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RESEARCH ARTICLE

Secretive marsh bird occupancy across a spectrum of hydroelectric reservoir management in western montane Canada

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Abstract

Dam construction projects have created opportunities for water security, targeted flood protection, and energy production but at the cost of increasing anthropogenic pressure on affected aquatic ecosystems. Wetland ecosystems are often among the most vulnerable, as underlying hydrological regimes influence overall wetland structure and function. Marsh bird species are wetland and riparian habitat specialists, many of which are experiencing population declines across North America. We examined how the alteration of hydrological regimes for generating hydroelectric power affected the occurrence of secretive marsh bird species in the western montane region of British Columbia, Canada. We established survey stations in wetlands across 2 regions, the West Kootenay and the Columbia Wetlands, sampling across a spectrum of hydrological regimes and other potentially relevant factors. At each station, we assessed wetland occupancy during the breeding season using broadcast-callback surveys focused on 5 secretive marsh bird species: American bittern (*Botaurus lentiginosus*), American coot (*Fulica americana*), pied-billed grebe (*Podilymbus podiceps*), sora (*Porzana carolina*), and Virginia rail (*Rallus limicola*). Additionally, we measured vegetation structure and the proximity and size

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of nearby water bodies for each survey station. We then used occupancy models to assess important correlates behind wetland occupancy for these marsh bird species, considering water management operations, regional differences, and local- and landscape-level wetland characteristics. Secretive marsh bird species were more likely to occupy wetlands in areas with less frequently altered hydrological regimes. Occupancy models highlighted local- and landscape-level characteristics as important correlates for wetland occupancy by marsh birds. Wetlands with frequently altered hydrological regimes had more open water cover and less tall vegetation present, conditions that were negatively associated with occupancy. Altered wetlands in this study were farther from the next nearest wetland, which was also negatively associated with occupancy. We suggest reservoir management is altering vegetation communities within these wetlands, indirectly promoting lower occupancy of secretive marsh bird species.

KEYWORDS
American bittern, American coot, occupancy model, pied-billed grebe, sora, Virginia rail, water management, wetland

Globally, more than half of the world's major river systems are affected by ≥1 large dam (Nilsson et al. 2005, Lehner et al. 2011, Grill et al. 2015). These projects have created opportunities for water security, targeted flood protection, and energy production but at the cost of increasing anthropogenic pressure on river and riparian ecosystems. The extent, type, and severity of these pressures can be site- and project-specific, requiring careful consideration of biogeophysical effects at multiple scales. The most apparent and arguably the most encompassing effects of these projects are disrupted or altered hydrological regimes.

Water reservoir projects can alter the amplitude, frequency, and seasonal timing of inundation, and can shift the hydrological regime within a given operational footprint. These changes can affect large areas in the surrounding regions, where entire ecosystems can experience shifts in their natural flow regimes and ecological functionality may be altered or lost entirely (Utzig and Schmidt 2011). Wetland ecosystems are frequently among the most vulnerable to reservoir project effects, as the underlying hydrological regime is a dominant influence on overall wetland structure and function. Effects include changes to water chemistry and quality (Toller 1994, Utzig and Schmidt 2011), disrupted sediment movement and deposition (Toller 1994, Toller and Nemetz 1997, Utzig and Schmidt 2011, Spellman 2015), and declines in primary productivity (Toller and Nemetz 1997, Utzig and Schmidt 2011). For example, emergent vegetation tends to dominate wetland environments and is well-adapted to seasonal flooding (Blom and Voesenek 1996); however, if inundation is too frequent or extreme, it can limit plant survival and establishment (Blom and Voesenek 1996, Campbell et al. 2016). This change can result in shifts to other vegetation assemblages and communities, a decline in overall diversity and complexity, invasive species colonization, or a loss of the wetland system (Bunn and Arthington 2002, Utzig and Schmidt 2011).

Marsh birds tend to be wetland and riparian habitat specialists, dependent on these communities for important periods of their life history. Marsh bird occupancy and density are often related to a combination of local- and landscape-level wetland characteristics. Greater availability of wetlands is often positively related to marsh bird species diversity (Brown and Dinsmore 1986, Fairbairn and Dinsmore 2001) and population densities (Fairbairn and Dinsmore 2001). The ratio of vegetation to open water cover, the vegetation community assemblage, and overall vegetation structure are often determinants of marsh bird presence (Kaminski and Prince 1981, Lor and Malecki 2006, Conway and Sulzman 2007, Baschuk et al. 2012, Nielson 2016). Altered hydrological regimes may be especially problematic if they skew open water-to-vegetation ratios in a less favorable direction or lead to the loss of key structural groups. These changes may ultimately result in wetlands that lack components necessary for marsh birds to survive and thrive.

Many marsh bird species are experiencing population declines across North America (Sauer et al. 2017), tied to the disappearing wetlands they depend on (Conway et al. 1994). While the requirements and status of some species are relatively well-studied, other species are more elusive. Secretive marsh birds, such as bitterns (subfamily Botaurinae), grebes (family Podicipedidae), and rails (family Rallidae), have cryptic coloration, are elusive, occupy densely vegetated areas, vocalize infrequently, and may vocalize very quietly (Conway 2011). Such species are often uncommon to see, making them challenging to study. The effects of wetland loss, degradation, and alteration on their populations are often poorly understood as a result. Secretive marsh birds are sensitive to altered hydrological regimes (Glisson et al. 2017, Harrity et al. 2020, Stevens and Conway 2020). Without a clear understanding of these populations and their requirements, conservation and management efforts can lack accurate targets and goals.

Our objective was to gauge whether increasing divergence from a natural regime influenced the occurrence of secretive marsh birds and characteristics of wetlands they inhabited. We predicted that as a landscape's hydrological regime became increasingly divergent from the natural regime, it would result in altered wetland characteristics and reduced availability of habitat across the landscape. Further, we predicted that wetlands that are never affected by management would feature wetland and landscape characteristics with which these species have co-evolved, making them most likely to be occupied by our study species.

STUDY AREA

We surveyed secretive marsh birds (i.e., marsh birds; Conway 2011) in the West Kootenay and Columbia Wetlands regions of British Columbia, Canada (Figure 1). Both regions are home to diverse wildlife communities. These communities also include several species of ungulate, such as white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and elk (*Cervus canadensis*), and carnivores, including grizzly bears (*Ursus arctos horribilis*), black bears (*U. americanus*), coyotes (*Canis latrans*), gray wolves (*C. lupus*), and cougars (*Puma concolor*). Our 2 study regions are both within the Columbia River watershed, which features the Columbia River flowing northwest through the Columbia Wetlands and turning southward through the West Kootenay region. The West Kootenay region features more developed waterways, while hydrological regimes within the Columbia Wetlands remain largely unmodified. Both regions are continental in climate, feature cold, snowy winters transitioning to hot summers, and encompass a range of wetland ecosystems. Peak water flows with the spring freshet from the surrounding mountain ranges generally occur between late May and early July. Timing and volume of the annual peak flow vary among locations and from year-to-year as a result of the preceding winter's snowpack, spring and summer temperatures, and rainfall. These factors affect natural wetlands and those associated with modified watercourses.

