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Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada

Glynnis A. Hood[a,b,*], *Suzanne E. Bayley*[a]

[a] *Department of Biological Sciences, CW 405, Biological Sciences Center, University of Alberta, Edmonton, Alberta, Canada T6G 2E9*
[b] *Department of Science, Augustana Faculty, University of Alberta, 4901-49 Avenue, Camrose, Alberta, Canada T4V 2R3*

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ABSTRACT

Shallow open water wetlands provide critical habitat for numerous species, yet they have become increasingly vulnerable to drought and warming temperatures and are often reduced in size and depth or disappear during drought. We examined how temperature, precipitation and beaver (*Castor canadensis*) activity influenced the area of open water in wetlands over a 54-year period in the mixed-wood boreal region of east-central Alberta, Canada. This entire glacial landscape with intermittently connected drainage patterns and shallow wetland lakes with few streams lost all beaver in the 19th century, with beaver returning to the study area in 1954. We assessed the area of open water in wetlands using 12 aerial photo mosaics from 1948 to 2002, which covered wet and dry periods, when beaver were absent on the landscape to a time when they had become well established. The number of active beaver lodges explained over 80% of the variability in the area of open water during that period. Temperature, precipitation and climatic variables were much less important than beaver in maintaining open water areas. In addition, during wet and dry years, the presence of beaver was associated with a 9-fold increase in open water area when compared to a period when beaver were absent from those same sites. Thus, beaver have a dramatic influence on the creation and maintenance of wetlands even during extreme drought. Given the important role of beaver in wetland preservation and in light of a drying climate in this region, their removal should be considered a wetland disturbance that should be avoided.

1. Introduction

During times of drought, the loss of water resources has devastating effects on both agricultural and natural resources (deMenocal, 2001; Schindler and Donahue, 2006), to the point of being considered a “landscape hazard” in situations where aridity is directly linked to soil erosion (Sauchyn et al., 2002). Although various data, including paleoclimatic (Laird et al., 2003), tree ring (Sauchyn et al., 2003), and anthropological data (deMenocal, 2001), suggest that decadal and multicentennial scale droughts have occurred in North America for at least two millennia; climate models predict the incidence of drought in some regions in the world, including parts of North America, will increase in frequency and duration over the next 100 years (Moore et al., 1997; Hengeveld, 2000; Hogg and Bernier, 2005; Schindler and Donahue, 2006). The combined impact of drought and anthropogenic wetland losses, with intensified industrial, urban and agricultural demands

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* *Corresponding author:* Address: Department of Science, University of Alberta, Augustana Faculty, 4901-46 Avenue, Camrose, Alberta, Canada T4V 2R3. Tel.: +1 780 679 1556; fax: +1 780 679 1590.
E-mail addresses: glynnis.hood@ulberta.ca (G.A. Hood), sbayley@ualberta.ca (S.E. Bayley).

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upon existing water resources, makes concerns of warming temperatures and decreased precipitation even more relevant to trends in wetland loss (Moore et al., 1997).

Biotic influences on the maintenance of wetlands, particularly in the context of climate change, have frequently been ignored. Beaver (*Castor canadensis* Kuhl), in particular, are often overlooked as a potential means to minimize the impacts of drought. This omission exists despite the well-documented role of beaver as a key species in creating and maintaining wetlands at landscape scales (Naiman et al., 1988; Johnston and Naiman, 1990a). Considering the value of wetlands as habitat for many aquatic and terrestrial species, the role of beaver (a keystone wetland species) in a comprehensive wetland management strategy seems critical, if incidence of drought does increase.

Several studies have sought to predict the long-term impacts of drought on wetland availability and function. Larson (1995) assessed the variability of water coverage in wetland basins across the prairie pothole region (PPR) relative to a suite of climatic variables. She found that climate explained over 60% of the variation in wet basins in the PPR, which in turn influenced the availability of habitat for breeding waterfowl. Johnson et al. (2005) found that drought conditions displaced waterfowl populations that would normally use the PPR into more northern areas where water levels were more consistently stable. These findings confirmed predictions by Poiani and Johnson (1991), whose climate-based simulation model forecasted lower waterfowl production due to a warmer, drier climate and an increase in dry basins in the PPR. However, despite more stable water availability, the peatlands of the boreal region are also vulnerable to climate change due to a predicted increase in wildfire and lower water inputs (Camill and Clark, 2000; Hogg and Bernier, 2005).

Climate change models for the prairie pothole and western boreal regions commonly predict reduced groundwater recharge and loss of wetlands due to less precipitation and higher temperatures. In fact, almost all models used to simulate various scenarios relative to global warming predict higher temperatures in these regions (Hogg and Bernier, 2005; Johnson et al., 2005). In their analysis of temperature data from Canada's western prairie provinces, Schindler and Donahue (2006) calculated an increase in temperature of 1–4 °C since 1970, which suggests such a trend has already begun. Although precipitation is more difficult to predict, even if there were an increase in precipitation, rising temperatures would result in greater evapotranspiration, therefore producing drier conditions in the southern boreal region (Hogg and Hurdle, 1995; Schindler and Donahue, 2006).

Wetland loss due to climate change is not unique to North America. Freshwater ecosystems across the circumpolar Arctic are very sensitive to climatic variability (Prowse et al., 2006) with some permanent water bodies now completely drying up over the summer months (Smol and Douglas, 2007). In Europe, where human activities have already significantly reduced the number and quality of wetlands, predicted rises in sea levels due to global warming would continue to compromise coastal wetlands (Airoldi and Beck, 2007).

Historical and current wetland loss over large expanses of North America due to urban, industrial, and agricultural development only serve to exacerbate wetland loss associated with current and future drought. Since European settlement, as much as 70% of the original non-peatland wetlands in Canada have been lost to development (National Wetlands Working Group, 1988) and as much as 53% in the United States (Dahl, 1990, 2006). This loss of wetlands in turn has eliminated highly valued wetland functions (e.g., groundwater recharge, nutrient removal, and wildlife habitat), which cannot always be mimicked through wetland restoration programs (Zedler, 2000). Anthropogenic disturbance causing the loss of wetlands can be as visually obvious as the drainage and infilling of wetlands, or as subtle as, but equally as serious, alteration of groundwater and surface water flows.

