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Research Article

Using Beaver Works to Estimate Colony Activity in Boreal Landscapes

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ABSTRACT Beaver ponds and beaver-impounded vegetation are indicators of past or present beaver activity that can be detected from aerial photography. A method to quantitatively relate these beaver works with the density of active beaver colonies could benefit beaver management, particularly in areas lacking beaver population data. We compared historical maps (1961–2006) of beaver works at Voyageurs National Park, Minnesota, USA with concurrent aerial surveys of beaver colonies. We tested 2 landscape-scale models of beaver colony density previously developed for a period of beaver population expansion (1940–1986), but they failed to predict colony density after 1986, a period of declining beaver population. We developed a new landscape-scale regression, calculating that 2.15% of the landscape would be flooded by every 100 additional beaver colonies ($R^2 = 0.53$, $P = 0.027$). Classification tree analysis of individual pond sites showed that open water pond and impounded marsh area were the primary predictors of beaver colony presence or absence, but that the classification trees were far better at identifying inactive sites (>93% correct) than active sites (35–38% correct). The area of open water in beaver ponds is a good but not perfect indicator of beaver activity that can be used by wildlife managers as a landscape-scale indicator of beaver colony density. Published 2015.

KEY WORDS *Castor canadensis*, dam, marsh, meadow, pond, population, Voyageurs National Park.

The North American beaver, *Castor canadensis*, is renowned for building dams that impound water and alter upstream vegetation, collectively called impoundments. Beaver dams are often detectable on aerial photos because of the upstream effects of inundation. Wildlife biologists began to use aerial photographic evidence of these beaver works (i.e., dams and impoundments) as an aid to management in the 1970s, when beaver populations were still recovering from near-extirpation due to historical over-trapping (Dickinson 1971, Parsons and Brown 1978). The use of aerial photographs (hereafter, photos) provided an additional advantage in the ability to document changes in beaver works over time. However, beaver works can persist long after the occupant's departure, so that their presence does not necessarily indicate current beaver activity. A more reliable metric of current beaver activity in the northern United States is a count of food caches, which are semi-submerged piles of twigs and branches stored by beavers near the lodge entrance in autumn as a supply of food for the winter. Beaver colony censusing typically uses aircraft overflights to detect these food caches before freeze-up in the autumn (Payne 1981, Brown and Parsons 1982, Swenson et al. 1983).

A variety of cover types occur within beaver impoundments. New ponds may contain live trees or shrubs that are tolerant of shallow inundation (e.g., black ash, *Fraxinus nigra*) or standing dead trees that have been killed by deeper, more prolonged inundation (Hyvönen and Nummi 2008, Johnston 2012). Older ponds may contain emergent marsh or submerged and floating-leaved macrophytes (Ray et al. 2001). Beaver dams also flood bogs, which may form peat mats that float up and down with water level fluctuations (Rebertus 1986, Reddoch and Reddoch 2005). Dewatered pond areas become beaver meadows, which are saturated wetlands vegetated by grasses and sedges (Wright et al. 2003, Little et al. 2012), and may succeed to shrubs after prolonged periods of abandonment (Remillard et al. 1987). The recovery of a beaver impoundment from altered to original state can take decades and can exhibit hysteresis, whereby vegetation changes are not merely the reverse of those that occurred during pond creation due to the conversion of forest lands to marshes and wet meadows (Johnston 1994, 2012).

Earlier aerial photo interpretation at Voyageurs National Park, Minnesota, USA (VNP) showed that the cover types of beaver impoundments changed between 1940 and 1986 as the beaver population expanded, with an increase in the proportion of pond and marsh and in total area affected (Johnston and Naiman 1990*b*). Broschart et al. (1989) used these impoundment data with independently collected beaver population data to develop 2 models of beaver colony density as a function of impounded vegetation, one based on marsh and meadow areas and the other based on marsh area alone, expressed as a proportion of the landscape. The 2 empirical models worked well based on the data available at

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that time, which represented a period of beaver population recovery and expansion. More recent census data show that the beaver population of VNP has declined, however, which may have affected model validity.

Our goal was to update and re-evaluate the relationships found in Broschart et al. (1989) to determine their applicability to a decreasing beaver population with increasing pond site abandonment. Specific objectives were to 1) describe trends over time (1958–2005) of VNP beaver colonies; 2) compare beaver colony densities from infrequent, complete aerial censuses versus densities calculated from widely spaced aerial transects sampled more frequently; 3) compare the water and vegetation cover characteristics of active versus inactive beaver pond sites, and determine if beaver activity of individual pond sites could be predicted from those characteristics; 4) quantify cumulative beaver landscape alteration caused by pond-building over time; and 5) determine if beaver colony density could be predicted from landscape vegetation characteristics using the previously developed models or other empirical models.