The West Kootenay region is situated between the Monashee and Purcell mountain ranges; we surveyed this area from 2013 to 2015 and 2017 to 2018. The complex geography of the region lends itself to an overall wetter climate compared to the Columbia Wetlands. Forested areas in the West Kootenay are generally dominated by coniferous species including western redcedar (*Thyja plicata*) and western hemlock (*Tsuga heterophylla*) in the lower elevations (Ketcheson et al. 1991), and Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in the higher elevations (Coupé et al. 1991). Land use varies throughout the

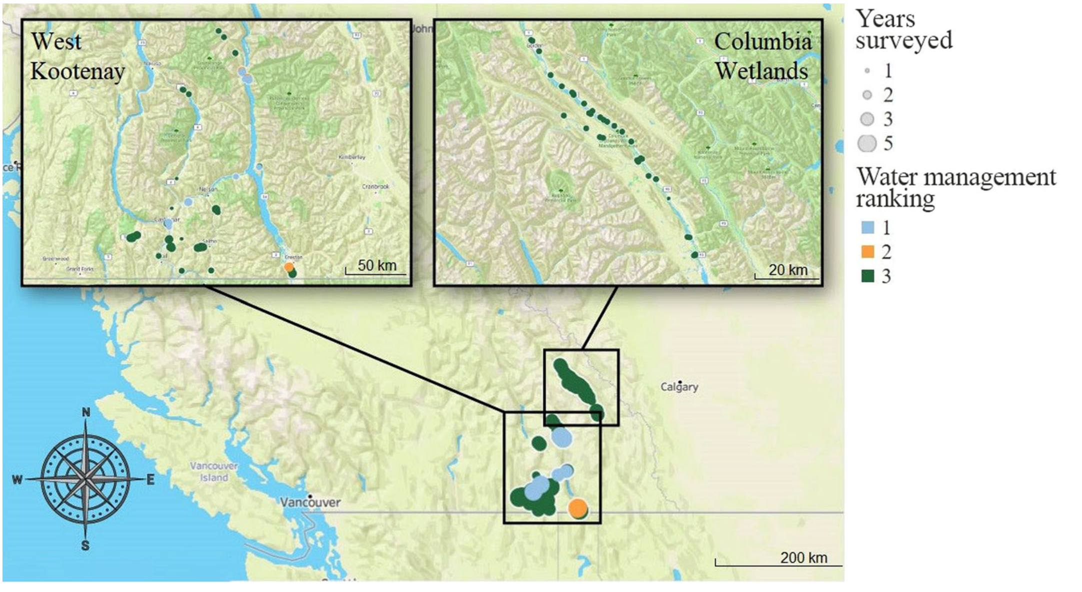

FIGURE 1 Southern British Columbia, Canada with insets of West Kootenay and Columbia Wetlands study regions. Relative size of points indicates the number of years the station has been surveyed, color indicates the frequency that a station was influenced by hydroelectric or water management projects (water management ranking). Water management rankings are categorized as 1 = station is always affected, 2 = station is occasionally affected, and 3 = station is never affected. The West Kootenay region was surveyed for marsh bird species from 2013 to 2015 and 2017 to 2018; the Columbia Wetlands region was surveyed from 2016 to 2018.

region, but includes outdoor recreation, forestry, mining, and agriculture. The West Kootenay region has been extensively developed by water management projects, including facilities operated by BC Hydro, FortisBC, Nelson Hydro, and Columbia Power. On a more localized scale, wetlands managed by Creston Valley Wildlife Management Area and Lower Kootenay Band are also present within the area. Reservoir operations affect the hydrological regime in complex ways (e.g., raising water levels upstream of the impoundment, modifying water-level fluctuations, altering flow regimes downstream). In the West Kootenay region, a chain of storage reservoirs exists such that 1 dam controls the water up to the next in such a way that upstream and downstream effects often overlap. Our West Kootenay study area covered approximately 2.2 million ha and encompassed multiple mountain ranges, lakes, and rivers. Survey stations within the West Kootenay region spanned elevations from approximately 420 m to 1,310 m above sea level.

The Columbia Wetlands are located within the Rocky Mountain Trench between the Rocky and Purcell mountain ranges; we surveyed this area between 2016 and 2018. These wetlands are the source of the Columbia River, occupying the floodplain from Canal Flats and flowing approximately 180 km north to the Kinbasket Reservoir (Pedology et al. 1983). The hydrological regime within the Columbia Wetlands between the communities of Canal Flats and Donald remains largely unaltered. Much of the Columbia Wetlands are relatively protected by their inclusion into the provincial Columbia Wetlands Wildlife Management Area and the federal Columbia National Wildlife Area, and in smaller parcels of private lands purchased by conservation land trusts. The Columbia Wetlands are internationally recognized as wetlands of importance under the United Nations' Ramsar Treaty, and represent a relatively unaffected region of habitat for a variety of wildlife species, including marsh birds (Darvill et al. 2023). The Columbia Wetlands study area covered >26,000 ha and encompassed a diverse mosaic of wetlands and other ecological communities. Survey stations within the Columbia Wetlands region spanned elevations from approximately 750 m to 1,300 m above sea level.

METHODS

Marsh bird surveys

Surveys were focused on 5 bird species: American bittern (*Botaurus lentiginosus*), American coot (*Fulica americana*), pied-billed grebe (*Podilymbus podiceps*), sora (*Porzana carolina*), and Virginia rail (*Rallus limicola*). These species are defined by Conway (2011) as secretive marsh birds and they vary in their degree of conspicuousness, diet, nesting preferences, and foraging strategies. These species potentially experience high or very high habitat-related effects from BC Hydro operations within the Columbia Basin (Manley and Krebs 2011). These qualitative ratings considered the effects of habitat alteration to individual wildlife species based on species-habitat associations and the risk of losing those habitats as a result of operations.

We selected survey stations to give an overall representation of wetlands in each region by sampling a range of wetland sizes, types, hydrological regimes, levels of productivity, elevations, relative isolation, and other potentially relevant factors (Table S1, available in Supporting Information). Given problems of road access to sites due to their remoteness and landowner permissions, we could not implement a stratified random sampling scheme. We sampled a variety of sites and habitat structures, given what was available and accessible, and so study sites are as representative as possible of the 2 regions. We recorded global positioning system coordinates of each survey station and spaced stations in accordance with the Standardized North American Marsh Bird Monitoring Protocol (Conway 2011).

