percent open was lowest and number of shrub patches highest in areas with oldest fire histories.

DISCUSSION

Our model results reinforce the importance of water depths documented in earlier studies (Bookhout and Stenzel 1987; Gibbs *et al.* 1991; Robert *et al.* 2000). Indeed, year and water depths contributed > 90% of the explanatory weight in the model. At the larger scale, recency of fire was the most important factor explaining Yellow Rail presence. Fire affected habitat features and attractiveness to Yellow Rails in ways that we were unable to detect by our direct measures and models. The small number of detections limited our

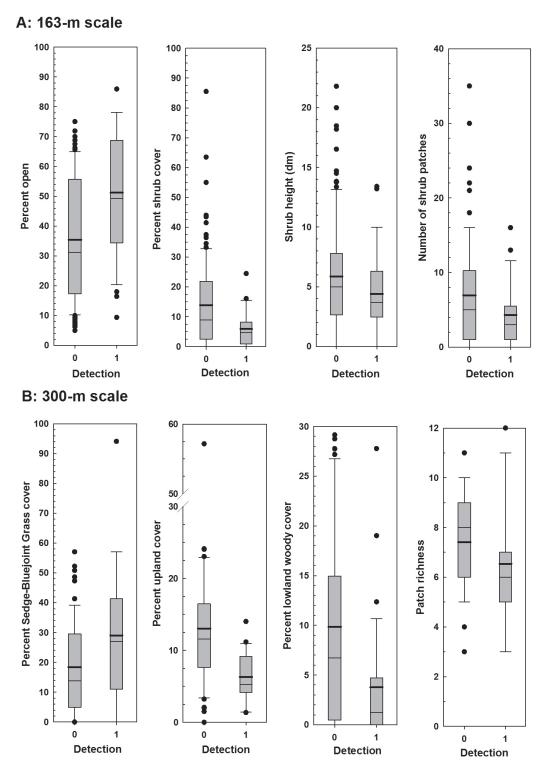


Figure 3. Box plots of habitat variables for survey points where Yellow Rails were detected (1) or not detected at (0) at the (A) 163-m scale and (B) 300-m scale at Seney National Wildlife Refuge, Michigan, during 2007-2009. Shrub measures were available only for 2007 and 2009. Box plots represent median (line in box), mean (bold line in box), 25-75% percentiles (shaded box), 10 and 90 percentiles, and dots outliers (dots).

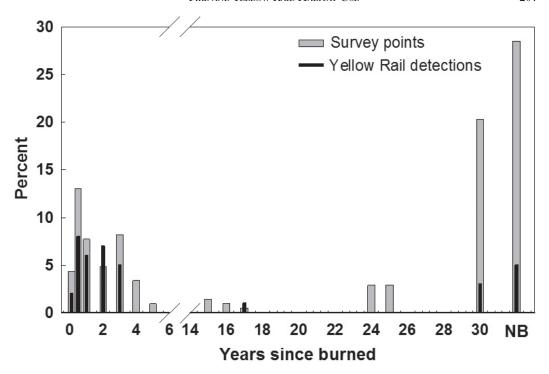


Figure 4. Distribution (%) of survey points and Yellow Rail detections by years since burned at Seney National Wildlife Refuge, Michigan, during 2007-2009. NB = no record of burning.

ability to examine more complex models (e.g., interactions or multi-variable logistic models, detection-occupancy models). However, examination of habitat and landscape data where Yellow Rails were present suggests a suite of features are important for Yellow Rails.

Yellow Rails appear to be the "goldilocks" of Rallidae, preferring water that is not too deep or too shallow. Maximum depths, which usually occur in May when birds are arriving on the breeding grounds, appear to be a key to habitat selection (Robert et al. 2000). Although some birds have been recorded at sites with water depths up to 46 cm (Bookhout and Stenzel 1987), water depths reported for most Yellow Rail locations range from saturated soils to 16 cm (Bart et al. 1984; Bookhout and Stenzel 1987; Gibbs et al. 1991; Robert et al. 2000). Further, nests are situated in water depths ranging from 0 (saturated soils) to 11 cm (Walkinshaw 1939; Elliott and Morrison 1979; Popper and Stern 2000; Robert et al. 2000). Interestingly, mean and maximum