During this period of wetland loss, a key species associated with the creation and maintenance of wetlands was also removed from the riparian and wetland ecosystems of North America. After European beaver (*Castor fiber*) were extirpated from many areas of Europe (Nolet and Rosell, 1998; Rosell et al., 2005), North American beaver were aggressively harvested in Canada and the United States from the 17th century to the early 20th century. By 1900, beaver were extirpated in most regions of North America, including many areas of Canada (Novak, 1987; Naiman et al., 1988). Beaver are well known for creating water impoundments and modifying channel geomorphology and hydrology (Naiman et al., 1986; Brochart et al., 1989). Johnston and Naiman (1990a) found that the rate of pond creation paralleled an increase in the population of beaver over a 46-year period. In the context of predicted increases in the incidence of drought and historic and current anthropogenic wetland loss, we hypothesized that beaver populations would play a key role in maintaining local wetlands.

With the creation of beaver impoundments comes an increase in the acid-neutralizing capacity of water flowing through beaver ponds (Smith et al., 1991), water storage, groundwater inputs, sediment storage (Naiman et al., 1988; Baker and Cade, 1995; Westbrook et al., 2006), and landscape heterogeneity (Brochart et al., 1989 Johnston and Naiman, 1990b). On the Colorado River in Rocky Mountain National Park, beaver dams increased both surface water and groundwater in both high- and low-flow periods and were able to attenuate declines in the water table during drier periods (Westbrook et al., 2006). High flow periods were generally during spring snowmelt. Beaver dams are also able to transform lentic habitats to a combination of both lentic and lotic habitats (Martell et al., 2006). Naiman et al. (1988) also found that streams with beaver impoundments have a high resistance to disturbance. Because of its ability to dramatically alter landscape form and function to the benefit of other species (Stevens et al., 2007), beaver are often considered a keystone species (Baker and Cade, 1995; Simberloff, 1998). Wetlands created by beaver enhance biodiversity by providing important habitat for fish (Snodgrass and Meffe, 1998; Schlosser and Kallemyn, 2000), water birds (Brown et al., 1996; Russell et al., 1998) and herptiles (Russell et al., 1998; Stevens et al., 2007).

Given the predicted increase in drought in key wetland regions of central North America, the beaver's ability to create and maintain wetlands over long time periods brings into question whether beaver can mitigate the effects of drought on shallow isolated sloughs, ponds, and lakes in glaciated landscapes. Beavers are known to increase the area of open water wetlands in streams and riverine systems (Johnston and Naiman, 1990b), but their ability to maintain relatively isolated wetlands in morainal landscapes has not been demonstrated. The availability of aerial photographs and beaver census data over a 54-year period from Elk Island National Park (EINP) in east-central Alberta, Canada, during a period that coincided with the most severe drought in the history of the area, provided a unique opportunity to examine the combined effects of climate and beaver on wetlands.

The overall objective of this study was to investigate whether beaver or climatic factors are more important in maintaining open water wetlands. Specifically, we (1) examined whether beaver (number of lodges/area) increase the area of open water in wetlands generally, (2) determined whether beaver also increase open water area during drought, (3) assessed the importance of precipitation and temperature in creating and maintaining open water wetlands in the presence of beaver, and (4) determined the effects of precipitation and temperature on open water in wetlands when beaver were absent from the models.

2. Study site and methods

2.1. Study site

Elk Island National Park (194 km^2) is located at the southern fringe of the mixed-wood boreal region of east-central Alberta, Canada (Fig. 1). The Park is in the heart of the Cooking Lake Moraine; a landscape predominantly covered by trembling aspen forest (*Populus tremuloides* Michx.). Balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh) occur in moist areas. Pockets of black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* [Moench] Voss) also occur, but are more common in the northern part of the Park. Fire was

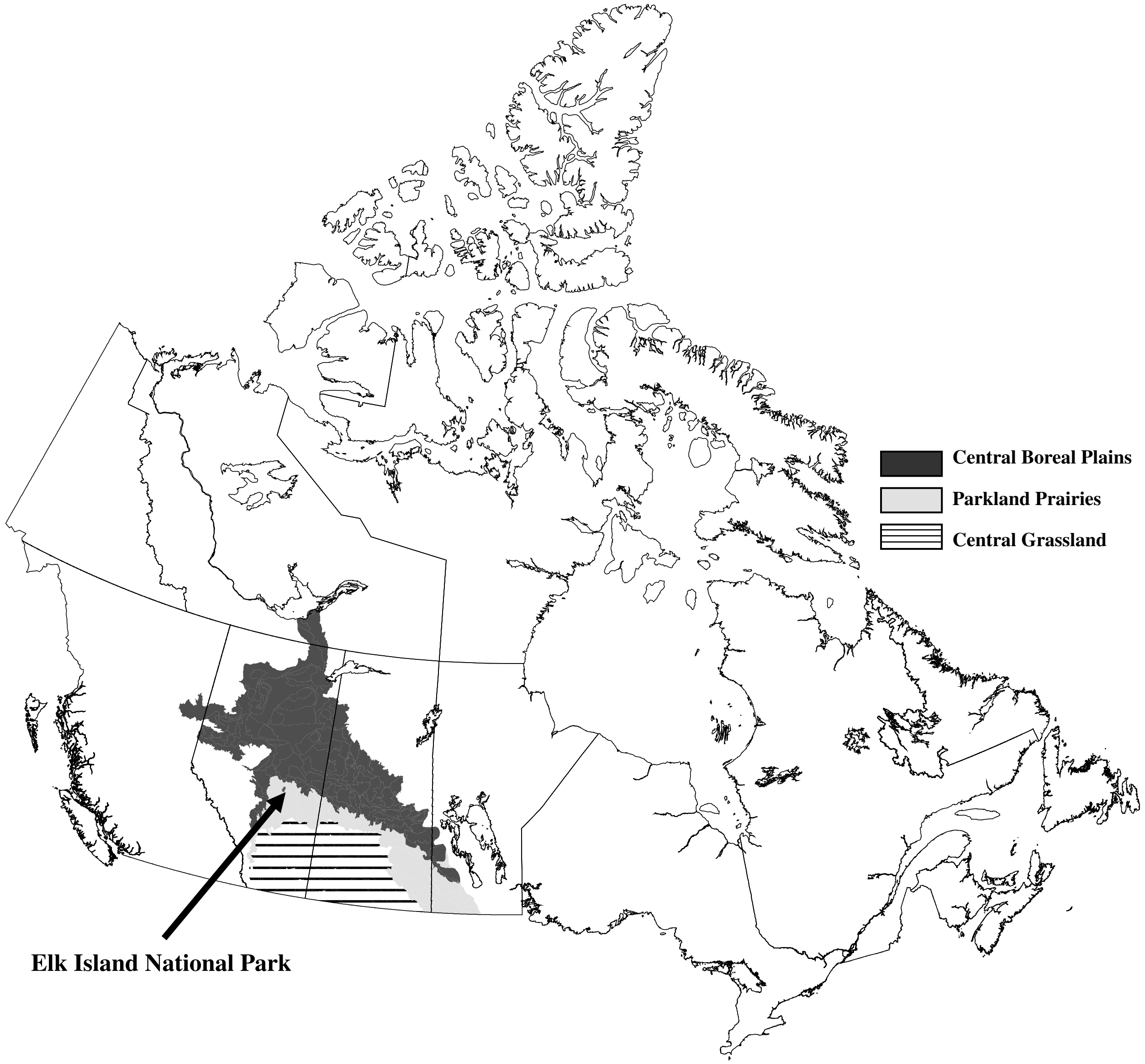

Fig. 1 – Location of Elk Island National Park in Alberta, Canada, relative to the prairie ecoprovinces (Marshall and Schut, 1999).