STUDY AREA

Our study area was the Kabetogama Peninsula of Voyageurs National Park (VNP), located 18 km east of International Falls, Minnesota on the United States–Canada border. The 305-km^2 Kabetogama Peninsula (48°30' N, 93°00' W) was the roadless core of the park, with portions in northern St. Louis and Koochiching Counties (Fig. 1). The mean annual temperature at International Falls was 2.4°C, and mean annual precipitation was 63 cm. Maximum topographic relief within the study area was only 80 m, with slopes ranging from flat glaciolacustrine plains to steep cliff faces. Upland forests were dominated by quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*; Faber-Langendoen et al. 2007).

METHODS

Beaver Population Data

We used 2 types of beaver population data, both collected as aerial observations from fixed-wing aircraft in late October: 1) census maps of active beaver lodges within VNP in 1984, 2000, and 2006 (lodge maps), and 2) number of active beaver lodges counted annually along transects crossing the Kabetogama Peninsula within St. Louis County from 1958 to 2005 (transect surveys). Lodge maps differed from transect surveys in their coverage area (comprehensive census vs. transect samples), recording methods (spatially explicit lodge maps vs. lodge count by transect), and frequency of acquisition (collected 3 times vs. 38 times). For both datasets, active beaver lodges were identified by the presence of a food cache and/or fresh mud on the lodge, as observed from a tandem-seat plane with a pilot and single observer flown at 180–210 m above the ground at approximately 130 kph. The 2000 census was flown at a slightly higher altitude (240–340 m above the ground) but similar flight pattern to other censuses. Although flight altitude is one of several factors that can bias detection rates in autumn beaver cache surveys (Romanski 2010), other factors that can potentially bias observation (aircraft type, speed) were consistent across all the aerial surveys. The lodge maps were created for the entire park by manually plotting locations of active beaver lodges on 1:50,000 scale topographic maps while in flight, and later converting the plots to geographic information system (GIS) point data. The transect surveys tallied active lodges on beaver ponds (pond lodges) and small (<125 ha) permanent lakes of the Kabetogama Peninsula interior (lake lodges), although these

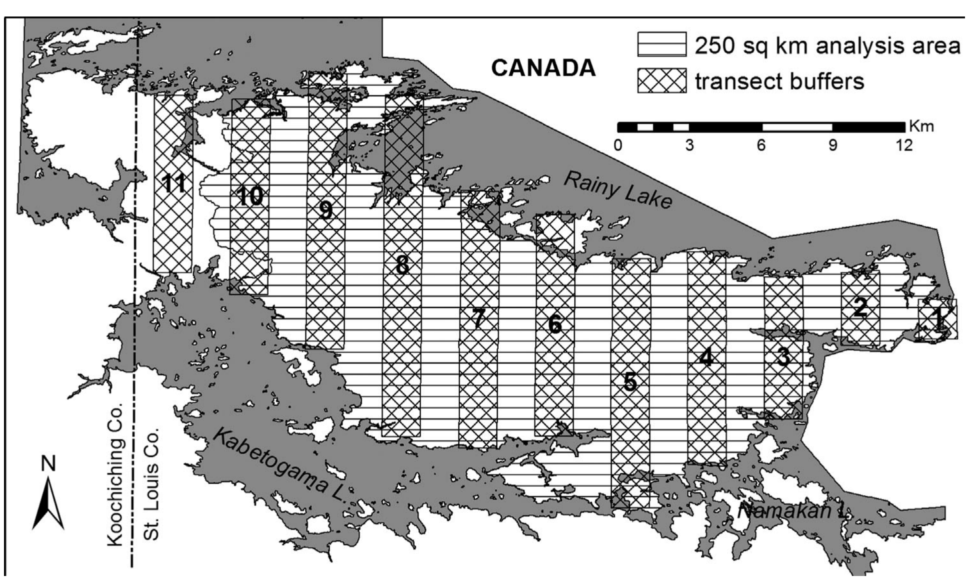

Figure 1. Site map of the Kabetogama Peninsula in Voyageurs National Park, Minnesota, USA, showing location of spatial analysis areas: 1) 11 transect buffers and 2) a single 250-km^2 area covering most of the St. Louis County portion of the Kabetogama Peninsula.