We conducted single-observer bird surveys following the Prairie and Parkland Marsh Monitoring Program (Bird Studies Canada 2010) and the Standardized North American Marsh Bird Monitoring Protocol (Conway 2011). Survey effort varied over the years because of access, logistics, and available funding. We sampled the West Kootenay region from 2013 to 2015 and 2017 to 2018. We surveyed the Columbia Wetlands region between 2016 and 2018. As per protocol, the first surveys began as early as 30 minutes prior to sunrise (earliest occurring at 0502) and were completed by 1000 in almost all instances, the latest survey occurring at 1015 in 2017. We surveyed each station 2–3 times between 1 May and 6 July annually, based on timing windows outlined by Conway (2011) and the local spring conditions in each region. We surveyed reserve lands with permission of the Yaqan Nukiy (Lower Kootenay Band) in the West Kootenay and Akisqnuk Band (of Ktunaxa First Nation) in the Columbia Wetlands. Upon completion of the final bird surveys in late June and early July, we surveyed vegetation at each station once annually according to the Prairie and Parkland Marsh Monitoring Program protocol (Bird Studies Canada 2010). Vegetation surveys were focused on the structural composition of major land cover types and vegetation communities within a 100-m radius of the station (Bird Studies Canada 2010).

We collected landscape-level characteristics for each station regarding the proximity and size of nearby water bodies based on the British Columbia Freshwater Atlas, a standardized dataset mapping British Columbia's hydrological features that defines watershed boundaries, and the connected network of streams, lakes, and wetlands (Province of British Columbia 2021). We used geographical information system software to calculate the distance from each station's focal point location to the nearest wetland or lake (as a source of open water), and the area of each water body.

Water management rankings

We derived a simple ranking system that allowed us to gauge how increasing divergence from the natural hydrological regime of the region may have influenced marsh birds and the characteristics of wetlands they occupy. This ordinal rank was based on how frequently the associated wetland at each station was affected by reservoir management-related activities, and was treated as a fixed attribute to each station throughout our study. We defined the rankings as 1 = station was always affected by reservoir management, 2 = station was occasionally affected, and 3 = station was never affected. Stations with a ranking of 1 were immediately adjacent to a body of water (reservoir) under control for generation of hydropower. We assigned a ranking of 2 to stations only influenced in years where regional water levels were elevated to the extent that its wetland connected to a managed waterway; these stations were sometimes affected by reservoir operations, depending on the year and water levels in the region. We assigned a ranking of 3 to stations with no direct influence from reservoir operations.

In the West Kootenay region, all stations >600 m in elevation were isolated from managed waterways and had a ranking of 3. Below 600 m in the West Kootenay region, all 3 rankings occurred at stations. In the Columbia Wetlands, regardless of elevation, all stations were not affected by water management activities related to dam or impoundment infrastructure. Therefore, all stations within the Columbia Wetlands had a rank of 3. A ranking of 3 indicates that the hydrological regime of the wetland is unaffected by water management actions but does not necessarily reflect whether other sources of ecological or anthropogenic disturbance currently or have previously affected the site.

Habitat analyses and occupancy modeling

We used occupancy models to assess the important correlates behind wetland occupancy for 5 secretive marsh bird species, considering water management operations, regional differences, and local- and landscape-level wetland characteristics. We began by examining whether local- and landscape-level wetland characteristics differed among the water management rankings and between study regions. Local-level wetland characteristics included relative percent cover of open water and floating vegetation, woody vegetation (i.e., trees and shrubs), emergent vegetation (all species present), and tall vegetation (specifically, cattails [*Typha* spp.], and rushes [*Scirpus* and *Juncus* spp.]), and elevation (Table 1). Landscape-level wetland characteristics included distance to and area of the nearest lake and wetland (Table 1) to the survey station. Shapiro-Wilk tests determined that data were not normally distributed (all $P < 0.05$). We used Kruskal-Wallis tests to consider differences between water management rankings (within the West Kootenay region) and Wilcoxon ranked-sum tests to consider regional differences (stations with a rank of 3 only) using R (R Core Team 2020).

TABLE 1 Descriptions of local- and landscape-level wetland characteristics considered to model wetland occupancy by secretive marsh bird species in the West Kootenay and Columbia Wetlands regions of British Columbia, Canada. Survey stations within the West Kootenay region were surveyed for marsh bird species from 2013 to 2015 and 2017 to 2018; stations within the Columbia Wetlands region were surveyed from 2016 to 2018.

Characteristic	Scale	Description
Open water and floating vegetation	Local	Relative percent cover of open water and floating vegetation within 100 m of a survey point.
Woody vegetation	Local	Relative percent cover of woody vegetation (i.e., trees and shrubs) within 100 m of a survey point.
Emergent vegetation	Local	Relative percent cover of emergent vegetation within 100 m of a survey point. Includes all herbaceous emergent vegetation species present in survey area, including but not limited to, cattails, rushes, reeds (*Phragmites* and *Phalaris* spp.), spike-rushes (*Eleocharis* spp.), horsetails (*Equisetum* spp.), and pondweed (*Potamogeton* spp.).
Tall vegetation	Local	Relative percent cover of tall vegetation (i.e., specifically cattails and rushes) within 100 m of a survey point.
Elevation	Local	Distance above sea level of survey point (m).
Distance to nearest lake	Landscape	Distance from a survey point to the nearest freshwater lake in m.
Area of nearest lake	Landscape	Area of the nearest freshwater lake to a survey point in m^2.
Distance to nearest wetland	Landscape	Distance from a survey point to the nearest wetland in m.
Area of nearest wetland	Landscape	Area of the nearest wetland to a survey point in m^2.

