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Distribution of Canadian Rocky Mountain Wetlands Impacted by Beaver

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Abstract Mountain wetlands, although limited in their spatial extent, provide many important hydrological and ecological services. There is a need to know existing beaver habitation patterns across mountain wetlands because of emerging interest in using beaver to restore and protect riparian and wetland habitats. However, there exist few inventories of wetlands, or their use as beaver habitat, for any mountain region of North America. We studied the distribution of beaver-impacted mineral wetlands and peatlands in a 7,912 km² area of the Canadian Rocky Mountains. Using aerial photography and an existing wetland database, we inventoried 529 wetlands at elevations of 1,215 to 2,194 m; peat soils were found at 69 % of the 81 field verified wetlands. Wetland distribution and beaver habitation varied by physiography and jurisdiction. While 75 % of the wetlands identified were located in the foothills region, beaver were twice as likely to inhabit those in the mountain region owing to differences in land use activities and wildlife conservation measures. Wetlands inhabited by beaver had an order of magnitude greater area of open water and 12 times the number of individual open water features than those without. Beaver-enhanced open water extent has far-reaching consequences for wetland ecohydrological and biogeochemical functioning.

Keywords *Castor canadensis* · Ecohydrology · Open Water · Peatlands · Mineral Wetlands · Inventory

Introduction

Beaver (*Castor canadensis* and *C. fiber*) have long been recognized as agents of hydrogeomorphic and ecological change, owing largely to their dam building abilities (Gurnell 1998). Although best known for building dams across streams that create and maintain wetland conditions in riparian areas (Westbrook et al. 2006), beaver can also inhabit pre-existing wetlands, including peatlands (Johnston 2012). The beaver population is believed to be rebounding in North America due to conservation measures (Gibson and Olden 2014). Climate change may also increase the beaver population; Jarema et al. (2009) predicted that the beaver population would respond to a warmer future climate with a modest range expansion a substantial increase in density in the range interior (Jarema et al. 2009). Other factors that affect the North American beaver population include new re-introduction efforts geared toward using beaver as a tool for wetland restoration (Conover 2011) and water management (Tömbloom et al. 2011), particularly in North America's water towers, the Rocky Mountains (Baldwin 2013; Pollock et al. 2014). Information on existing beaver pond density is therefore desirable (Butler 2012), but unfortunately, there exist few inventories of wetlands (Chimner et al. 2010), or their use as beaver habitat, for any mountain region of North America. The purpose of this research is thus to better understand how beaver modify the environment by evaluating the distribution and abundance of beaver ponds in mineral wetlands and peatlands across varying land management jurisdictions in the Northern Rocky Mountains.

Evaluating wetland extent and distribution in the mountains is challenging because a wide range of wetland types occurs over very short distances. This is because the supporting hydrological characteristics can change at small spatial scales owing to variations in topography, geology and geochemistry (Cooper et al. 2012). Although there has yet to

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be a systematic inventory of wetland distribution in the Rocky Mountains as a whole, it is estimated that they make up 2 % of the land cover, with peatlands being the most common wetland type (Cooper et al. 2012). Inventories of peatlands in select areas of the Rocky Mountains have been conducted at both fine (Chadde et al. 1998; Chimner et al. 2010) and coarse (Vitt et al. 1996; Halsey et al. 1997; Zoltai et al. 2000) spatial scales, using aerial or satellite imagery. These inventories commonly report the presence of beaver ponds (Cooper et al. 2012), despite reports in the literature of peatlands being marginal beaver habitat (Rebertus 1986; Pastor et al. 1993).

Beaver can dam stream channels in both mineral wetlands and peatlands (Watters and Stanley 2007; Janzen and Westbrook 2011), but they do not require channels to build dams (Racine and Walters 1994; Walbridge 1994). Where channelized surface drainage is lacking, beaver dredge canals and dam groundwater seepage (Mitchell and Niering 1993). This causes anchored mat vegetation to be eliminated or partially sheared, thereby resulting in open water formation (Ray et al. 2001; Cunningham et al. 2006). The tight arrangement of small branches in beaver dams, as compared to debris dams, is an architecture that further promotes upstream pooling of water at the land surface (Bisson et al. 2006). An increase in open water can fundamentally modify wetland structure and function, through affecting processes such as water storage-runoff relations (Tardif et al. 2009), water table dynamics (Janzen and Westbrook 2011) and carbon accumulation rates (Blodau 2002) at the local (Wieder et al. 1981) or regional scale (Rebertus 1986). Modification to wetland structure and function by beaver may be temporally persistent (Gorham et al. 2007) because dams and ponds in wetlands are less prone to washout than those in riverine environments due to the flowing water having less energy (Ray et al. 2001). As a result, ponds could remain in a stable state in mineral wetlands and peatlands for centuries (Westbrook et al. 2013). The objectives of this research are to: 1) determine the distribution and abundance of mineral wetlands and peatlands in the Northern Rocky Mountains; 2) assess beaver habitation patterns of these ecosystems; and 3) determine the impact beaver activity has on one ecohydrologically important variable, open water extent.