suppressed in the Park until 1979 when a prescribed fire program was established to restore vegetation communities and enhance wildlife habitat. Approximately 51% of the Park area was burned by 2002. The Park is dominated by knob and kettle terrain and lacks any major riverine systems. Open water areas are represented by lakes, intermittent or slow-moving streams, shallow open water, and marshes. Fens, bogs, and swamps are also present throughout the Park (Nicholson, 1993).

The Park's climate is classified as continental with warm summers and cool winters (Crown, 1977). Much of the atmospheric inputs into wetlands in the Park come from rainfall, rather than seasonal snowmelt originating from mountainous areas. Average precipitation from 1940 to 2002 was 457 mm, although variability from wet to dry years is common (Fig. 2).

Although there have been no groundwater studies within the Park, there have been groundwater assessments in the counties that surround the Park (Hydrogeological Consultants Ltd., 1998, 2001). The areas immediately adjacent to the Park are almost evenly classed as groundwater recharge and groundwater transition areas. Recharge wetlands are higher than the surrounding groundwater table and water flows out of the wetland to the groundwater (Mitsch and Gosselink, 2000), while in groundwater transition areas, groundwater is well below the surface and there is no gradient.

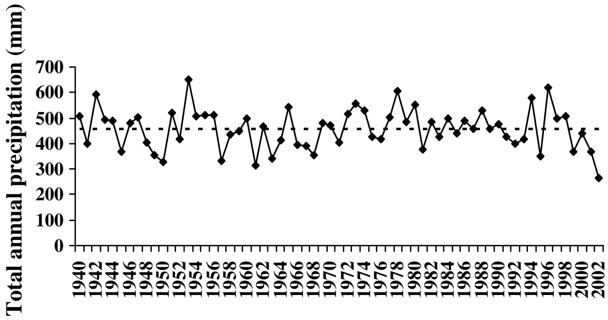

Fig. 2 – Total annual precipitation (solid line) from January 1 to December 31 and average precipitation (dashed line) from 1940 to 2002 at Elk Island National Park, Canada. Data from Environment Canada (http://www.climate.weatheroffice.ec.gc.ca/climatedata).

Beaver were extirpated from the Park and much of east-central Alberta by the mid-1800s (Blyth and Hudson, 1987) and not successfully reintroduced until September 1941. Park-wide beaver census data have been gathered since their reintroduction. The initial spread of beaver was very slow. Since the mid to late 1950s there has been a well-established beaver population within the Park.

2.2. *Data acquisition and development*

2.2.1. *Aerial photographs*

There is an extensive aerial photo record for EINP dating back to 1923 and beaver population data (lodge occupancy) from 1941. For this study we were able to analyze 12 separate years of data between 1948 and 2002 using complete vertical aerial photo coverage of the entire Park, corresponding beaver census data and, appropriate climate data. Aerial photos for each year were scanned at a minimum of 600 dpi (dots per inch) as greyscale images and made spatially relevant by georectifying them in a Geographic Information System (GIS) using ArcMap 8.1 (ESRI, 2001). We then created a mosaic in ArcMap from the aerial photos to develop a single geographically accurate aerial representation of the study area. In 1995 and 2001 there were existing aerial photo mosaics available in the GIS. For 2002, the driest year on record, Landsat-7 ETM imagery was the only imagery available. Only the black and white band 8 image was used to obtain the best resolution for the area (Table 1). Landsat imagery differs from aerial photographs and can pick up more water reflectance in surrounding emergent vegetation; however, it is commonly used for wetland assessment and offers good results when consistent cover classes are analyzed (Ramsey and Laine, 1997). For years where digital and non-digital aerial photographs were available, individual wetlands that were difficult to delineate in the GIS were confirmed with a binocular mirrored stereoscope using the original aerial photos.

The study area comprised approximately 79 km^2 of the Park that had never been exposed to fire during the Park's history. By excluding the burned areas of the Park, we eliminated

Table 1 – Images used in the analysis of the effects of beaver and climate on the area of open water in Elk Island National Park, 1948 to 2002

Year	# of photos used	Scale and resolution	Date taken
1948	33	1:36 000 (600 dpi)	September 1948
1950	20	1:40 000 (600 dpi)	September 1950
1962	20	1:31 680 (600 dpi)	May 1962
1964	50	1:20 000 (600 dpi)	July 1964
1967	29	1:31 680 (600 dpi)	August 1967
1973	45	1:15 840 (600 dpi)	September 1973
1980	12	1:60 000 (600 dpi)	April 1980
1982	30	1:30 000 (600 dpi)	August 1982
1995	N/A (orthophoto)	1:40 000 (600 dpi)	August 1995
1996	37	1:30 000 (800 dpi)	May 1996
2001	N/A (orthophoto)	N/A, 1200 + dpi	May 1996
2002	Landsat-7, ETM	N/A, 12.5 m	August 2002

N/A = not available.

the possible confounding effects of fire on wetlands and beaver lodge occupancy. In an associated study, it was determined that beaver lodge occupancy is lower in areas that have been burned than in unburned areas in the Park (Hood et al., 2007).

Using a consistent study area for all years, we digitized all open water in wetlands for each of the 12 sets of aerial photo coverage and calculated their areas in the GIS. Summed areas provided the total area (in hectares) of open water within the study area for each of the 12 years. Because large lakes (>150 ha) could not be manipulated by beaver, four big lakes (Flyingshot, Bailey, Goose and Blackfoot Lakes) within the study area were excluded from the analysis.

2.2.2. *Climate*

Temperature and precipitation data were obtained from Environment Canada (http://www.climate.weatheroffice.ec.gc.ca/climatedata). For the years when accurate climate data were not available for EINP, data from the Edmonton Municipal Airport (approximately 45 km to the west) were used instead.