We examined wetland occupancy of marsh bird species using the unmarked package in R (Fiske and Chandler 2011). Occupancy modeling separates the probability of detection (p) from the probability of occupancy (Ψ), and we used a staged approach in the model selection. We first looked at seasonal differences in detection (Conway and Gibbs 2011), followed by a sequential series of model suites examining occupancy considering regional differences, local variables, and then both, incorporating the best models from the prior suite into the next. In the first step, we modeled p as a function of seasonal timing, considering linear and quadratic relationships between detection probability and date while holding Ψ constant. In the second step, we examined how water management ranking, year, and region influenced Ψ using the best supported model for detection from the first step. This step produced a base model of detection and occupancy, which we could then use to further consider the role of local- and landscape-level wetland variables. We first considered these variables separately, modeling occupancy as a function of local- and landscape-level wetland characteristics. In both study regions, relative percent cover of open water and emergent vegetation were strongly negatively correlated (Columbia Wetlands: $r = -0.89$, $P \leq 0.001$; West Kootenay: $r = -0.85$, $P \leq 0.001$). Therefore, we removed emergent vegetation from further modeling. In the final step, we considered the local- and landscape-level characteristics from the highest-ranking models together to produce a final occupancy model. At each stage, we ranked models based on Akaike's Information Criterion (AIC; Burnham et al. 2011) values, and selected the model with the lowest AIC value to move into the next stage of complexity, with a few exceptions to account for model fit and convergence. This approach allowed us to first address any methodological considerations that might have affected detection rates; determine whether any broad differences in occupancy exist across the water management categories, regions, or study years; and lastly investigate what, if any, local- and landscape-level wetland characteristics might be influencing these differences. We centered and scaled local- and landscape-level wetland characteristics using the scale function within R prior to modeling. We used a parametric bootstrap function using a χ^2 statistic and 100 replicates to assess the goodness of fit for the final model.

RESULTS

We surveyed between 34 and 53 stations in the West Kootenay (Table 2), and between 33 and 35 stations in the Columbia Wetlands (Table 3) each year of the study. Water management rankings varied in the West Kootenay: 5–9 stations assigned a rank of 1 (always affected), 7 stations assigned a rank of 2 (sometimes affected), and 22–37 stations assigned a rank of 3 (never affected) were surveyed each year (Table 2). All stations within the Columbia Wetlands were assigned a rank of 3 (Table 3).

The 5 focal species varied in abundance. We never detected American bitterns within the West Kootenay region (Table 2) and detected them only at a few stations in the Columbia Wetlands (on average 2% of the stations/year; Table 3). American coot, pied-billed grebe, and sora had moderate frequencies of detections (i.e., 18–35% of stations/year) in the West Kootenay (Table 2), and were observed with higher rates of detections in the Columbia Wetlands (i.e., 33–82% of stations/year; Table 3). Virginia rail had moderate rates of detection (~33% of stations/year) in the West Kootenay and Columbia Wetlands regions (Tables 2 and 3).

Wetland characteristics

Wetland characteristics at local- and landscape-level spatial scales varied with water management rankings and, to some extent, region (Table 4; Figures 2 and 3). All wetland characteristics differed significantly between rankings in the West Kootenay region (Table 4). Among local-level wetland characteristics, open water cover was highest at rank 1 stations, emergent and tall vegetation cover were both highest at rank 2 stations, and woody vegetation cover was highest at rank 3 stations (Figure 2). The relative percent cover of open water and emergent vegetation was not significantly different between regions, but woody and tall vegetation cover were both higher at the

TABLE 2 Summary of stations, survey effort, occupancy, and number of detections by year and water management ranking in the West Kootenay study region, British Columbia, Canada. Survey stations within the West Kootenay region were surveyed for marsh bird species from 2013 to 2015 and 2017 to 2018. Stations occupied summarizes the percentage of stations where ≥1 bird was detected during ≥1 survey/season and in parentheses are the number of birds detected. Survey effort denotes the number of surveys conducted. Water management rankings are categorized as 1 = station is always affected by water management operations, 2 = station is occasionally affected, and 3 = station is never affected. Averages are weighted to consider annual survey effort.

				% Stations occupied (number of detections)				
Year	Ranking	Stations	Survey effort	American bittern	American coot	Pied-billed grebe	Sora	Virginia rail
2013	1	9	24	0 (0)	11 (4)	11 (1)	33 (3)	0 (0)
	2	7	20	0 (0)	71 (60)	86 (29)	71 (21)	57 (16)
	3	34	95	0 (0)	24 (33)	12 (7)	35 (39)	41 (41)
	Total	50	139	0 (0)	28 (97)	22 (37)	40 (63)	36 (57)
2014	1	9	27	0 (0)	11 (1)	22 (6)	44 (6)	0 (0)
	2	7	21	0 (0)	57 (36)	71 (18)	57 (17)	71 (16)
	3	37	103	0 (0)	19 (28)	5 (4)	27 (43)	35 (51)
	Total	53	151	0 (0)	23 (65)	17 (28)	34 (66)	34 (67)
2015	1	9	26	0 (0)	0 (0)	0 (0)	33 (9)	11 (6)
	2	7	20	0 (0)	43 (7)	43 (2)	86 (33)	43 (17)
	3	37	106	0 (0)	14 (29)	22 (19)	32 (46)	43 (81)
	Total	53	152	0 (0)	15 (36)	21 (21)	39 (88)	38 (104)
2017	1	5	15	0 (0)	20 (2)	0 (0)	60 (4)	40 (4)
	2	7	21	0 (0)	43 (49)	43 (10)	71 (23)	43 (6)
	3	28	84	0 (0)	14 (18)	7 (9)	18 (30)	29 (26)
	Total	40	120	0 (0)	20 (69)	12 (19)	33 (57)	33 (36)
2018	1	5	15	0 (0)	0 (0)	0 (0)	20 (5)	20 (2)
	2	7	21	0 (0)	57 (54)	29 (8)	100 (33)	57 (13)
	3	22	64	0 (0)	23 (28)	18 (7)	14 (23)	36 (34)
	Total	34	100	0 (0)	27 (82)	18 (15)	33 (61)	38 (49)
Average	1	7	21	0 (0)	8 (1)	7 (1)	38 (5)	14 (2)
	2	7	21	0 (0)	54 (41)	54 (13)	77 (25)	54 (14)
	3	32	90	0 (0)	19 (27)	13 (9)	25 (36)	37 (47)
	Total	46	132	0 (0)	23 (70)	18 (24)	35 (67)	36 (63)

Columbia Wetlands stations. Among landscape-level characteristics, rank 1 stations tended to be farther from the next nearest lake and wetland; however, the next nearest lakes tended to be very large (Figure 3). The 2 study regions did not differ significantly in distance to the nearest wetland but differed in distance to the nearest lake and in the area of both nearest lake and wetland (Figure 3).

TABLE 3 Summary of stations, survey effort, occupancy, and number of detections by year in the Columbia Wetlands, British Columbia, Canada. Survey stations within the Columbia Wetlands region were surveyed from 2016 to 2018. Stations occupied summarizes the percentage of stations where ≥1 bird was detected during ≥1 survey/season and in parentheses are the number of birds detected. Survey effort denotes the number of surveys conducted. All stations have a water management ranking of 3 (i.e., the stations are never affected by water management or hydro operations). Averages are weighted to consider annual survey effort.