water depths for Yellow Rails correspond to mean and maximum depths of the litter mat (Bookhout and Stenzel 1987; Robert et al. 2000). Prolonged submergence of the litter mat increases its decomposition rate (Neckles and Neill 1994). Given the importance of the litter mat for cover, nesting, and structure for Yellow Rail foods (e.g., arthropods and snails; Walkinshaw 1939; Robert et al. 1997), deep and prolonged flooding would reduce the mat's depth and value for Yellow Rails in that and subsequent years. Conversely, low water depths in May, when maximum depths usually occur, likely provide Yellow Rails a good indication that favorable water conditions will not be sustained through the breeding season.

Fire history was the most important variable explaining presence of Yellow Rails at the 300-m scale, with continued contribution of water depths. Yellow Rails were most likely to be present in areas burned 2-5 years ago, but they also were likely to occur in areas burned within the previous

Table 3. Results of linear mixed model analyses with repeated measures (year) to examine the effect of time since burning on habitat variables at survey points for Yellow Rails at Seney National Wildlife Refuge, Michigan, 2007-2009. Different letters within a row indicate significant differences (P < 0.05) between fire histories and are highlighted in bold. Shrub-specific measures were available only for 2007 and 2009. Degrees of freedom of F tests were 2 and 123 for all variables except shrub height, percent shrub cover, number shrub patches, and shrub patch size, where they were 2 and 59.

		Analysis Results		Years Since Last Burned LSMean (SE)			
Variable	n	F	P	≤1 year	2-5 years	> 10 years	
Mean percent cover	197						
Open		2.58	0.080	39.4 (1.6)	38.5 (1.9)	35.3 (1.1)	
Moss		0.38	0.684	2.6 (1.0)	1.9 (1.2)	1.6(0.7)	
Fine sedges		2.66	0.074	38.6 (2.0)	41.2 (2.6)	43.6 (1.6)	
Coarse sedges		0.96	0.385	5.1 (1.4)	7.8 (1.7)	6.6 (1.0)	
Cattail		0.57	0.566	0.7(0.3)	0.3(0.3)	0.6(0.2)	
Forbs		0.01	0.988	7.9 (1.0)	7.9 (1.2)	7.7 (0.7)	
Grasses		0.95	0.388	7.8 (1.2)	5.6 (1.5)	7.3 (0.9)	
Low shrubs		1.19	0.308	2.2 (1.1)	1.7 (1.4)	3.9 (0.9)	
Tall shrubs		0.04	0.957	0.9(0.3)	0.9(0.3)	0.8(0.2)	
Other woody		0.20	0.817	0.1 (0.3)	0.1 (0.3)	0.2(0.1)	
Other		2.38	0.096	0.9 (0.6)	1.9 (0.7)	2.1 (0.4)	
Litter depth (cm)	197						
Mean		3.67	0.028	7.7 (0.5) A	9.6 (0.5) B	8.5 (0.3) AB	
SE		16.06	< 0.001	0.6 (0.0) A	1.0 (0.1) C	0.7 (0.0) B	
Minimum		0.99	0.376	1.9 (0.3)	1.4(0.4)	2.0 (0.2)	
Maximum		13.98	< 0.001	15.5 (0.9) A	22.8 (1.1) B	17.4 (0.6) A	
Graminoid height (cm)	197						
Mean		0.63	0.536	30.5 (1.5)	29.9 (1.8)	28.6 (1.0)	
SE		5.12	0.007	5.5 (0.2) A	5.9 (0.3) A	5.0 (0.1) B	
Total VOR	197						
Mean		1.47	0.234	28.1 (1.8)	30.2 (2.2)	26.4 (1.6)	
SE		0.50	0.611	2.6 (0.3)	3.0 (0.4)	2.7 (0.2)	
Minimum		3.89	0.023	15.0 (1.1) AB	16.8 (1.3) A	12.9 (0.7) B	
Maximum		0.67	0.514	53.0 (3.9)	54.9 (4.8)	49.1 (3.0)	
Ground-level VOR	197						
Mean		3.41	0.036	88.5 (1.8) AB	92.6 (2.2) A	86.0 (1.4) B	
SE		0.83	0.437	3.6 (0.6)	2.9 (0.7)	4.0 (0.4)	
Minimum		1.32	0.271	78.5 (3.1)	84.1 (3.8)	77.1 (2.2)	
Maximum		2.85	0.062	94.6 (1.2)	97.7 (1.5)	93.7 (0.9)	
Shrub height (dm)	132						
Mean		0.11	0.894	5.3 (0.8)	5.8 (1.0)	5.7 (0.6)	
SE		0.22	0.801	0.8 (0.2)	0.8 (0.3)	0.9 (0.2)	
Min		0.33	0.719	3.1 (0.6)	3.8 (0.8)	3.4 (0.4)	
Max		0.39	0.679	8.6 (1.8)	8.6 (2.4)	10.3 (1.3)	
Mean % shrub cover	132	0.68	0.509	10.4 (2.3)	12.4 (3.0)	13.5 (1.8)	
No. shrub patches	132	2.51	0.090	5.1 (1.1)	4.2 (1.4)	7.5 (0.9)	
Shrub patch size (cm)	132	2.03	0.140	27.2 (5.7)	43.8 (7.5)	35.9 (4.2)	