Aerial photos were taken in spring and summer months, but the months were not always consistent among the years examined. In addition, extreme weather events after the aerial photos were taken could bias the precipitation values if the typical annual hydrologic year was used (November 1 to October 31). For these reasons, we calculated annual precipitation, temperature, and total annual effective precipitation (precipitation – potential evapotranspiration; Sass et al., 2007) as the 12 months prior to the month the aerial photographs were taken. For example, if an aerial photo was taken in June of 1948, annual precipitation and temperature values were calculated from June 1947 to May 1948. Longer climatic intervals (e.g., 3-year average precipitation) were calculated by the same method. This approach is consistent with methodologies in other studies where multiple sets of aerial photographs were used in the analysis of wetland areas (Johnston and Naiman, 1990a; Larson, 1995). Initial climatic variables included: mean and mean maximum annual temperature, total annual precipitation (*P*), total annual rainfall, total annual snowfall, and total annual effective precipitation (precipitation – potential evapotranspiration). For total annual effective precipitation, potential evapotranspiration (PET) was calculated using methods by Hamon (1963). We also examined the effects of hydrologic year (November 1 to October 31), seasonal precipitation (3 months prior to the time the photograph was taken), and 2-, 3-, and 5-year time lags for total annual precipitation.

Because it could be argued that the relationship between the presence of beaver and the area of open water is correlative rather than causal, we examined differences in water area and activity in 80 individual ponds over four separate years – in 1948 and 1950 when there were no beaver present in the study area and in 1996 and 2001 when beaver were well established. The year 1996 represents a year with average total annual precipitation (377 mm, measured from 12 months prior to the month the air photo was taken), and 2001 represents a year of slightly below average precipitation (370 mm). The year 1948 had the highest precipitation of all 4 years (471 mm), and 1950 was the lowest (342 mm).

2.2.3. *Beaver*

We selected all the ponds in the study area that had active beaver colonies in both 1996 and 2001 ($N = 40$) and an additional set of ponds that had no beaver activity in them in both 1996 and 2001 ($N = 41$). By default there was no beaver activity in any of these ponds in 1948 and 1950. Ponds were classified into two groups – (1) ponds that did not have beaver in them in 1948 and 1950, but did have active beaver colonies in 1996 and 2001, and (2) ponds that did not have beaver in them in any of the 4 years. The area of each of these ponds was determined from the digitized 1948, 1950, 1996, and 2001 wetland data. Although it was impossible to find any ponds in 1996 and 2001 that did not have beaver in them at some point in their history, every effort was made to ensure the pond did not have an active colony in it for at least 5 years. Each year provided an individual measure of the area of open water for each pond relative to its future or current beaver activity. For example, ponds 1 through 40 were given a classification as "active" because they supported beaver in 1996 and 2001. These same ponds were considered as future active ponds in 1948 and 1950. Ponds 41 through 80 were classified as "inactive" because they did not support beaver in 1996 and 2001 and, by default, in 1948 and 1950.

Park staff have conducted censuses of beaver lodges in the Park since 1941 when beaver were re-introduced. Until the mid-1950s the beaver population was limited to Astotin Lake (outside the study area), but in 1952 beaver subsequently recolonized the entire Park including our study area. In their census, conducted in late fall and winter months, each active lodge was assumed to represent one family unit. We observed an average of six beaver per lodge during our study. In each census, all lodges were classified as active or inactive and mapped. These data were transferred to the GIS for each of the 12 years. The total number of active and the total number of lodges (active + inactive) were calculated for each year. Beaver density in the Parks is relatively high compared to many other areas where beaver have been studied (Skinner, 1984).

Wetlands in the Park are generally isolated and lack the linear surface water connectivity found in many other areas with riverine connectivity where beaver have been studied extensively (e.g., Naiman et al., 1988; Johnston and Naiman, 1990b; Syphard and Garcia, 2001). Beaver in EINP construct dams, but dams were generally smaller and less numerous than those found in areas with more rivers and streams. A large dam in EINP would average approximately 20 m across and 1.7 m in height. By capturing overland flow in this morainal landscape, beaver were able to facilitate groundwater recharge as well as increase the overall area of open water. Although some form of dam was common, there were active beaver ponds that lacked any dams. Counting lodges, rather than dams has been an effective way to monitor beaver activities within the Park.

2.3. Data analysis

Multiple linear regression was used to determine the relationship between the area of open water in wetlands (response variable) and a number of independent variables including the number active beaver lodges, inactive beaver lodges, all beaver lodges (active + inactive), precipitation, and temperature.

A suite of 14 independent variables was derived from the climate and beaver data. From these variables we ran several regression models. To avoid collinearity, no variables that were derivatives of the same data (e.g., using two precipitation variables in the same analysis) were used together when conducting model runs. Only the beaver and climate variables that best explained the variation in open water were included in the final model. The final model was also tested to identify possible interactions between the explanatory variables. Finally, we used a relative Pratt index (*dj*) to determine the relative importance of each explanatory variable by attributing the proportion of the overall R^2 to each one (Thomas and Zumbo, 1997). A variable was considered "important" if $dj > 1/(2 \times [\#\text{ of explanatory variables}])$. The level of significance was $\alpha = 0.05$.

To determine whether beaver were able to mitigate the loss of open water during drought, we compared the open water coverage for the two driest years, 1950 (with no beaver) and 2002 (with beaver) by overlaying the water coverage areas in the GIS. To further assess the effects of climate, we developed a regression model that included only precipitation and temperature variables to determine their overall effect on open water cover in wetlands while excluding beaver from the model.

From the data gathered for individual ponds in 1948, 1950, 1996, and 2001, repeated measures ANOVA was used to test for the effect of year and beaver activity over time on the mean change in the area of open water for individual ponds for each of the 4 years. Because the value for total annual precipitation within a year was a single number, the year itself was representative of its annual precipitation. Year was a within-subjects factor while beaver activity (future and current) was a between subjects factor (StatSoft Inc., 2003). We then used a Tukey's HSD test for post-hoc comparisons. All results were significant at $\alpha = 0.05$.