Methods

Study Area

Wetland and beaver pond distributions were evaluated in a 7,912 km² area of the Canadian Rocky Mountains west of Calgary, Alberta (Fig. 1). The study area consists of the entirety of Kananaskis Country (a series of protected areas – provincial parks and improvement areas), part of the Stoney-Nakoda First Nations reserve, and three Municipal Districts.

The boundary of the study area was determined by the availability of recent (2007 and 2008) high-resolution aerial images, and the geographical limit of the foothills region. It is bordered to the west by Banff and Jasper National Parks. The study area forms the western margin of the Western Canada sedimentary basin and is therefore geologically complex. The strata (sandstone, limestone, shale and dolomite) are folded and faulted, range in age from Cambrian to Cretaceous (Toop and de la Cruz 2002), and are covered by glacial, lacustrine and fluvial materials (Gignac et al. 1991).

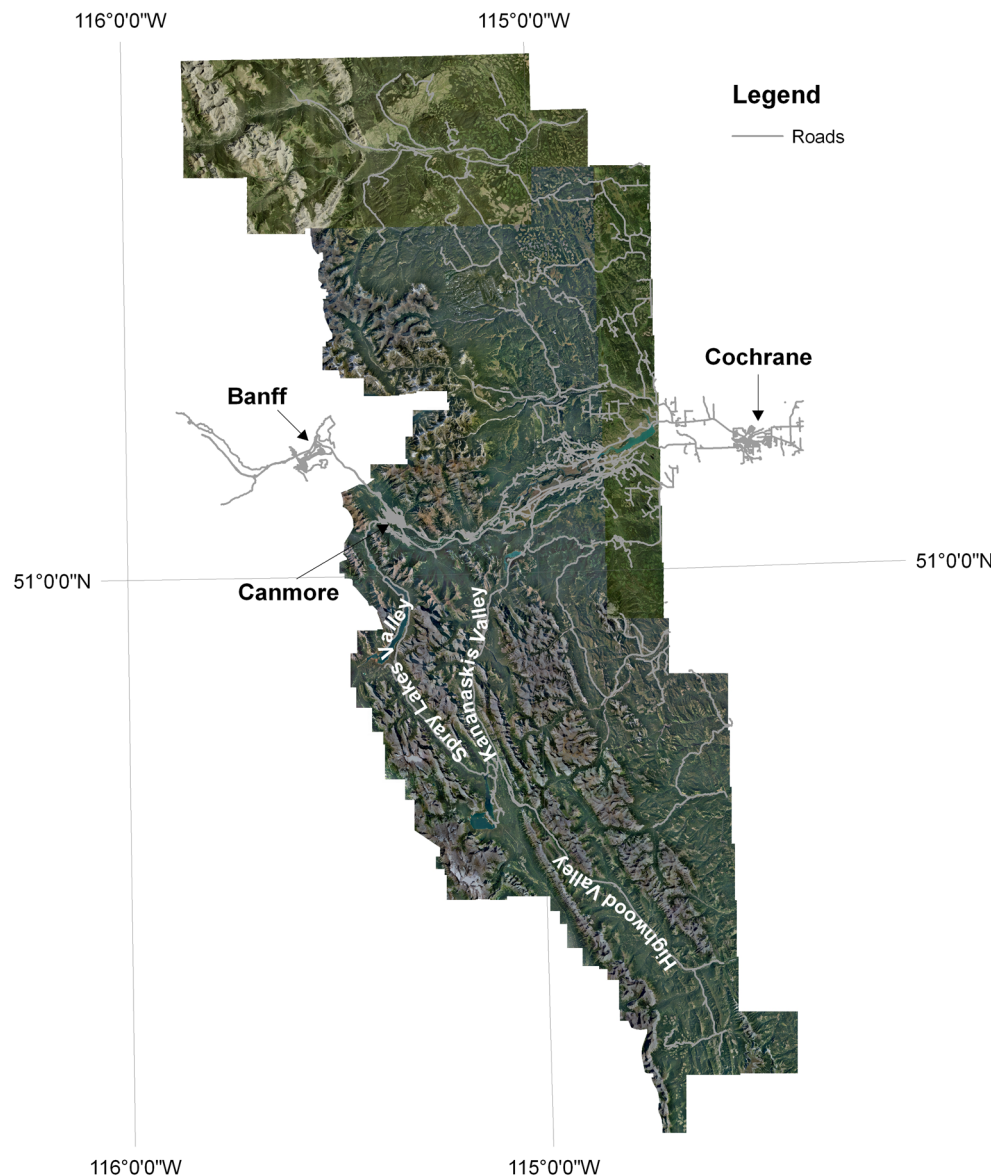
Elevation of the study area ranges from 1,161 to 3,427 m, with the highest areas occurring in the Kananaskis Range in the south. The mountain region is characterized by glaciated U-shaped valleys, with tarns, cirques and moraines at higher elevations and valleys bisected by rivers at lower elevations. Land use activities are restricted across the entire mountain region, with uses such as forest harvesting permitted in the Improvement Districts but not the Provincial Parks. The foothills region is characterized by a rolling topography and more varied land uses, such as ranching, recreational vehicle use, and forestry.