year. Burkman (1993) detected more Yellow Rails in areas burned 1.5-2 years previously, but also found 16 Yellow Rails in the C3 Pool over 3 years (1991-1993) despite

absence of fire in that area for > 15 years. Stenzel (1982) detected the greatest abundance of Yellow Rails northwest of Marsh Creek Pool and low abundance in the C3

Pool, both of which had burned 3-4 years previously; other areas with low densities of Yellow Rails had no record of fire (Seney NWR, unpubl. data). Similarly, Conway et al. (2010) reported increased numbers of Yuma Clapper Rails (Rallus longirostris yumanensis) and Virginia Rails (R. limicola) 0.5-2.5 years following late-winter prescribed burning of wetlands in the lower Colorado River, and a suggestion of diminishing effects by 4.5 years after burning. However, they detected no fire effects for California Black Rails (Laterallus jamaicensis coturniculus) or Soras (Porzana carolina). Time since burning affects several measures of habitat structure that correspond with non-water features generally described for Yellow Rail habitat: dense stands of sedges or other emergent vegetation and a thick senescent litter mat (e.g., Bart et al. 1984; Bookhout 1995; Conway et al. 2010). In our study, ground-level VOR was highest during the first 5 years after burning, corresponding with trends of declining percent open and increasing cover of fine graminoids over time. Mean litter depth increased to its peak 2-5 years after burning, then tended to decline. Litter depth was most variable 2-5 years after burning when litter depths peaked; this may reflect combined influences of spatially variable productivity and fire effects. More than 5 years after burning, litter mats appear to decline despite additional years of aboveground productivity, likely due to compaction and partial decomposition. Kost and de Steven (2000) also noted peak litter depths two seasons after burning sedge meadows and high live biomass the first season after burning, which would contribute to high groundlevel VOR. Seven years after burning, differences in litter, live biomass, and relative cover of plant forms between burned and unburned areas had disappeared.

That we detected no differences in shrub cover or height among fire history classes is not entirely surprising. Recent burns were light to moderate in severity, and the dominant shrubs (speckled alder, bog birch, and leatherleaf) are tolerant of burning and resprout readily fol-

lowing burning (e.g., Pavek 1993; Fryer 2011). The mixed and often temporary results of burning to suppress woody vegetation in sedge meadows also relates to fire intensity, season, and patchiness. Most studies involved single, low-intensity fires conducted during the dormant season or early spring, which typically result in high survival of shrubs, resprouting, and only temporary reduction in woody cover or height (Kost and de Steven 2000; Middleton 2002; Briggs et al. 2005; Brisson et al. 2006). Further, spatial variability of fuels (litter and live biomass), water, and microclimate often result in patchy fire effects. Slow, hot fires during late summer or early fall, while shrubs are still actively growing, are more likely to be effective in reducing shrub cover and stem densities (Linde 1969). Water conditions immediately after disturbance are another important factor influencing survival or recruitment of woody species in wetlands (Keddy and Reznicek 1986; Toner and Keddy 1997). Woody seedlings generally do not tolerate flooding but can become established under drier conditions. Hence, actions to suppress woody establishment or survival needs to consider timing of burning or other disturbances relative to water conditions and growing season.