3. Results

The area of open water in wetlands closely paralleled the number of active beaver lodges over time (Fig. 3A). The best model that explained the greatest amount of variability in the area of open water in EINP included active beaver lodges, mean maximum annual temperature, and mean 2-year precipitation ($R^2 = 0.87$, $P < 0.00075$):

$$\begin{aligned}\text{area of open water} = {} & -78.14 + 0.81(\text{active lodges}) \\ & + 0.17(\text{mean max temp}) \\ & + 0.18(\text{2YrPrecip}) + 97.27\end{aligned}$$

The presence of beaver had a dramatic effect on the amount of open water in wetlands in EINP (Fig. 3B). The presence of active beaver lodges was the strongest predictor of open water coverage in the Park (relative Pratt index $dj = 0.8492$). Neither the mean maximum temperature (relative Pratt index $dj = 0.0784$) nor 2-year mean annual precipitation (relative Pratt index $dj = 0.0733$) significantly affected the amount of open water in wetlands (Fig. 4). We did not find any interaction effects among the explanatory variables.

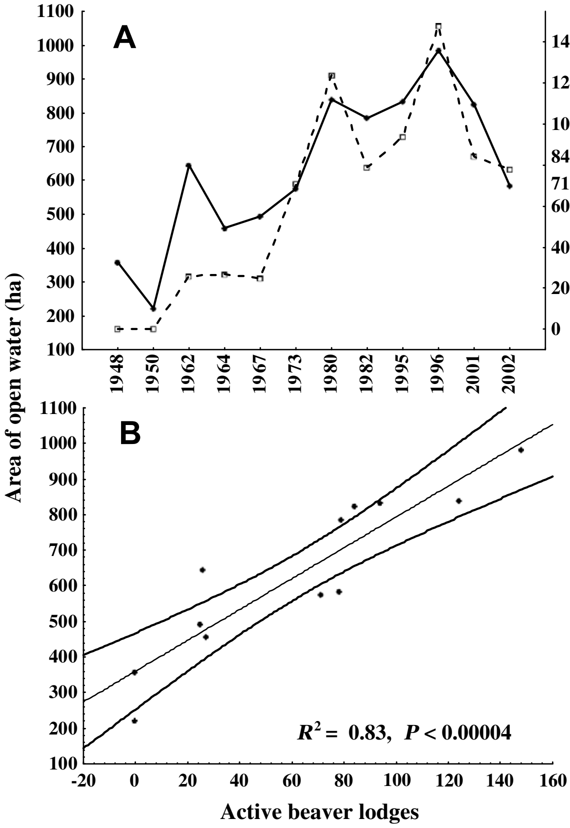

Fig. 3 – Relationship between beaver lodges and area of open water in all wetlands in study area. Graph (A) shows the area of open water (solid line) and the number of active beaver lodges (dashed lines) from 1948 to 2002 in Elk Island National Park, and graph (B) represents the regression between the area of open water (Y) and number of active beaver lodges (X) where Y = −58.43 + 0.19X. Outer lines represent 95% confidence limits.

Beaver were not present in the study area between 1948 and 1950, but were present in 1962 (Fig. 3). They steadily increased in the area until reaching a peak in active beaver lodges in 1996 (348 active lodges). In 1950, the second driest year of the study period, there was 47% more precipitation (316.7 mm) than in 2002, the driest year on record (215.9 mm). In 1950, when beaver were not present, wetlands held 61% less open water (228.7 ha) than in 2002 when beaver were well established (593.90 ha, Fig. 5).

When active beaver lodges were excluded from the analysis, the remaining variables (mean maximum annual temperature and mean 2-year precipitation) explained 38% of the variability in the area of open water in wetlands ($P = 0.12$). Mean maximum annual temperature was the strongest predictor in the model (relative Pratt index $dj = 0.5546$) followed by mean 2-year precipitation (relative Pratt index $dj = 0.4454$).

$$\begin{aligned}\text{area of open water} = {} & -720.80 + 0.51(\text{mean max temp}) \\ & + 0.47(\text{2YrPrecip}) + 197.86\end{aligned}$$

For all other variables used in the initial analyses, only the variable representing all beaver lodges (active + inactive) had a significant effect on the area of open water in wetlands ($R^2 = 0.45$, $P = 0.017$, Table 2). Despite documented residual effects of abandoned beaver dams on water retention (Naiman