				% Stations occupied (number of detections)				
Year	Ranking	Stations	Survey effort	American bittern	American coot	Pied-billed grebe	Sora	Virginia rail
2016	3	35	100	0 (0)	43 (106)	74 (104)	83 (143)	23 (10)
2017	3	34	102	3 (6)	24 (34)	74 (97)	79 (89)	41 (29)
2018	3	33	99	3 (4)	33 (45)	67 (66)	85 (99)	30 (23)
Average		34	100	2 (3)	33 (62)	72 (89)	82 (110)	31 (21)

TABLE 4 Comparing wetland characteristics between water management rankings in the West Kootenay (ranking, Kruskal-Wallis tests) and stations that are never affected (rank 3) in both study regions (region, Wilcoxon rank sum tests) in British Columbia, Canada. Survey stations within the West Kootenay region were surveyed for marsh bird species from 2013 to 2015 and 2017 to 2018; stations within the Columbia Wetlands region were surveyed from 2016 to 2018.

Variable	Comparison	Test statistic	df	*P*-value
Open water and floating vegetation	Ranking	$\chi^2 = 39$	2	≤0.001
	Region	W = 7,432	1	0.577
Emergent vegetation	Ranking	$\chi^2 = 31$	2	≤0.001
	Region	W = 3,321	1	0.958
Tall vegetation	Ranking	$\chi^2 = 15$	2	≤0.001
	Region	W = 11,662	1	≤0.001
Woody vegetation	Ranking	$\chi^2 = 44$	2	≤0.001
	Region	W = 9,322	1	0.006
Distance to nearest lake	Ranking	$\chi^2 = 7$	2	0.026
	Region	W = 5,740	1	≤0.001
Area of nearest lake	Ranking	$\chi^2 = 11$	2	0.003
	Region	W = 10,879	1	≤0.001
Distance to nearest wetland	Ranking	$\chi^2 = 23$	2	≤0.001
	Region	W = 7,966	1	0.707
Area of nearest wetland	Ranking	$\chi^2 = 39$	2	≤0.001
	Region	W = 11,034	1	≤0.001

Marsh bird occupancy

We were able to model the occupancy of wetland stations for American coot, pied-billed grebe, sora, and Virginia rail (Figure 4; Table S2, available in Supporting Information). There were not enough detections to reliably model the occupancy of wetlands by American bitterns (Tables 2 and 3).

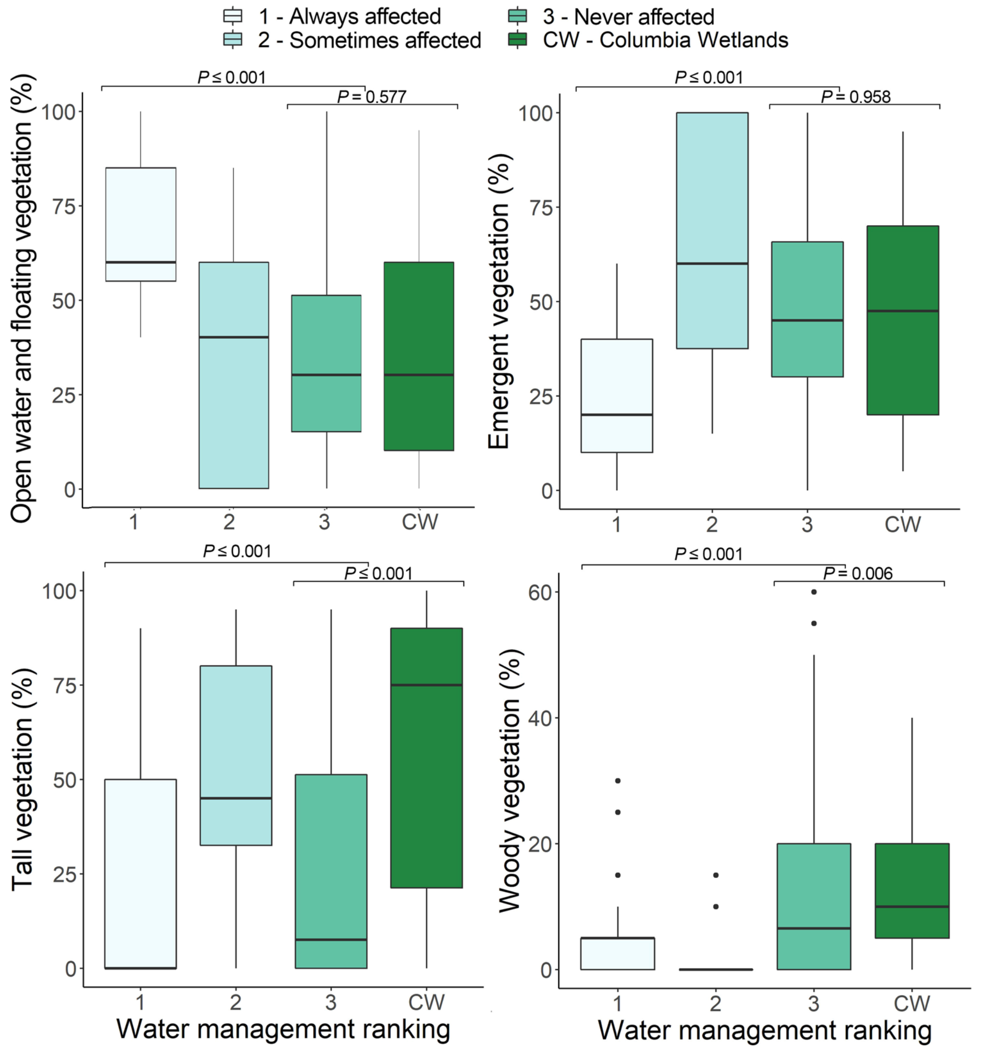

FIGURE 2 Box plots depicting relative percent cover of wetland characteristics at survey stations in the West Kootenay and Columbia Wetlands regions of British Columbia, Canada. Survey stations within the West Kootenay region were surveyed for marsh bird species from 2013 to 2015 and 2017 to 2018; stations within the Columbia Wetlands region were surveyed from 2016 to 2018. Stations in the West Kootenay are partitioned by water management rankings categorized as 1 = station is always affected by water management operations, 2 = station is occasionally affected, and 3 = station is never affected. Columbia Wetlands stations are all categorized as rank 3 and are included as reference. Tall vegetation (cattails, sedges, and rushes only) is a subset of emergent vegetation (all emergent species). Bold, horizontal lines within each plot indicate median value and the box summarizes the inter-quartile range. Results of Kruskal-Wallis (West Kootenay, comparison between water management rankings) and Wilcoxon rank sum (comparison between both regions, water management ranking of 3) tests are displayed above respective groupings of box plots.