Beaver were extensively trapped in the study area from the 1790s through the mid-1800s, with several fur trading outposts on the nearby Bow (Peigan Post), Kootenay (Kootenae Post) and North Saskatchewan (Rocky Mountain House) rivers (Moore 2012). The history of fur trading with the Ktuxana, Piikani, and Niitsitapi First Nations indicates that there was an abundant beaver population into at least the beginning of the 1800s (Moore 2012). Aerial photography from 1949 shows no evidence of beaver activity in the study area; however, in the 1970s, there was abundant evidence in the images, suggesting that the beaver population rebounded in the 1950s and 1960s.

Wetland Identification and Mapping

Inventorying of wetlands in the study area involved both a general analysis of the 2007 and 2008 aerial photography imagery (scale 1:30,000 in nearly all instances) within a geographic information system (GIS) and field verification of a subset of the GIS identified wetlands. The 2007 images were taken in October, and contained 202 of the wetlands. The 2008 images were taken between mid-August and mid-September, and contained 327 of the wetlands. Wetland shapefiles available from the National Topographic Database (NTDB; Natural Resources Canada) were used as a starting point for the GIS wetland delineation. The wetland NTDB shapefiles are a summary of data gathered between 1972 and 1996. Owing to the fact that the metadata for this GIS layer did not describe the method by which it was produced, the wetland shapefile was overlain on the 2007 and 2008 aerial imagery and manually inspected to ensure that it did coincide with apparent wetland features. This assessment revealed that

Fig. 1 The 7,912 km² study area in the Canadian Rocky Mountains, Alberta. Aerial images are from 2007 and 2008; linear grey features are roads



the majority of the wetland polygons coincided with apparent wetlands on the aerial images as assessed manually. The accuracy of the shapefiles in depicting wetland location was also assessed during field verification, where 100 % of wetland sites identified from the shapefiles proved to be wetlands on the ground. We recorded the UTM coordinates of the wetland centroid, wetland area, physiographic region and jurisdiction. The smallest wetland identified in the GIS analysis was 0.2 ha; however, many wetlands smaller than this were observed during the field verification.

To distinguish peatlands from mineral wetlands, soil organic composition and peat thickness were measured during the field verification stage using cores. The distinction between peat and mineral soils was based on soil organic matter content by mass, where peat has >30 % organic matter content and >17 % organic carbon content (Soil Classification

Working Group, 1998). In each field-verified wetland, multiple cores (up to 10) were collected using a Russian corer (50 cm in length). The sampling location with the thickest peat deposit was used for organic matter analysis; samples of the top 40-cm from the core were sealed on-site in polypropylene bags and refrigerated within 10 h until lab analysis. Samples were dried at 105 °C for 24 h, homogenized, and subsampled. Subsamples were burned in a muffle furnace at 500 °C for 5 h to determine the percentage of organic matter. We broadly defined peatlands as both wetlands that were true peatlands (i.e. had at least 40 cm of peat; Soil Classification Working Group (1998)) and wetlands that were peat-forming, (i.e. had at least 20 cm of continuous peat in the surface 40 cm). Although a wetland must technically have at least 40 cm of peat to be considered a peatland, the sloping gradient common to mountain wetlands meant highly variable depths

to peat within a single wetland. This variability was compounded by interbedded mineral material in a peat matrix, which was found in many of the wetlands.

Assessment of Wetlands as Beaver Habitat

All delineated wetlands were assessed for evidence of beaver habitation by visually inspecting the aerial images. Two basic identifiers were used: 1) wetlands with ponds that had clear indications of being created by beaver because of identifying features such as dams (linear structures), lodges (circular features within ponds), and visible food caches; and 2) wetlands with relict beaver structures that indicated past beaver activity, but were not accompanied by the presence of ponded water on the surface at the time that the image was taken. These structures included relict dams (broken linear structures) and patches of relatively homogenous vegetation that were different than the surrounding area (see Wright et al. 2003).