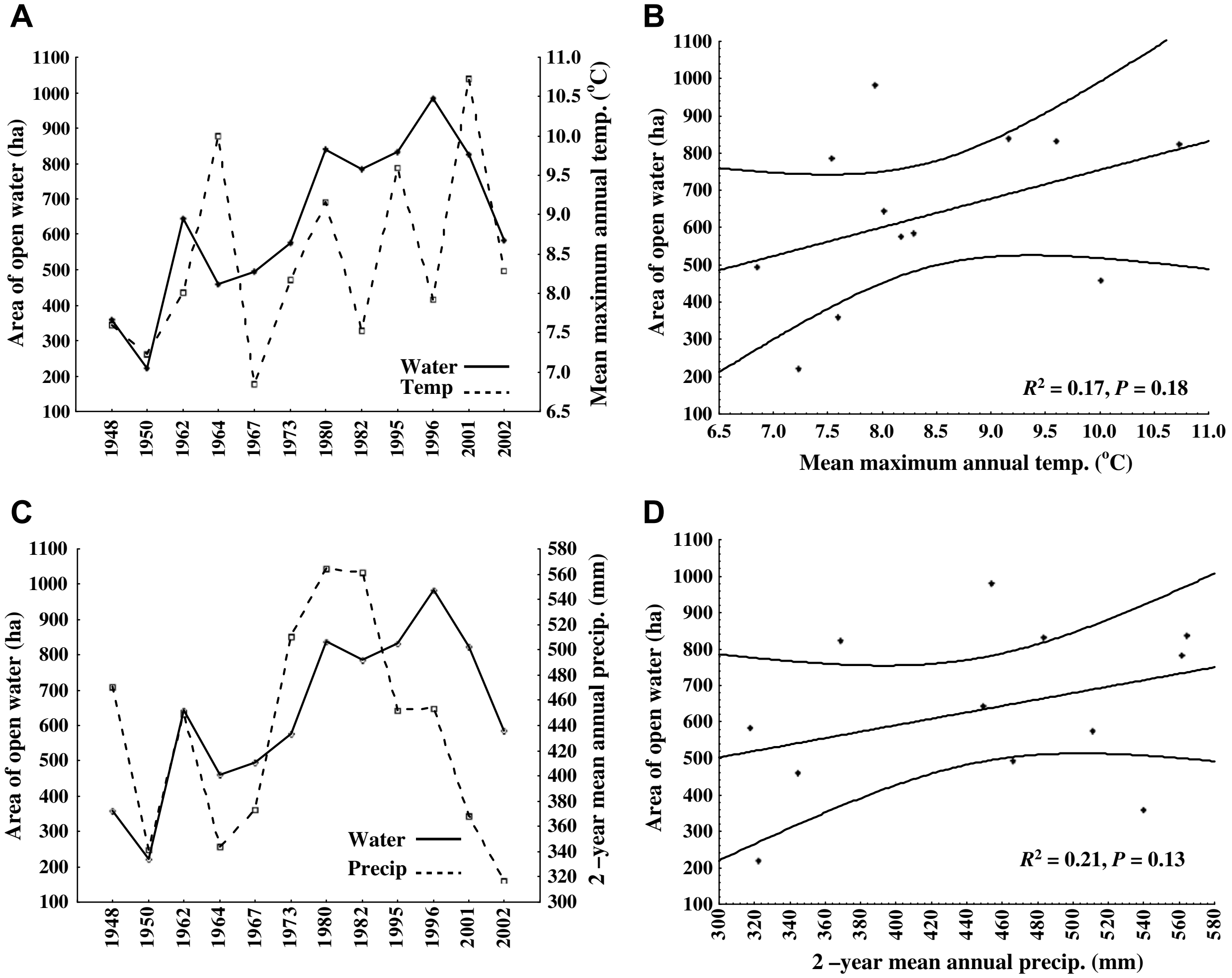

Fig. 4 – Relationship between the area of open water in the study area and climatic variables. Graph (A) shows the area of open water (solid line) and the mean maximum annual temperature (dashed lines) from 1948 to 2002 in Elk Island National Park; and the regression (B) between the area of open water (Y) and the mean maximum annual temperature (X) where Y = 7.08 + 0.002X. Graph (C) represents the area of open water (solid line) and the 2-year mean annual precipitation (dashed lines) from 1940 to 2002 in Elk Island National Park; and the regression (D) between the area of open water (Y) and 2-year mean annual precipitation (X) where Y = 358.78 + 0.14X. Outer lines represent 95% confidence limits. For graph C, precipitation is extended to 1940 to give a broader context to the drought year in 1950.

et al., 1988), in this analysis inactive lodges explained only 29% of the variability in the area of open water in EINP and was not a significant variable ($P = 0.07$, Table 2). Because the variable representing the number of active beaver lodges was a better predictor of the area of open water than the combined variable representing all (active and inactive) beaver lodges, only the data for active lodges were used in the overall model. The delayed effect of precipitation inputs into wetlands has also been described as a key factor driving open water retention in wetlands (Larson, 1995). We tested for the influence of 2-, 3-, and 5-year time lags in precipitation in the analyses, but found only the 2-year time lag was influential.

When water areas for individual ponds were repeatedly measured over 4 years within the study period (1940, 1950, 1996, and 2001) relative to their beaver activity, there was a significant effect of year ($F_{2,237} = 28.5$, $P < 0.001$), beaver activity ($F_{1,79} = 6.53$, $P = 0.01$, Fig. 6), and the interaction between year and beaver activity ($F_{3,237} = 6.54$, $P = 0.0003$). Ponds with active beaver colonies in 1996 and 2001 had an average open water area of 35.5 ha, compared to an average of 3.9 ha of open water in those same ponds without beaver in 1948 and 1950 (Fig. 7), despite 1948 having above average precipitation (Fig. 2). The ponds that did not have active beaver colonies in them during any of the years (i.e., the 41 ponds measured in 1948, 1950, 1996, and 2001) also had less open water area than ponds with active beaver colonies ($F_{1,79} = 6.53$, $P = 0.01$, Fig. 6). There was no difference in area of open water in any of the ponds measured in 1948 and 1950; however, on average these ponds had approximately nine times less open water than both active and inactive ponds in 1996 and 2001($F_{1,322} = 43.52$, $P < 0.001$). It is important to note that, although these ponds were unoccupied, it was impossible to find any ponds in 1996 and 2001 that had not had beaver in them at some point in their history.