The presence of American coot was best modeled with the probability of detection as a negative linear function of survey date, indicating a decline over the season (logit-scale beta ± SE = −0.52 ± 0.14). After accounting for detection, the best model suggested that there were regional differences in station occupancy (−2.10 ± 0.59, odds ratio [OR] = 0.12), with American coot being more likely to occupy stations in the Columbia Wetlands than the West Kootenay. There was evidence that station occupancy was affected by water management for American coot, with

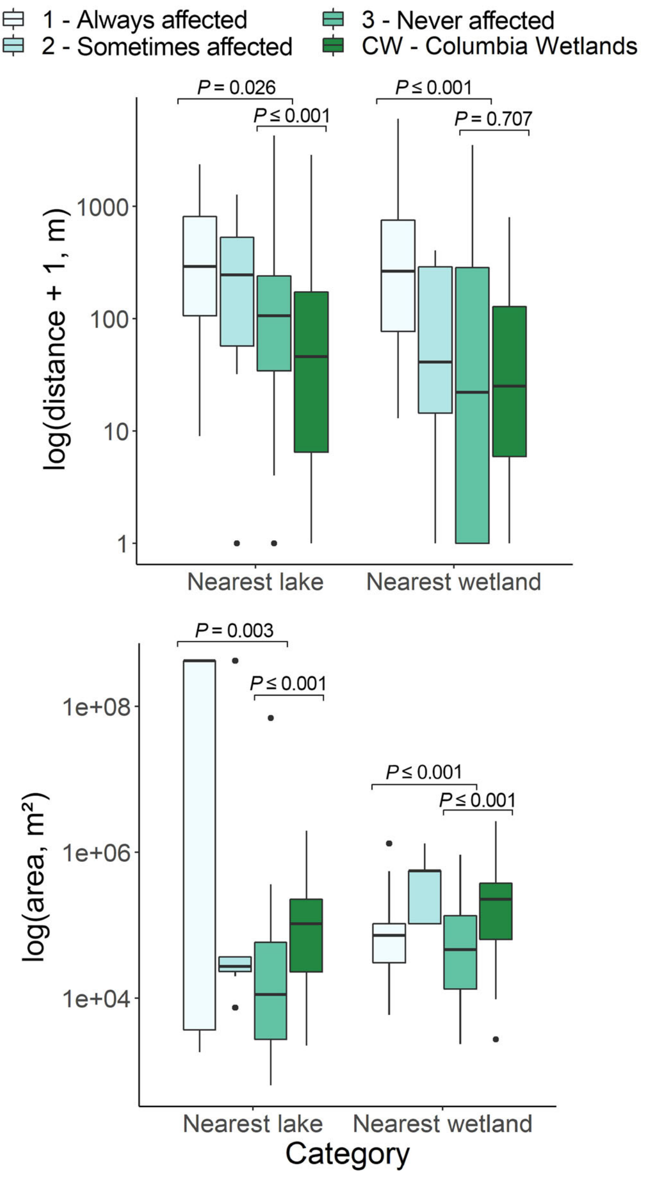

FIGURE 3 Box plots depicting the area and distance to the nearest lake and wetland from each survey station in the West Kootenay and Columbia Wetlands regions of British Columbia, Canada. Survey stations within the West Kootenay region were surveyed for marsh bird species from 2013 to 2015 and 2017 to 2018; stations within the Columbia Wetlands region were surveyed from 2016 to 2018. Area is log-transformed and distance is shown as log(distance + 1) to include distances of zero. For reference, the mean distance to the nearest lake was 421 m (range = 0–4,283 m) and to the nearest wetland was 300 m (range = 0–6,045 m), respectively. The mean area of the nearest lake was 31,869,406 m^2 (range = 641–422,658,880 m^2) and of the nearest wetland was 274,263 m^2 (range = 2,330–2,664,020 m^2), respectively. Stations in the West Kootenay are partitioned by water management rankings, which are categorized as 1 = station is always affected by water management operations, 2 = station is occasionally affected, and 3 = station is never affected. Columbia Wetlands stations are all categorized as rank 3 and are included as reference. Bold, horizontal lines within each plot indicate median value and the box summarizes the inter-quartile range. Results of Kruskal-Wallis (West Kootenay, comparison between water management rankings) and Wilcoxon rank sum (comparison between both regions, water management ranking of 3) tests are displayed above respective groupings of boxplots.