Field verification was performed for 15 % of the 529 delineated wetlands at a ratio of 3:1 beaver impacted to non-beaver impacted wetlands. A ranked list of the 161 beaver impacted wetlands identified on the aerial imagery was created in the database, as was a number of other metrics like accessibility by road, number of wetlands nearby, and accessibility during the usually wet summer conditions. Of the 129 potential wetlands listed, 81 were visited between 1 July and 20 August 2012.

The GIS analysis indicated that 59 of the wetlands had recent evidence of beaver impact and 22 did not. Field visits showed that of the 59 wetlands predicted to show beaver impact, two were misidentified due to an oversight during the site selection phase, as confirmed by repeating the desktop methods for those sites. Of the 22 wetlands predicted to show no clear evidence of beaver, 20 were correctly identified. The two wetlands misidentified as not having evidence of beaver impact were a result of relict features being small and overgrown, and the aerial imagery not having the necessary resolution for identification. Therefore, the GIS delineation was mostly accurate, with limitations in photograph quality more likely to lead to an underestimate of beaver impacted sites rather than an overestimate.

Open Water

Polygons were manually digitized in ArcGIS for each water open water feature in each wetland using the aerial images from 2007 and 2008. Although the smallest identifiable wetland in the GIS analysis was 0.2 ha, the smallest identifiable area of open water within any identified wetland was 5 m². Open water area for wetlands impacted and not impacted by beaver activity was compared using the Wilcoxon test because data were non-normal.

Results

Distribution and Abundance of Wetlands

Wetlands occurred at elevations between 1,215 m and 2,194 m throughout the study area and those that were field verified occurred at 1,286–1,968 m. Wetland distribution varied by both physiographic location and jurisdiction. The GIS inventory of wetlands identified that of the 529 wetlands, 25 % were in the mountain region and 75 % were in the foothills region. Wetland density in the study area was 0.067/ km², but there was a clear difference between the physiographic regions, with the mountains having a lower wetland density (0.026/ km²) than the foothills (0.137/ km²). Alberta Parks (0.020/ km²) and Improvement Districts (0.026/ km²) had lower wetland density than Municipal Districts (0.121/ km²) and First Nations Reserves (0.146/ km²). The Municipal Districts contained the greatest number of wetlands of all the jurisdictions.

We found peat soils at 69 % of the 81 field-verified wetlands (Fig. 2) at elevations of 1,286–1,889 m. Proportionally fewer wetlands in the mountains were peatlands (57 %) than in the foothills (71 %). The jurisdiction with the greatest proportion of peatlands was the Municipal Districts (75 %), which was located wholly in the foothills region (Table 1). Unfortunately, field verification for wetlands in the Stoney-Nakoda First Nation was not possible as land access was not granted.

Wetlands as Beaver Habitat

Beaver impacts were evident in 30 % of the wetlands identified (Fig. 3) across nearly the entire elevation range (1,215–2,152 m; Fig. 4). Distribution of beaver-created features differed by both physiographic and jurisdictional region (Table 1). In the mountain region, 43 % of wetlands had evidence of beaver impact, whereas only 26 % of foothill

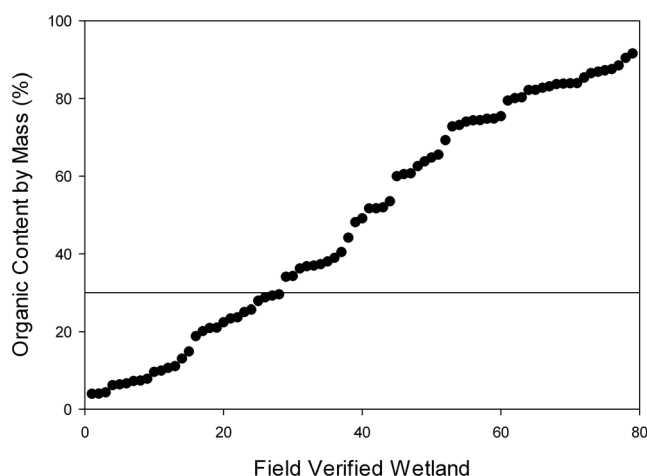
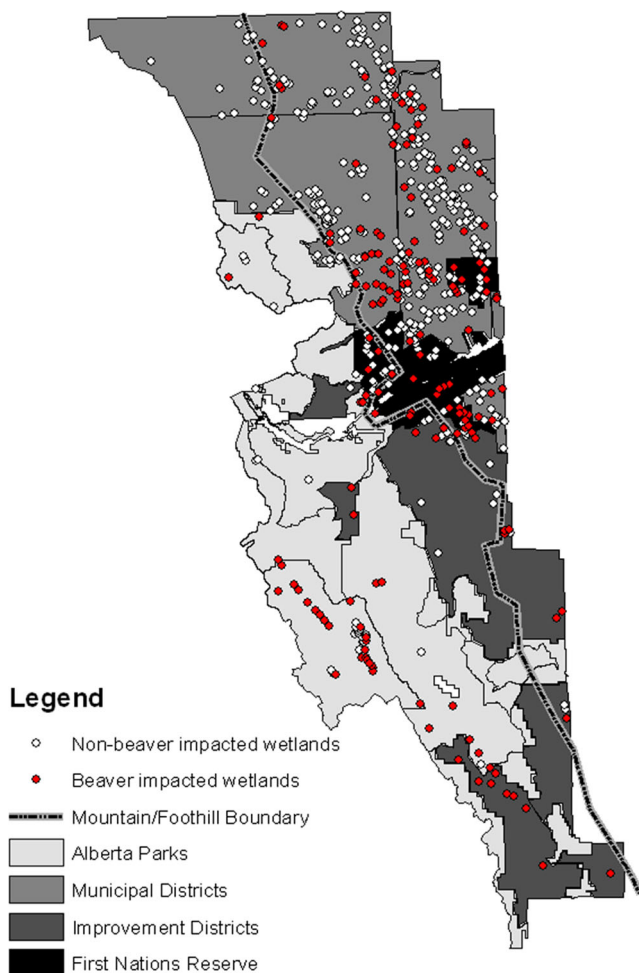