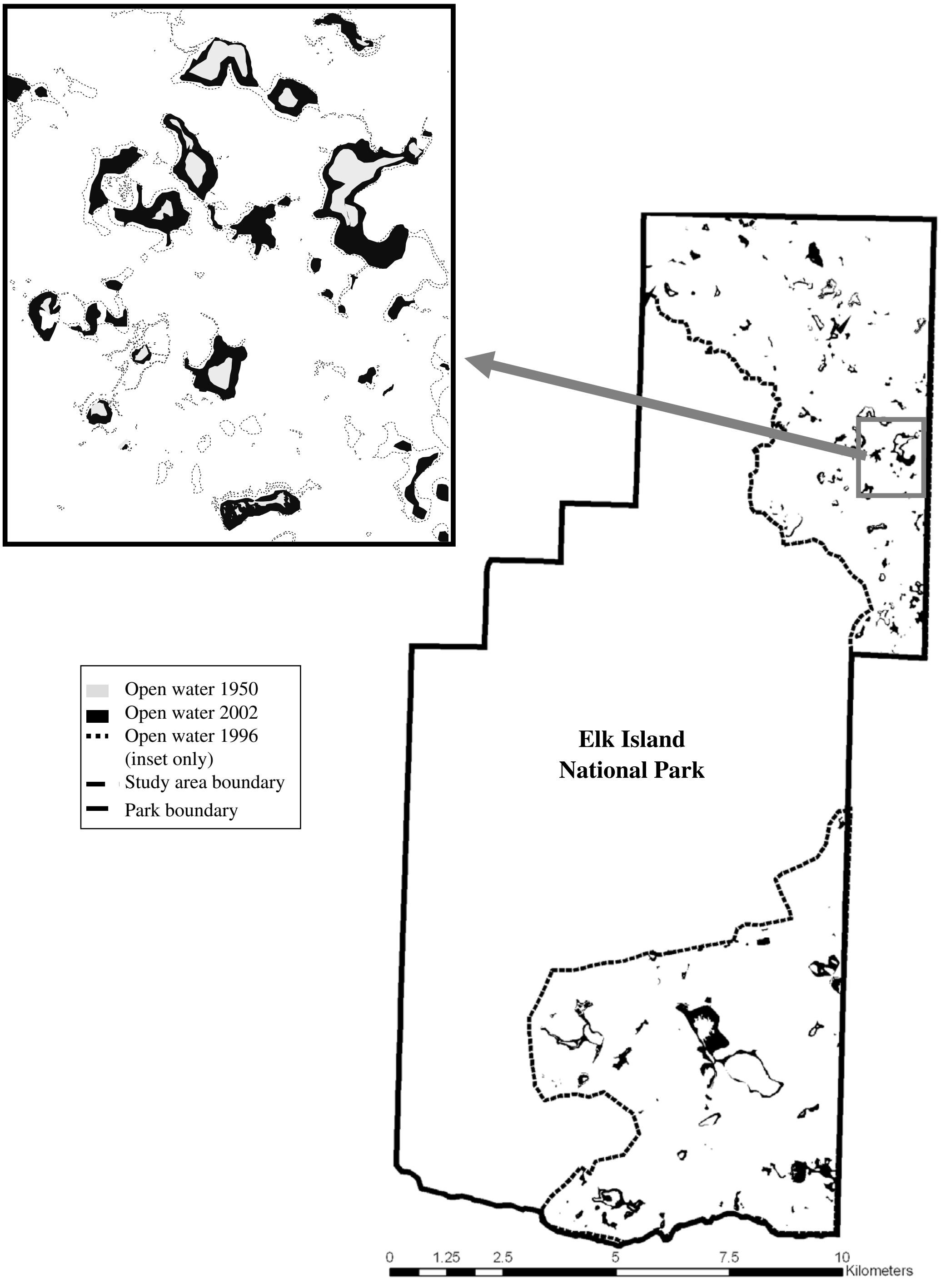

Fig. 5 – The area of open water in 2002 (black) overlaid with the area of open water in 1950 (gray) in Elk Island National Park, Canada. There were no beaver present in the study area in 1950, but they were well established by 2002. The dashed line (– – –) represents the study area boundary, the black line (—) indicates the Park boundary, and the dotted line (.....) in the inset represents the water area in 1996 (a year with average to high levels of precipitation).

4. Discussion

Rarely do we have the opportunity to examine long-term data where we can compare the effects of climate, beaver activity, and open water coverage in wetlands on the same scale. We determined that the presence of beaver increases open water in wetlands despite fluctuations in precipitation and temperature. Specifically, the presence of active beaver lodges accounted for over 80% of the variability in the area of open water in wetlands of EINP over a 54-year period. This ability of beaver to manage water is remarkable, considering the isolated nature of wetlands in this area and the lack of

Table 2 – Regression results for the variability in the area of open water (ha) predicted by individual climatic and beaver population variables for the period of 1948 to 2002 in Elk Island National Park, Canada

Ranking	Explanatory variable	R^2-value	P-value
1	Number of active beaver lodges	0.83	0.00004*
2	Number of all beaver lodges (active + inactive)	0.45	0.02*
3	Number of inactive beaver lodges	0.29	0.07
4	2-Year total annual precipitation	0.21	0.13
5	Total annual rainfall	0.18	0.67
6	Mean maximum temperature	0.17	0.18
7	5-Year total annual precipitation	0.14	0.23
8	Hydrologic year (November 1 to October 31)	0.14	0.23
9	3-Year total annual precipitation	0.11	0.30
10	Seasonal precipitation (3 months prior)	0.05	0.47
11	Total annual precipitation	0.032	0.58
12	Total annual snowfall	0.031	0.58
13	Mean annual temperature	0.028	0.61
14	Annual precipitation–potential evapotranspiration (PET)	0.02	0.70

Values are for simple linear regression models that include only one predictor variable. Results area ranked by the variable's R^2 value.

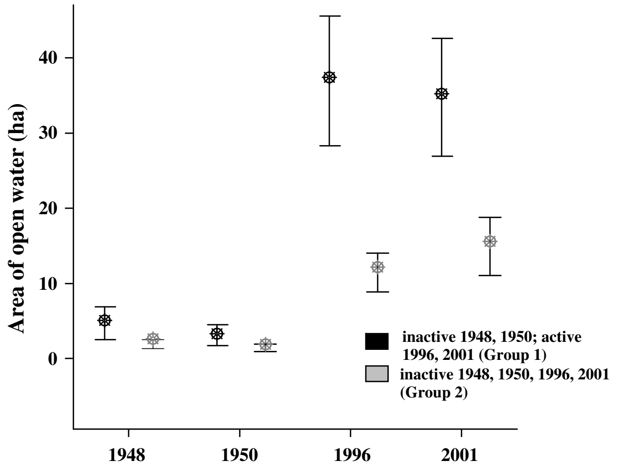

Fig. 6 – Mean area of open water for individual ponds measured in 1948, 1950, 1996, and 2001 in Elk Island National Park, Canada. Ponds were classified into two groups: (1) ponds that did not have beaver in them in 1948 and 1950, but did have active beaver colonies in 1996 and 2001 (black; established post-1950) and (2) ponds that did not have beaver in them in any of the 4 years (grey). Lines indicate ±1.0 standard error of the mean.

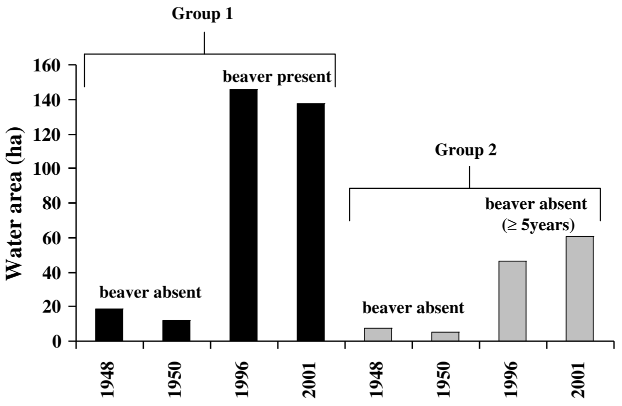

Fig. 7 – Total area (ha) of the area of open water for individual ponds measured in 1948, 1950, 1996, and 2001 in Elk Island National Park, Canada. Ponds were classified into two groups: (1) ponds that did not have beaver in them in 1948 and 1950, but did have active beaver colonies in 1996 and 2001 (black) and (2) ponds that did not have beaver in them in any of the 4 years (grey).

significant stream flow. Although precipitation and temperature were a factor in the amount of open water area, their contributions were minor relative to those of beaver activities. Morainal ponds, such as those found in EINP, likely respond quickly to heavy rainfall events, as suggested by Ferone and Devito (2004) in their investigations of shallow peatland complexes in the boreal plains. Winter (1999) also proposed that local flow systems are more important than regional flow systems with morainal wetlands. The ponds in the study area are typically isolated ponds and "valleys" best described as morainal depressions. EINP generally lacks the permanent streams or creeks examined in other studies where researchers have shown beaver to have significant influences on water resources (e.g., Naiman et al., 1988; Johnston and Naiman, 1990a, b; Westbrook et al., 2006). Our results confirmed that beaver have an overwhelming influence on wetland creation and maintenance and can mitigate the effects of drought.