2 lodge types were not differentiated in data reports until 1979. Tallies were separately recorded for each of the 11 north-south aerial transects within the St. Louis County portion of the Kabetogama Peninsula (Fig. 1). The transect surveys were conducted nearly annually from 1958 to 2002 by the Minnesota Department of Natural Resources (MNDNR, unpublished data), then continued by the National Park Service (NPS). Thirty-five of the 38 transect surveys were conducted by 3 observers, each of whom trained their successor.

We digitized the transect flight lines in ArcGIS 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA) and generated an 800-m buffer along both sides, corresponding to the sight distance that observers were instructed to use in their counts. We divided the original transect survey data (count per length of survey route) by buffer area to compute colony density/km^2. We also clipped the lodge maps for 1984 and 2000 with the 800-m transect buffers to test the assumption that detection probability was 1.0 within the transect buffers. No transects were flown in 2006, so the 2006 lodge maps could not be compared with transect surveys.

Lake, Beaver Impoundment, and Pond Site Maps

We used aerial photos from multiple years to delineate beaver ponds and associated wetlands in which elevated water levels from beaver dams had flooded, killed, or otherwise altered the vegetation present. We delineated beaver impoundments manually or electronically on aerial photo prints or digital images according to National Wetlands Inventory conventions (Cowardin et al. 1979) and codes (Table 1) but mapped only beaver-altered ponds and wetlands rather than all wetlands. Impoundment boundaries were generally distinct on the aerial images except when beavers raised the water level in pre-existing peatlands, where we used ponded water or dead woody vegetation to identify the outer extent of beaver influence. All mapping was done by 3 photo interpreters, who checked each other's work for consistency. We generated the GIS versions of all beaver impoundment maps as described in Johnston and Naiman (1990*b*) and Host and Meysembourg (2010).

The beaver impoundment maps did not distinguish individual dams; they delineated polygons of contiguous vegetation of the same class. To identify the complex of vegetation and open water associated with an individual dam, we intersected the beaver impoundment maps with a pond site GIS layer. Pond sites are bounded at the downstream end by the beaver dam that caused the ponding, and at the upstream end by unimpounded vegetation or the next upstream beaver dam. Pond sites usually contain a complex of water and wetland vegetation, and are rarely merely open water.

Beavers do not create lakes, yet lakes support active beaver lodges that were enumerated in the census maps and transect counts. Because we were interested only in beaver works, we excluded or kept distinct the area of lakes and permanent ponds and their associated wetlands in our GIS data. This included 27 lakes and ponds $<$125 ha within the peninsula interior (see Table S1, available online at www.onlinelibrary.wiley.com). We used aerial photos taken in 1927 to identify 6 unnamed permanent ponds based on the absence of beaver dams and the presence of floating bog mats around pond peripheries. We generated a separate GIS data layer by selecting the polygons for the 27 permanent water bodies from the National Hydrography Dataset (http://nhd.usgs.gov/). The GIS data layers of the permanent water body and beaver impoundment maps can be viewed and downloaded online (Johnston and Windels 2015).

GIS and Statistical Analyses

We generalized impoundment vegetation classes into 6 cover types (Table 1), and summarized classes at 3 different spatial resolutions: 1) individual pond sites ($n = 734$, average area = 4.04 ha); 2) transect buffers ($n = 11$, average area = 1,346 ha); and 3) a single 250-km^2 area covering most of the St. Louis County portion of the Kabetogama Peninsula (hereafter, peninsula). We intersected the beaver impoundment maps with these boundaries to extract vegetation data that would spatially match the beaver population data in the form of transect surveys (transect buffer resolution) and lodge maps (pond site resolution). We performed all GIS analyses in ArcGIS 10.1.

At the pond site resolution, we used the 3 lodge maps to identify active beaver ponds as of 1984, 2000, and 2006, which we matched with the 1986, 2003, and 2005 beaver impoundment maps, respectively (the closest temporal

Table 1. Grouping of original National Wetlands Inventory (NWI) classification codes into 6 general classes. The system for all NWI classes used was palustrine (P). Water regimes included: temporarily flooded (A), saturated (B), seasonally flooded-saturated (E), semi-permanently flooded (F), and permanently flooded (H). Additional information about classes at http://www.fws.gov/wetlands/Data/Wetland-Codes.html