Fig. 2 Organic content of the top 50 cm of soil at each field verified wetland. Soils with an organic matter content of 30 % or greater were considered peat

Table 1 Distribution of field verified mineral wetlands and peatlands by physiography, land management jurisdiction and beaver habitation

		Peat-forming wetlands		Mineral wetlands	
Wetland land status	Number of wetlands	Total	Beaver impacted	Total	Beaver impacted
<i>Physiography</i>					
Mountains	28	16	16	12	12
Foothills	51	36	20	15	12
<i>Jurisdiction</i>					
Alberta Parks	21	12	12	9	9
Municipal Districts	40	30	17	10	8
Improvement Districts	18	10	7	8	7

wetlands did. Wetlands in protected areas (i.e., Alberta Parks 59 % and Improvement Districts 60 %) were most frequently impacted by beavers (Table 1). In contrast, the more densely populated Municipal Districts had few beaver impacted wetlands (20 %), although there was a cluster of beaver impacted wetlands in the southern part of this jurisdiction (Fig. 3). About 40 % of wetlands in the First Nation had evidence of beaver habitation.

**Fig. 3** Distribution of wetlands, as impacted by beaver, as related to physiographic location and jurisdiction

Evidence of recent or current beaver activity was found at 69 % of the field verified peatlands and 89 % of the mineral wetlands. However, there were regional and jurisdictional differences in beaver activity (Table 1). In the mountain region, 100 % of field verified peatlands and mineral wetlands had evidence of past or present beaver habitation whereas only 56 % of peatlands and 80 % of mineral wetlands in the foothills did. All field verified peatlands and mineral wetlands in the Alberta Parks had evidence of beaver habitation whereas 57 to 88 % of the peatlands and mineral wetlands located in the Municipal Districts and Improvement Areas did. There was a clustering of peatlands with evidence of beaver activity in the southwestern area of the Municipal Districts (Fig. 3).

Open Water

Of the 529 wetlands inventoried, 40 % had open water. Open water area varied greatly, ranging by four orders of magnitude (27 to $2.6 \times 10^4 \text{ m}^2$). There was twice as much open water area, on average, in mountain wetlands than foothill ones (Table 2). Open water area accounted for 2.4 % of total wetland area in the mountain region and 0.8 % in the foothill region. Municipal district wetlands had considerably less open water

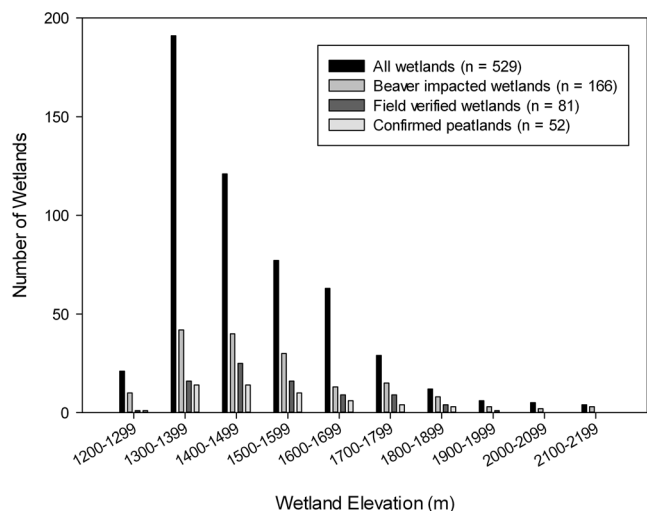
**Fig. 4** Histograms of mapped and field verified wetland elevations

Table 2 Area and abundance of open water in mapped wetlands for each physiographic location and jurisdiction