Because beaver are a semi-aquatic mammal, it could be argued that the relationship between the area of open water is correlative rather than causal. However, in all cases where beaver were absent from individual ponds in 1948, 1950, 1996, and 2001, water levels were significantly lower than in areas with active beaver colonies. The area of water in ponds that did not yet have beaver in them, but would in future years, was also consistently lower prior to being colonized by beaver. We were unable to find any ponds consistently without beaver following re-colonization of the Park. It is possible that because of lag effects from abandoned dams and channels, inactive ponds in 1996 and 2001 retained significantly more open water than inactive ponds in both 1948 and 1950. This 9-fold difference existed despite the fact that 1996 and 2001 had less combined total precipitation than

1950 and 1948. Other studies have noted the continued effects of beaver on water resources even after the site had been abandoned (see Naiman et al., 1988; Westbrook et al., 2006) and it is possible that lag effects from high water also affected groundwater and surface water recharge in EINP, even during drought.

Climate change is a topic of increasing importance on both a global and local scale. The effects of a warming climate are anticipated in many sectors including forestry (Hogg and Bernier, 2005; Breshears et al., 2005), agriculture (Smit and Skinner, 2002), and resource management (Dawson et al., 2003; Johnson et al., 2005). Climate change is of particular concern within protected areas due to their role in conserving species at risk and their associated habitats, and their larger role in supporting high biodiversity. An assessment of the potential effects of climate change on Canada's National Parks predicted lower soil moistures and increased drought in Parks such as EINP, if predictions of current global circulation models (GCM) are accurate (Scott and Suffling, 2000). The predicted loss of open water and increased water temperatures would have direct effects on fish, amphibian, and waterfowl populations and could potentially cause more northerly shifts both in vegetation and wildlife populations. Several studies predict biome shifts in forest and grassland ecosystems due to temperature increases predicted in GCMs (Scott and Suffling, 2000; Camill and Clark, 2000; Hogg and Bernier, 2005). In other regions of the world predicted to be influenced by global warming, beaver may play a similar role. As yet, this role does not appear to home been well-studied relative to climate change.

Our findings indicate that beaver could mitigate some of the adverse effects of climate change due to their ability to create and maintain areas of open water. Naiman et al. (1988) suggested that beaver impoundments have a high resistance to disturbance (e.g., flooding). We argue that this resistance extends to drought. During the drought of 2002, wetlands lacking active beaver lodges were visibly drier (some of which became mudflats) than those with beaver. During the height of the drought, many farmers grazed their cattle in areas with active beaver impoundments to water their animals.

Despite their ability to maintain wetlands, beaver are not impervious to repeated or long-term droughts, which could compromise the survival of beaver colonies. During the drought of 2002, much of the activity around the lodges was spent digging channels in their receding impoundments to maintain critical access to resources and appropriate water depths at the food cache areas in front of their lodges. These caches must be accessible under the water for the duration of the winter for the colony to avoid starvation. We found that some colonies were able to over-winter with as little as 70 cm of water at their food caches. Others, whose food caches were completely frozen into the ice, died from either predation when they tried to escape their lodges in search of food or starvation inside their lodges. The number of beaver lodges in EINP decreased by approximately 7% from 1999 to 2002, loss which can partly be attributed to low water levels and lack of access to food caches.

As with our study, both Johnston and Naiman (1990a,b) and Syphard and Garcia (2001) used historic aerial photography to study the influence of beaver activities over a period of 46 and 41 years, respectively. Johnston and Naiman (1990a) found that pond sites increased from 71 to 835 between 1940 and 1986 in northern Minnesota, USA. In the Chickahominy River study, Syphard and Garcia (2001) found that, although beaver only accounted for 1% of wetland gain, their activities accounted for 23% of change in wetland types from 1953 to 1994. In EINP, the area of open water increased from 365 ha in 1948 to 991 ha in 1996, when beaver populations reached their peak. Current levels are somewhat lower due to the recent drought (593.9 ha in 2002).

This study differs from other long-term studies in that we were able to examine 12 years of data over a 54-year period, while the other studies were only able to obtain data covering 2–6 years of their study period (Johnston and Naiman, 1990a, b; Syphard and Garcia, 2001). We were also able to use mapped beaver census data, while other studies relied on indications of beaver activity from analysis of aerial photography. In addition, long-term climate data were readily available and included temperature and precipitation extremes.

Analyses were limited to 12 years of data due to either a lack of photographic coverage when data on beaver were available, or a lack of beaver census data when aerial photographs existed. In addition, no photographic coverage was available for the extreme drought of the 1930s; a period when drought was extreme in the area, thus limiting the number of extremely dry years we could examine. The 2002 drought was drier than that of the "Dirty 30s" and because current annual precipitation levels continue to be low, its duration may also be comparable to the 1930s. Due to a lack of hydrological data for the Park, we were unable to assess possible effects on groundwater in this study. Future hydrologic studies in the area would not only help assess the effects of beaver on groundwater, but also the effects of extreme climatic events, such as drought, on the overall water resources in the area.

Given the recent predictions of warming and drying trends for the PPR and the southern boreal regions in North America, beaver will likely play an important role in maintaining open water and mitigating the impact of drought. Considering their role as a keystone species in wetlands, their positive impact on biodiversity alone is a significant benefit (Naiman et al., 1986; Pollack et al., 1996; Nolet and Rosell, 1998). Increased removal of wetlands and beaver from the landscape for urban, industrial and agricultural demands warrants further investigation. As with drought, fire is also expected to increase with predicted drying trends and future research that incorporates fire into the model would be warranted.

5. Conclusions

Given their ability to create and maintain areas of open water wetlands, the removal of beaver from aquatic systems should be recognized as a wetland disturbance equivalent to in-filling, groundwater withdrawal, and other commonly cited wetland disturbances (Mitsch and Gosselink, 2000; Zedler, 2000). Although beaver have recovered in much of their former range after their near extirpation at the start of the 20th century, they are often in conflict with human activities and are subject to extensive management. Alternatives to direct removal of beaver colonies have been suggested by Lisle (2003) in his design and use of flow devices. In habitats where potential conflicts are minimal, but the benefits of wetland restoration is high, beaver should be seen as a natural alternative to wetland restoration and enhancement due to their ability to mitigate extreme weather events such as drought. Removal of beaver should be considered a wetland disturbance, much in the same way as infilling, peat mining, and industrial water extraction, and should be avoided.

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