General class	NWI system, class and subclass	Description of NWI class and subclass	NWI water regime(s)
Dead woody	PSS5	Scrub/shrub dead	B, E, F
	PFO5	Forested dead	B, E, F
Pond	PAB3	Aquatic bed rooted vascular	F, H
	PUB	Unconsolidated bottom (i.e., open water)	F, H
Meadow	PEM1	Emergent persistent	A, B, E
Marsh	PEM1	Emergent persistent	F
Bog	PSS3	Scrub/shrub broad-leaved evergreen	A, B, E, F
	PSS4	Scrub/shrub needle-leaved evergreen	A, B, E, F
	PFO3	Forested broad-leaved evergreen	A, B, E, F
	PFO4	Forested needle-leaved evergreen	A, B, E, F
Deciduous swamp	PSS1	Scrub/shrub broad-leaved deciduous	A, B, E, F
	PFO1	Forested broad-leaved deciduous	A, B, E, F

match for each). Pond sites appearing on the impoundment maps that were not designated as active by their corresponding lodge maps were considered to be inactive. We performed 2 analyses of vegetation within active versus inactive pond sites. The first compared average areas of pond sites and their vegetation classes within active versus inactive groups for each of the 3 lodge map census dates, using Welch two-sample *t* tests. The second analysis distinguished pond sites into those that had been active once, twice, thrice, or inactive during the years represented by the lodge maps, and compared their average area and vegetation using analysis of variance (ANOVA) followed by Tukey honest significant difference (HSD) comparisons. Because of the possibility of spatial mismatch between lodge points and pond sites, we included only pond sites with an area of 0.5 ha or more in the analysis.

At the transect resolution, we used the 11 transect buffers to clip the beaver impoundment maps for the following years: 1961, 1972, 1981, 1986, 1988, 1990, 1997, 2003, and 2005. We used linear regressions to relate the number of active lodges counted in all transects versus beaver pond water as a percent of total transect buffer area (148 km^2). We repeated the analysis after excluding lake lodges and lake area to relate active pond lodges versus pond water as a percent of transect buffer land area (131 km^2). Because most of the aerial photos used to generate the impoundment maps were flown in May, we matched the impoundment maps with transect count data from the previous autumn where possible (1961 and 2005 aerial photos and transect count data were acquired during the same year).

One- and 2-variable empirical models were previously developed that estimated beaver populations as a function of area impounded using data from the 1940 to 1986 maps (Broschart et al. 1989):

$$Y = 0.09 + 61.86(W)$$

$$Y = 0.26 + 94.14(W) - 45.33(X)$$

where Y = number of beaver colonies/km of survey route, W = proportion of total land area impounded as marsh, and X = proportion of total land area impounded as seasonally flooded meadow. We applied these formulas to the new summary data for the 250-km^2 area as mapped in 1987–1990, 1997, 2003, and 2005, and compared the resulting beaver population estimate to the actual count per km of transect, using linear regressions to evaluate the results. We performed all statistical analyses using R version 3.1.1. (R Core Team 2014).

We constructed classification tree (CART) models to relate beaver activity to pond site vegetation characteristics, using the recursive partitioning and regression trees package for R (RPART version 4.1-8; Therneau et al. 2014). We used the 1984, 2000, and 2006 pond sites (classified as active or inactive) as response variables, and the following vegetation characteristics as potential predictors: the area of each general class (Table 1) within the pond site (6 variables), the area of pond plus marsh (i.e., the 2 wettest classes) within the pond site (1 variable), total pond site area (1 variable), and the proportion of each general class relative to total pond site area (6 variables). The RPART package allows cross-validation runs on the data to determine the optimally sized tree, selected as the sub-tree that performs best in a validation set. We performed a 10-fold cross-validation, where each run consisted of 10 random divisions of the data into 90% learning and 10% test sets. For each split, we computed the complexity parameter (CP), a measure of how much additional accuracy a split must add to the entire tree to warrant the additional complexity. Any split that did not decrease the overall lack of fit by a factor of CP was pruned from the tree. We determined the optimal tree size from the table of cross-validation error values for various tree lengths as the number of splits corresponding to the minimum cross-validation error, and pruned each tree to the CP value for this optimum. We conducted an error analysis of the CART models by applying the resultant models to the original lodge map data to determine user's accuracy (the probability that a site modeled as a particular class really was that class) and producer's accuracy (the probability that a particular class identified on the lodge map was correctly modeled as such).