	No. Wetlands	No. wetlands with open water	Total wetland area	Mean individual wetland area	Total open water area	Mean open water area	
Physiographic location			$\text{m}^2 \times 10^5$	$\text{m}^2 \times 10^5$	$\text{m}^2 \times 10^5$	$\text{m}^2 \times 10^3$	SE
Mountains	133	75	130.75	0.99	3.10	2.31	0.29
Foothills	396	135	604.42	1.50	4.85	1.22	0.21
Total	529	210	735.59	1.4	7.92	1.50	
Jurisdictional location							
Alberta Parks	59	42	42.68	0.83	1.38	2.27	0.43
Municipal Districts	361	106	556.35	1.52	2.88	0.80	0.13
Improvement Districts	42	25	56.04	1.23	1.81	4.30	1.27
First Nations Reserve	67	30	81.14	1.36	1.85	5.00	0.57
Total	529	210	735.59	1.4	7.92	1.50	

area on average than the other jurisdictions owing to a greater total wetland area. Wetlands with beaver impact had significantly more ($p < 0.001$) open water than those not impacted (Table 3). The number of individual open water features per wetland was 12 times higher on beaver impacted wetlands compared to non-impacted ones (Table 3).

Discussion

We found that most of the wetlands inventoried in this Northern Rocky Mountain region were peatlands, and that there were differences in whether beaver used the wetlands as habitat based on physiography and land status. Wetlands used as beaver habitat had many more open water features than those not inhabited, which has wide-ranging implications for wetland form and functioning.

Distribution and Abundance of Wetlands

In the greater Kananaskis region of Alberta, wetlands occur at a density of $0.07/\text{km}^2$, with their distribution reflecting the physiography of the landscape. In the mountain region, wetlands tended to occur primarily in the major valleys, particularly those of the Spray Lakes, Upper Kananaskis and Highwood (see Fig. 1). Wetlands are common in valley bottoms because this physiographic position lends itself to a convergence of flow paths that can maintain wet conditions

at the near surface (Cole et al. 1997; Westbrook et al. 2006). In the foothills region, wetlands also occur in low-lying positions, but these are more evenly distributed owing to the rolling topography. Where the topography was steep in the foothills, wetland density was lower.

Although we identified 529 wetlands in this inventory, it is likely that there are more wetlands in the study region, especially small ones. While the field verification showed that the wetlands on the GIS layer were indeed wetlands out in the field, we observed a number of wetlands not captured by the GIS data layer. There may be several reasons for this: i) these wetlands may have formed after the GIS layer was produced; ii) they may have been too small for the original analysis method to detect; or iii) they may have been obscured by trees or snow cover on the imagery used to develop the GIS layer. Technology has developed since the GIS layer was created, which has improved the ability to remotely sense wetlands (Halabisky et al. 2013). The accuracy of the manual wetland inventory in the United States, for example, was improved 25 % by using a 1-m LiDAR based DEM (Maxa and Bolstad 2009) in part because LiDAR can be used to detect wetlands obscured by the forest canopy (Lang and McCarty 2009). When LiDAR becomes available for the study area, wetland mapping should be repeated to ensure this important ecological resource is properly inventoried.

Our study provides a detailed estimate of the distribution of individual peatlands in the southern Canadian Rockies. We

Table 3 Comparison of open water area and number of individual open water features in beaver impacted and non-impacted mapped wetlands

	No. Wetlands	No. wetlands with open water	Mean open water area	No. Individual ponds	SE
			$\text{m}^2 \times 10^3$		
Beaver impacted	166	147	3.9	782	0.47
Non-beaver impacted	363	63	0.4	155	0.12
Total	529	210	1.5	937	

identified 77 % of the field-verified wetlands as peatlands or peat forming wetlands. Our research complements Halsey et al.'s (1997) provincial peatland inventory and Zoltai et al.'s (2000) national inventory by providing a regionally dense dataset. Extending our field results to the GIS inventory indicates that ~397 of the 529 identified wetlands could be peatlands. This is a much higher number than Chadde et al. (1998) reported for the Rocky Mountains in the northern United States (61 peatlands in Idaho, Washington, Montana and Wyoming). If the ecological value (in terms of uniqueness and ecosystem services) of peatlands presented in Chadde et al. is similar for those in our study area, then the peatlands of the greater Kananaskis region represent a substantial regional natural resource. Given the expansiveness of the Canadian Rockies, its peatland resource is likely to be large.

The challenges encountered while inventorying the peatlands have important implications for relying solely on remote sensing imagery for this task, such as is the current trend (Krankina et al. 2008). We discovered out in the field that wetlands that appear as peatlands at the land surface, based on their vegetation composition and wetness, had a stratigraphy in the upper 40 cm that ranged from pure peat to heavily stratified with mineral layers; layers of pure peat and stratified peat were found not only in different wetlands but also often at different locations within the same wetland. Many of those heavily stratified ended up not meeting the criteria of >17 % organic carbon by weight in the upper 40 cm (Soil Classification Working Group, 1998) and thus could not be considered a peatland despite having many of the requisite functional characteristics.