In our models, local and landscape habitat variables contributed little to explaining Yellow Rail occupancy and, therefore, did not provide direct support for our hypotheses regarding shrub cover and landscape composition. In a similar study conducted in southeastern Manitoba, Yellow Rail occupancy was influenced by shrub cover at the patch (wetland) scale in the drier of two years but not in the wetter year, when water depths averaged 12 cm (Martin 2012). Water conditions overwhelmingly influence the probability of occupancy by Yellow Rails, and influence the habitat features in both positive and negative ways; e.g., the influence of shrubs occurred only in drier conditions (Burkman 1993; Robert et al. 2000; Martin 2012). A more comprehensive understanding of what wetland features influence Yel-

low Rail occupancy will therefore require studies encompassing multiple years and areas that capture combinations of hydrological conditions and habitat features.

One of the assumptions of logistic regression models that may have been violated in this study is that probability of detection is constant across survey points (MacKenzie 2006), which might bias parameter estimates. Important habitat and landscape covariates may appear unimportant due to non-detection error or, if detection is related to some of the habitat or landscape covariates, the models may overstate the effect of those covariates on occupancy (Gu and Swihart 2004). The importance of water depth is nearly universal in Yellow Rail studies and seems unlikely to have influenced detection or results. However, vegetative structure (e.g., lowland woody cover) and topography (pine islands) could muffle Yellow Rail calls and reduce the probability of detecting them, and may have inflated the importance of lowland shrub cover in our results. Given the ecology of Yellow Rails and sedge systems, we believe further investigation into the relationship between these features and Yellow Rail use is warranted.

Although wetland habitat in the refuge was impacted by attempted drainage in the early 1900s and the creation of permanent pools in the 1930s, wetland habitats used by Yellow Rail in this study (primarily sedge-bluejoint grass and lowland shrub with woody cover $\leq 60\%$) today comprise 34% of the refuge's area. To what extent these habitat types have been lost to woody encroachment has not been investigated but is apparent for some areas, based on earlier reports and imagery. Long-term effects of drainage ditches dug in the early 1900s (Wilcox et al. 2006) and infrequent fires between 1976 and 2000 provided the conditions for woody encroachment into once-open wetlands. Refuge records compiled for this study indicate that the lowland shrub and sedge meadow areas we surveyed were burned zero to three times between the historic 1976 fire and 2000, when the current prescribed burning program was initiated. Drainage and infrequent fire, and fire suppression, likely also contributed to wetland losses documented in the region around Seney NWR. Based on records recorded in the General Land Office survey notes (1840-1856), Zhang *et al.* (2000) estimated that the proportion of wetlands in the poorly-drained Seney subdistrict (406,000 ha) declined from 22.6% to 10.8% by 1991 – a 46% decline.

Seney NWR has long been noted as an important breeding area for Yellow Rails, but may represent one end of the spectrum (sedge meadows intermixed with lowland woody and upland cover), whereas the extensive, homogeneous sedge meadows of southern James Bay (Robert *et al.* 2004) may represent the other end. While not all sedge meadow systems may be vulnerable to woody encroachment, further study is needed across the Yellow Rail's breeding range to clarify the relationship between shrub cover and Yellow Rail use and potential significance, and risk, of shrub encroachment into sedge meadows.

Our results suggest Yellow Rails use areas with moderate water levels, deep litter and low ground-level visibility at levels that are not too decadent or closed to encumber movement (Conway et al. 2010), and relatively low shrub cover and shrub heights, as well as use landscapes having low amounts of lowland woody or upland cover types. While these conditions may be sustained in some areas by natural flooding regimes, many sedge meadows are fire-dependent (Curtis 1959) and require both seasonal flooding and periodic fire. Our data suggest burning every 2-5 years is appropriate for providing the litter, ground-level cover, and woody conditions attractive to Yellow Rails. Where shrub cover is high, more intense or frequent fires, or fire in combination with mechanical treatment (Reuter 1986; Briggs et al. 2005), may be needed to reduce their dominance to levels more attractive to Yellow Rails. Managers seeking to restore and sustain these wetland systems for Yellow Rails would benefit from further investigations into how flooding and fire create habitat conditions attractive to breeding Yellow Rails.

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