RESULTS

Comparability of Transect Versus Comprehensive Census Data

Linear regressions relating the 1984 and 2000 transect survey counts with corresponding data clipped from 1984 and 2000 lodge maps using the transect buffers were highly significant (1984 $R^2 = 0.770$, $P < 0.001$; 2000 $R^2 = 0.887$, $P < 0.001$), indicating that comparable data were collected by both approaches within their common observation areas. Furthermore, the slopes of the regressions were approximately 1, indicating that the transect counts are indeed estimating the number of colonies within the 800-m wide observation bands as specified in the transect survey standard operating procedure. The 0.99 slope of the regression between the 2000 transect survey and its corresponding lodge map also validates our assumption that the higher aircraft altitude used to construct the 2000 lodge map did not unduly reduce cache detection.

Beaver Colony Density

At the transect scale, beaver colony density changed over time as the VNP beaver population expanded, stabilized, and declined (Fig. 2, solid line). Total active lodge density was only 0.33/km^2 during the first transect survey in 1958, increasing to 1.1/km^2 during the mid-1980s through the mid-1990s then decreasing to 0.9/km^2 thereafter. Beaver colony density computed for the St. Louis County portion of the Kabetogama Peninsula using the 3 lodge maps was similar: 0.97/km^2 in 1984, 1.00/km^2 in 2000, and 0.76/km^2 in 2006. Lake lodges were distinguished from pond lodges in transect surveys beginning in 1979, and constituted 8.5% of all active lodges counted in 1979–2005, ranging from 4.3% to 17.4%. Removal of lake lodges from the 1979 to 2005 transect survey data had minimal effect on computed densities (Fig. 2, dashed line).

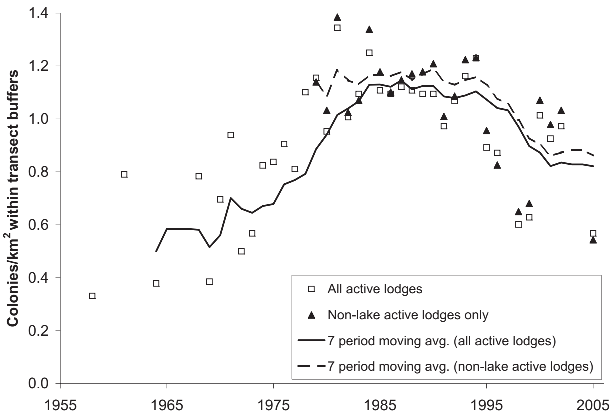

Figure 2. Beaver colony density at Voyageurs National Park, Minnesota based on aerial survey transects, 1958–2005. Point symbols indicate average annual colony density per square km, including and excluding lake lodges. Linear trends are 7-period moving averages of the point data.

Vegetation of Active Versus Inactive Beaver Pond Sites

None of the 734 pond sites mapped completely disappeared over the period of study; the high water mark outlines remained discernable in the form of altered vegetation despite pond dewatering after abandonment. Wetland vegetation was the major cover type in both active and inactive pond sites (Fig. 3). Of the 171 active pond sites in 2006, only 11 were predominantly (>90%) pond water, and 10 contained no mapped water bodies at all, consisting entirely of wetland vegetation.

In each pair for a given date, active pond sites were larger and contained greater pond and marsh area than did inactive ponds (*t* tests, $P < 0.001$; Fig. 3A). Sites active 2 or 3 times were significantly larger than the 2 other site groups, and the area per pond site of open water pond and marsh increased significantly with increasing frequency of beaver occupancy (Fig. 3B). The area of wet meadow vegetation was greater in twice-active than inactive pond sites, but wet meadow as a fraction of total pond site area was greatest in once-active and inactive pond sites (data not shown). On average, bog vegetation constituted 12–16% of pond site area regardless of beaver activity, and the area of bog vegetation was significantly greater in thrice-active than in inactive pond sites. Dead woody vegetation, which is created when dam-induced flooding kills intolerant trees and shrubs, was not significantly different across the groups. These data illustrate that the same vegetation classes occur in both active and inactive pond sites, but that the area and relative proportion of open water and herbaceous vegetation classes differ across levels of beaver activity.

Beaver Landscape Alteration

The cover types of beaver impoundments exhibited 3 different periods of change (Fig. 4). During 1940–1981, impoundment area and the relative proportion of pond and marsh cover increased; during 1986–1990, pond area stabilized at around 29% of impoundment area; and during 1997–2005, pond area decreased to only about 16% of impoundment area and meadow became the prevalent cover type (29% of impoundment area in 2003 and 2005). These changes were concurrent with increases, stabilization, and decreases in transect counts of active beaver colonies (Fig. 2).