Beaver Habitation Patterns

Beaver disturbance varied by wetland physiographic location and jurisdiction. Even though there were fewer wetlands in the mountain region, beaver impacts were twice as likely there than the foothills region. While there could be a number of causes for this, the most likely one is differing priorities of the main land managers in each jurisdiction. The mountain area consists primarily of Improvement Districts and Provincial Parks whereas the foothills region consists primarily of Municipal Districts and a First Nations Reserve. None of these jurisdictions have an official published policy on beaver management, although there is a provincial quota system to limit the beaver harvest. The Government of Alberta (2012) reports that the average harvest of beaver pelts from 2008 to 2012 was 12,075. Beaver are also removed in many Alberta municipalities as part of regular road maintenance and in response to landowner complaints. Trapping and land/infrastructure removal are thus likely to be the main causes of the low proportion of wetlands (20 %) in the municipal districts found to have beaver ponds. Ranching and forestry may also contribute to low pond densities in the Municipal Districts as

beaver tend to be perceived as a nuisance to these two industries (Bhat et al. 1993; Conover 1994; Messmer 2000; Törnblom et al. 2011).

In the Improvement Districts, the proportion of beaver impacted wetlands is 40 % higher than the Municipal Districts. This jurisdiction does not have the same intensity of forestry or ranching found in the Municipal Districts. Further, it contains some wildlife protection areas that are mostly used for recreational purposes. Thus beaver are more likely to be tolerated as they are rarely directly impacting peoples' livelihoods. Indeed, in many cases their presence could be seen as beneficial. For example, beaver ponds are known to provide good conditions for fishing, and wildlife viewing as they attract a plethora of other wildlife (Conover 2011). Other factors that may be important in influencing the local beaver population are food availability and predator density. For example, the interaction of predators such as wolves with their prey can be complex. Elk herbivory can reduce the available food source for beaver (Wolff et al. 2007), but the predation of wolves on elk reduces this impact (Hebblewhite et al. 2005). Wolves are discouraged from living in areas of high human population (Hebblewhite et al. 2005), which impacts their distribution and density.

The Alberta Parks jurisdiction had a similar proportion of wetlands impacted by beaver as the Improvement Districts. There are stringent rules on development and a high degree of wildlife protection in the park area. The unofficial policy of Alberta Parks is to adapt management practices to allow co-existence with beaver, and to remove them only when absolutely necessary to protect infrastructure (M. Percy, pers. comm.). That there were similar proportions of inhabited wetlands in the parks and Improvement Districts indicates that the suitable wetland habitat in both jurisdictions is already colonized, and that land management and land use practices in the Improvement Districts are sufficient to protect beaver populations. The similarity is perhaps surprising as logging and seasonal grazing does occur in the Improvement Districts. It may be that licensing of these activities provides adequate protection of beaver, compared to logging and ranching practices on private land, but further study is needed.

Interestingly, the proportion of wetlands on the First Nations reserve with evidence of beaver activities (40 %) fell halfway between that of the protected regions and the Municipal Districts. Physiographically, the reserve sits in the foothills region, and so should be more densely impacted by beaver than the Municipal Districts. Beaver management policy is decided at the reserve level, and was not publicly available for the Stoney-Nakoda First Nation. Without knowing more about the way beaver are managed on the reserve, specific conclusions cannot be drawn other than to note that sharing of management strategies across jurisdictions in the region could aid in the development of a regional beaver management policy

that provides a balance of protection of both beaver and human interests while promoting the important ecosystem services provided by beavers.

Although the Municipal Districts generally had a low density of beaver-impacted wetlands, there was a high-density cluster in one Municipal District, coincident with the Ghost Valley Forest Recreation Area (GVFRA). Land use in GVFRA is restricted to recreation activities such as ATV trails and fishing and this land was an Improvement District until 1988. Interestingly, the average distance from wetlands to a road was higher within this cluster (average of just over 3 km) than for other wetlands in the Municipal District (average of 1.5 km). High road density fragments habitats and increases beaver mortality through road kills (Gunther et al. 1998). Our results suggest that the proportion of wetlands impacted by beaver can be changed through modifying socioeconomic forces and/or land and wildlife management practices. If practices are designed in a way that increases beaver inhabitation of wetlands, this approach is likely to help towards balancing human interests with the improvement of wetland functions and services (Tömbblom et al. 2011).