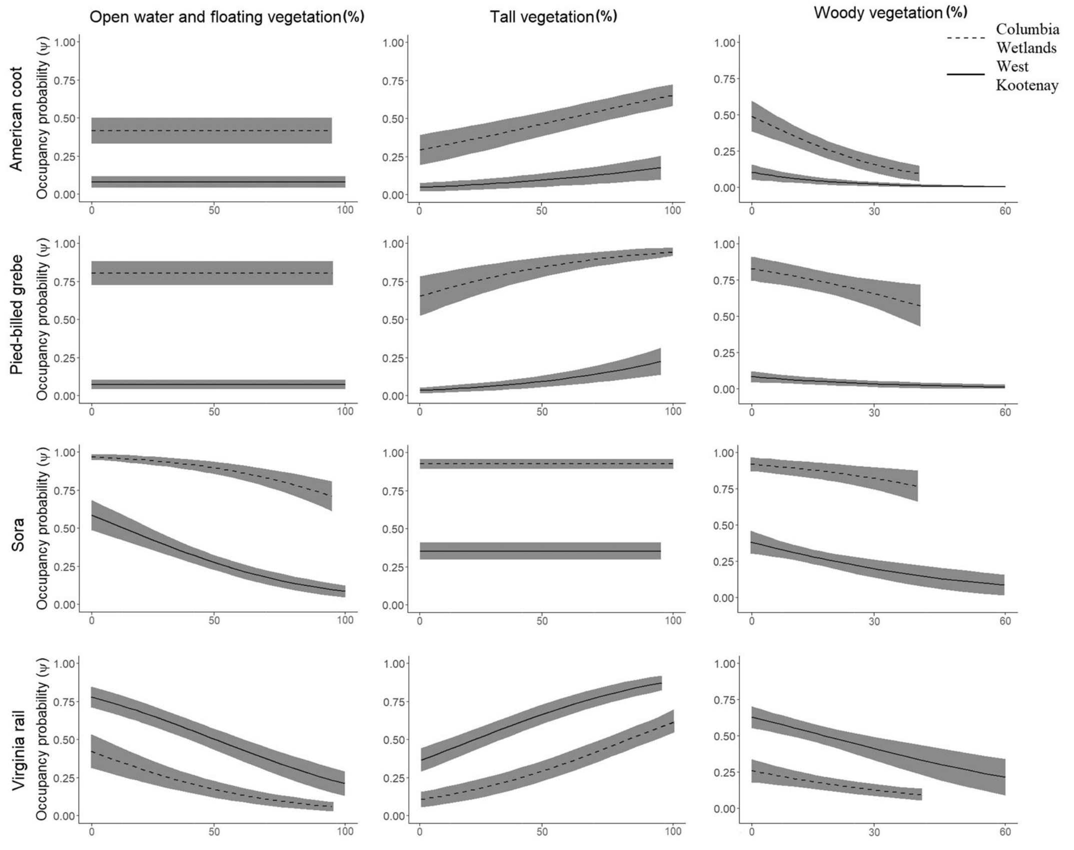

FIGURE 4 Plots depicting the probability of occupancy (Ψ) as predicted by wetland characteristics in both the West Kootenay (solid) and Columbia Wetland (dashed) regions in British Columbia, Canada. Survey stations within the West Kootenay region were surveyed for marsh bird species from 2013 to 2015 and 2017 to 2018; stations within the Columbia Wetlands region were surveyed from 2016 to 2018. Plots are based on the top model predicting occupancy of American coot, pied-billed grebe, sora, and Virginia rail, and examine Ψ as a function of the relative percent cover of open water and floating vegetation, tall vegetation, and woody vegetation. Plots assume remaining variables are at the median observed value in this study for each region. The *x*-axis depicts each wetland characteristic from its minimum and maximum observed values. Shaded areas depict standard error.

an increasing probability of occupancy at stations that were less frequently affected by reservoir operations (rank 2 = 2.76 ± 0.75, OR = 15.83; rank 3 = 3.42 ± 0.83, OR = 30.47). Additionally, American coot were more likely to occupy stations at lower elevations (−2.83 ± 0.64, OR = 0.06), with more tall vegetation (0.57 ± 0.20, OR = 1.76) and less woody vegetation (−0.72 ± 0.28, OR = 0.49). There was no evidence that American coot occupancy of wetlands was influenced by distance to and area of the nearest lake and wetland.

The presence of pied-billed grebe was best modeled with the probability of detection as a quadratic function of survey date (day: 1.99 ± 0.52, day^2 = −1.94 ± 0.52). The probability of detecting pied-billed grebes increased from the beginning of May until a peak around 12 June before declining for the remainder of the season. After controlling for detection, the best model indicated regional differences in occupancy (−3.96 ± 0.68, OR = 0.02), with pied-billed grebe being more likely to occupy stations in the Columbia Wetlands compared to the West Kootenay. There was evidence that occupancy for pied-billed grebe differed by water management rank (rank 2 = 2.18 ± 0.75, OR = 8.83; rank 3 = 1.78 ± 0.74, OR = 5.95). Additionally, pied-billed grebes were more likely to occupy stations at lower elevations (−1.70 ± 0.48, OR = 0.18), with more tall vegetation (0.82 ± 0.23, OR = 2.26), and less woody vegetation (−0.41 ± 0.29, OR = 0.66). At the landscape-level, pied-billed grebes were less likely to occupy stations with increasing distance to the nearest lake (−0.44 ± 0.22, OR = 0.64) and more likely with increasing size of the nearest wetland (0.47 ± 0.31, OR = 1.61).

The top model for sora in the candidate set examining temporal effects on detection was the null model, although χ^2 tests suggested this model did not adequately fit the data. The model considering a quadratic function of survey date was also well-supported (ΔAIC < 2) and provided adequate model fit; therefore, we selected this detection model to move forward. This model indicated probability of detecting sora increased from the beginning of May until a peak around 12 June before declining for the remainder of the season (day = 0.51 ± 0.41; day^2 = −0.48 ± 0.41). After controlling for detection, the best model suggested regional differences in station occupancy (−3.13 ± 0.48, OR = 0.04), with sora being more likely to occupy stations in the Columbia Wetlands compared to the West Kootenay. Station occupancy was affected by water management for sora (rank 2 = 1.09 ± 0.68, OR = 2.97; rank 3 = 0.36 ± 0.52, OR = 1.43). Additionally, sora were more likely to occupy stations at lower elevations (−1.00 ± 0.21, OR = 0.37), with less open water (−0.77 ± 0.22, OR = 0.46), and less woody vegetation (−0.50 ± 0.20, OR = 0.61). When modeling landscape-level characteristics, the models incorporating area of and distance to the nearest lake had problematic convergence, and so we selected the models with the next lowest ΔAIC values to move forward. At the landscape-level, sora were more likely to occupy stations with increasing size of the nearest wetland (0.78 ± 0.34, OR = 2.19).

The presence of Virginia rail was best modeled with the probability of detection as a linear function of survey date with indications that probability of detection increased through the season (0.53 ± 0.12). After controlling for detection, models considering water management ranking exclusively and in combination with region were both well-supported and provided adequate model fit based on χ^2 tests. Both base models produced similar results in subsequent modeling stages; however, we felt there were important considerations for retaining regional differences within the model. Therefore, we selected the model including both region and water management ranking as the best model to move forward. This model indicated regional differences in station occupancy (1.57 ± 0.43, OR = 4.82); however, in contrast to the other species, Virginia rail were more likely to occupy stations in the West Kootenay rather than the Columbia Wetlands. Station occupancy was affected by water management for Virginia rail, with an increasing chance of occupancy with decreasing frequency of management (rank 2 = 1.36 ± 0.75, OR = 3.90; rank 3 = 2.56 ± 0.72, OR = 12.98). Additionally, Virginia rail were more likely to occupy stations at lower elevations (−0.87 ± 0.25, OR = 0.42), with more tall vegetation (0.97 ± 0.21, OR = 2.63), less open water (−0.73 ± 0.20, OR = 0.48), and less woody vegetation (−0.39 ± 0.19, OR = 0.68). At a landscape level, Virginia rail were less likely to occupy stations with increasing distance to the nearest wetland (−0.82 ± 0.35, OR = 0.44).

DISCUSSION

The Columbia Basin has been altered by water management projects built for flood control and hydroelectric power production (Toller and Nemetz 1997). While water management projects provide socioeconomic value and services to human communities, they do so with ecological costs to connected river and riparian ecosystems. The Columbia Basin is no exception, as projects in this watershed contributed to wetland loss and alteration (Utzig and Schmidt 2011). Recent population declines of many marsh bird species are closely tied to disappearing wetlands, making it imperative that we gain a better understanding of these secretive species to assist with management and conservation efforts. Given the specialist nature of marsh birds, we initially predicted that occupancy would be at least partially influenced by altered hydrological regimes. We predicted that as the hydrological regime of a landscape became increasingly divergent from a natural regime, we would observe increasingly altered wetland characteristics and reduced availability of habitat across the landscape. Additionally, we predicted that wetlands that were never affected by management would be most likely to be occupied, as they would feature wetland and landscape characteristics with which these species have co-evolved. In keeping with this prediction, we expected that there would be a clear preference for the Columbia Wetlands, a relatively unaffected refuge of wetland habitat relative to the West Kootenay. While our modeling results largely supported these predictions, we did find unexpected nuance in the occupancy of some species.