Peatlands, in particular, appear to be good beaver habitat: 73 % of the peatlands visited had evidence of beaver habitation. The widespread use of peatlands as beaver habitat contradicts descriptions from the literature of peatlands as marginal habitat (Rebertus 1986; Pastor et al. 1993), but these assertions were not based on scientific evidence. Studies focused on peatlands have shown that beaver commonly inhabit them. For example, Milbrath (2013) described beaver colonization patterns in nine peatlands in the Rocky Mountain foothills of Montana, and although Rebertus (1986) concluded that peatlands were marginal habitat, he documented that 42 % of the peatlands studied his northcentral Minnesota study site had evidence beaver impact. Further, researchers studying other peatland attributes have noted the presence of beaver at their study sites (Yavitt et al. 1990; Roulet et al. 1997; Turetsky and St. Louis 2006). At a continental scale, Gorham et al. (2007) showed that there is evidence of beaver in peatlands throughout the Holocene. This finding suggests that beaver readily colonize peatlands. It would be interesting to revisit Rebertus' study site to determine if more (or fewer) peatlands have been colonized by beaver since his research, given that Johnston and Naiman (1990) concluded that the rate of pond creation after the first two decades of beaver recolonization of a landscape becomes limited by lack of geomorphically suitable habitat.

One Ecohydrological Impact of Beaver on Wetlands

Our results indicated beaver commonly use mountain peatlands as habitat, which opened the question of resulting impacts on peatland function. We focused our attention on one ecohydrological impact, open water area, and found that

peatlands inhabited by beaver had much more of it. The idea that beaver enhance open water extent in ecosystems they inhabit is not new; there are many descriptions in the literature of increased open water area in riverine systems dammed by beaver, and how it turns lotic habitat into lentic (Johnston and Naiman 1987; Gurnell 1998). However, the changes incurred to pre-existing wetlands (mineral and peat) are often quite different than those in riverine systems. In shallow open water wetlands, such as those common in the western boreal forest of Canada, beaver can increase the extent of flooding (Hood and Bayley 2008). For other types of wetlands though, beaver create open water features where they did not previously occur. Although the formation of open water features by beaver activity in wetlands, particularly peatlands has been previously documented (see Johnston et al. 1990), the area is only infrequently quantified, and linkages to peatland hydrologic function have yet to be explored. The form of beaver ponds are similar to peat pools in that they are open water bodies within the peat matrix, but they are different in that their persistence is influenced by dam intactness (Woo and Waddington 1990). Although they did not study beaver ponds, Tardif et al. (2009) showed that the presence, shape and location of pools changed the way peatlands store and release rain water. An important research avenue is the exploration of rainfall and snowmelt runoff generation in mountain mineral wetlands and peatlands as impacted by beaver ponds.

Biogeochemical impacts of open water areas of peatlands have been studied, and been shown to be distinct from non-open water areas. In particular, carbon (C) sequestration and release are impacted by changed wetness conditions (Belyea and Malmer 2004; Strack et al. 2005; Ise et al. 2008). For example, Roulet et al. (1997) reported a C flux from a beaver pond in a boreal peatland as more than 200 g C/m² per year and Crill et al. (1988) found that methane flux from an open peat bog was 107 g C/m² per year. Given the differences in the climate and peatland forms present in the Canadian Rockies as compared to the boreal forest, along with the large enhancement of open water features documented here, investigations of C dynamics in Rocky Mountain peatlands, as affected by beaver, are warranted.

Conclusions

Wetlands are abundant in this Rocky Mountain environment and, despite their small areal extent, provide critical elements of landscape diversity. They were physiographically constrained mainly to valley bottom positions in the mountain region and more evenly distributed in the foothills region owing to the rolling topography. Challenges encountered when mapping peat wetlands serve as a cautionary note for relying solely on digital mapping to infer wetland type. In

several cases wetlands appeared as peatlands based on their functional characteristics, but could not be classified as such because the coring revealed heavily stratified soils that did not meet the criteria for organic soil.

Our research also highlights the widespread use of mountain wetlands, both mineral wetlands and peatlands, as beaver habitat. Although our study design did not permit an in-depth evaluation, research is needed on the differences in the ways beaver use mineral wetlands vs. peatlands. Even though there were fewer wetlands in the mountain region, beaver impacts were twice as likely there than in the foothills region, reflecting different land use zoning and wildlife management strategies. Human-wildlife interactions also appear to greatly enhance pooling of water on the surface of wetlands. Open water has far-reaching implications for wetland ecosystem function and service, in particular, water storage-runoff relations and nutrient cycling. Specifically, the role of beaver in delaying the transmission of runoff to downstream water bodies is under-researched, which is important to know for mountain wetlands, as they tend to be located at the critical juncture between mountain hillsides and major rivers. Changes in the abundance of keystone species, in this case beaver, that influence water and nutrient dynamics should thus be monitored to protect key wetland ecosystem functions.

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