In both regions of our study, a range of available wetlands were present, varying in size, vegetation assemblage, level of productivity, elevation, relative isolation, and other potentially relevant factors. Therefore, in addition to sampling across a spectrum of water management regimes, our site selection also considered an overall representation of the variation in available wetlands. Reservoir management influences wetland occupancy at a wetland-scale, landscape-scale, or both, depending on the species. American bitterns were absent from the West Kootenay region and were only observed at a few sites within a particular area in the Columbia Wetlands, highlighting that this species may be most frequently found in relatively remote and pristine areas. Water management rankings were a significant correlate of wetland occupancy for American coot, pied-billed grebe, sora, and Virginia rail. Further supporting our initial predictions, American coot, pied-billed grebe, and sora were more likely to occupy sites within the Columbia Wetlands. Virginia rail differed from the other species and were more likely to occupy wetlands in the West Kootenay.

Our water management rankings provided a gauge of increasing divergence from the natural hydrological regime of the region. While effect sizes suggested that water management ranking was generally the strongest correlate of wetland occupancy, it alone did not explain all the variation in occupancy. Local- and landscape-level characteristics provided additional context for modeling occupancy in all 4 species. Stations that were always affected by reservoir management tended to have more open water and less emergent vegetation present, conditions that generally promoted lower occupancy across our study species. Hydrological regime is an important determinant of the physical and biological composition of aquatic and semi-aquatic ecosystems (Bunn and Arthington 2002). Altered flow and inundation can spur habitat loss or alteration (Utzig and Schmidt 2011) and shift vegetation communities (Blom and Voesenek 1996, Nilsson et al. 1997, Ellis et al. 2009, Campbell et al. 2016). The relationship between breeding marsh bird species and emergent vegetation cover is well-established in other managed wetland systems (Fairbairn and Dinsmore 2001, Lor and Malecki 2006, Darrah and Krementz 2009, Bolenbaugh et al. 2011, Baschuk et al. 2012), and seems to hold in the western montane regions of Canada. Marsh-specialists rely on the emergent vegetation community to provide protective cover, nesting material (Gorenzel et al. 1982, Forbes et al. 1989), and sources of food (Horak 1970). Further, dead stems of fibrous plant species such as cattails and rushes tend to persist over-winter, often providing valuable early spring cover and nesting material before live material has begun to establish (Gorenzel et al. 1982, Forbes et al. 1989, Lor and Malecki 2006). Limited tall vegetation coupled with extensive open water may have deterred marsh birds from using the stations, especially in spring when they are likely searching for adequate protective cover and potential nesting sites with readily available nesting material. Negative relationships between marsh birds and woody vegetation cover are also well-supported in the literature (Naugle et al. 1999, Darrah and Krementz 2010, Bolenbaugh et al. 2011, Nielson 2016, Tozer 2016). This relationship is less well-understood, and a possibility could be that woody vegetation creates more perching sites and foraging areas for predators (Naugle et al. 1999, Darrah and Krementz 2010), which may deter marsh birds.

Wetlands consistently affected by hydro reservoir management were farther from the next nearest lake or wetland. With these wetlands, the next nearest lake also tended to be larger, though the next nearest wetland tended to be comparable in size. Habitat connectivity and relative isolation are frequently associated with species richness and assemblages (Brown and Dinsmore 1986, Craig and Beal 1992). The importance of these features varied among species, possibly depending on whether the species was nesting or foraging when it was detected (Craig and Beal 1992). Generally, local-level characteristics tended to be stronger correlates of occupancy than landscape-level traits. This result is similar to previous studies involving our focal species (Tozer 2016), possibly indicating the need to prioritize local wetland characteristics in management plans. We caution, however, that this does not mean that landscape-level considerations should be neglected in planning and decision-making. As evidenced in this study, and others (Toller 1994, Toller and Nemetz 1997, Utzig and Schmidt 2011), landscape-level decisions and conditions can have local-level effects.

While the secretive marsh bird species in our study exhibited lower occupancy at the most frequently affected wetlands, wetlands that were never affected were not necessarily the most likely to be occupied. Both pied-billed grebe and sora were most likely to occupy wetlands that were occasionally affected (rank 2). For pied-billed grebe and sora, these stations may offer a more favorable balance of local- and landscape-characteristics. Wetlands within this category are typically only affected by reservoir management in years where water levels are high enough to connect them to managed waterways. This mild-to-moderate influence on the natural disturbance regime may be enough to enhance conditions for emergent vegetation establishment and renewal without overwhelming that growth. The increased vegetation cover within wetlands and larger wetland area within the landscape likely explain the preference of pied-billed grebe and sora for these occasionally affected stations. A similar phenomenon was noted in wetlands managed for waterfowl, where moderately managed wetlands tended to have higher marsh bird occupancy (Bradshaw et al. 2020). It should be noted, however, that this does not necessarily reflect the diverse needs of other wetland species during their breeding seasons, which may be adversely affected by these influences.

As hydrological regimes were increasingly altered by reservoir operations, habitat changes were observed at local- and landscape-levels, shifting towards a wetland state that was less desirable for breeding marsh birds. Generally, local-level wetland characteristics were stronger correlates of occupancy than those at the landscape level; however, landscape-level pressures have direct implications for local-level habitat, evidenced in our study by the strong differences in habitat features among the 3 hydro rankings. Overall, focal marsh bird species in our study were more likely to occupy wetlands with a less altered hydrological regime, largely driven by a desirable balance of local- and landscape-level characteristics.

MANAGEMENT IMPLICATIONS

Our study demonstrates that sites with more natural hydrological regimes, little woody vegetation, small to moderate amounts of open water, moderate to ample amounts of tall emergent vegetation, and closer proximity of large wetlands tended to promote higher wetland occupancy of secretive marsh bird species. Wetlands more frequently affected by reservoir management tended to have less emergent vegetation, more open water, and the next nearest wetlands tended to be farther away, all conditions that negatively influenced wetland occupancy. Ideally, wetlands within a region will possess diverse conditions with varying ratios of interspersed open water and emergent vegetation to meet the needs for a range of species. Secretive marsh birds in regions where water levels are heavily managed for the purpose of hydropower generation will be best supported by conserving wetlands that are relatively ecologically intact and restoring desirable habitat features in wetlands that have been degraded or altered.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All surveys conducted as part of this research were observational and required no handling of birds. Care was taken to limit disturbance to wetland birds during the breeding season in the West Kootenay and Columbia Wetlands regions of British Columbia, Canada.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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