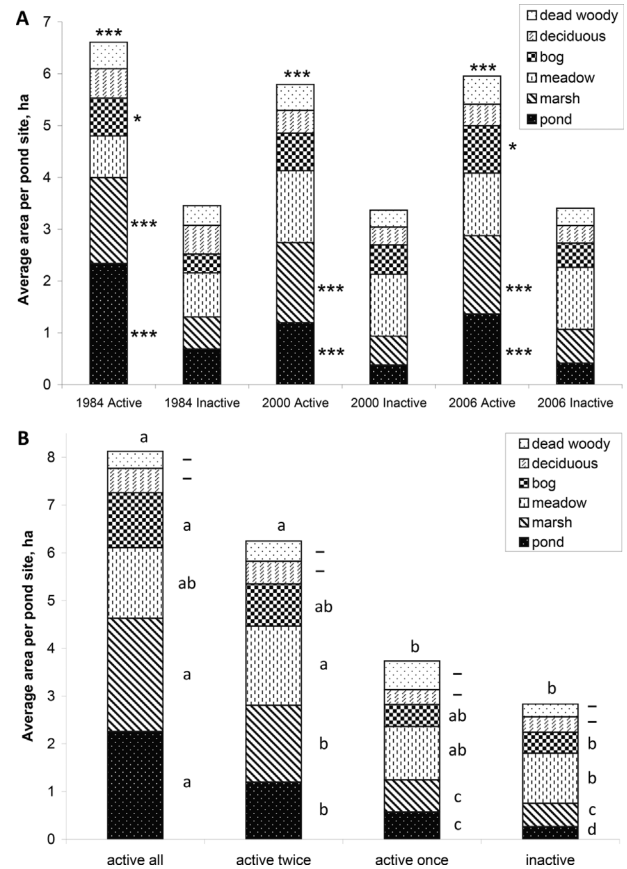

Figure 3. Vegetation types associated with active versus inactive beaver pond sites in Voyageurs National Park, Minnesota. (A) Average area of vegetation types for active versus inactive pond sites during lodge map census years 1984, 2000, and 2006. Bars or portions of bars with * indicate significant differences (*** $P < 0.001$, * $P < 0.05$). (B) Average area of vegetation types for beaver pond sites that had been active once, twice, thrice, or inactive according to lodge maps. Bars or portions of bars sharing the same lowercase letter are not significantly different (Tukey multiple comparisons of means, $P < 0.05$). — = no significant difference among groups.

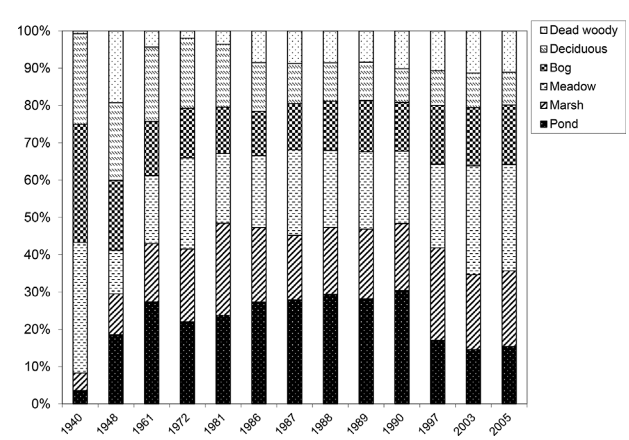

Figure 4. Average vegetation composition of all beaver impoundments (active and inactive) as a fraction of impounded area in Voyageurs National Park, Minnesota, 1940–2005. Data from 1940 through 1986 after Broschart et al. (1989).

Landscape Models of Beaver Colony Density

The 2 peninsula-wide models developed by Broschart et al. (1989) worked well for the time period on which they were based, but they failed to predict colony density after 1986 ($R^2 = 0.13$ for the 1-variable model; $R^2 = 0.01$ for the 2-variable model). The models failed because they were based on a period of beaver expansion, when marsh as a proportion of all land area was greatly increasing as the burgeoning beaver population flooded new pond sites. This pattern changed after 1986, as available pond sites were used up and beaver reoccupied previously established pond sites.

However, there was a positive relationship ($R^2 = 0.53$, $P = 0.027$) between number of active pond lodges and beaver pond area as a proportion of land area during 1986–2005 (Fig. 5). Exclusion of the 2002–2003 outlier strengthened this relationship ($R^2 = 0.78$, $P = 0.003$). Inclusion of lake lodges and lake area yielded a linear regression with a smaller intercept but a comparable fit ($R^2 = 0.53$, $P = 0.027$) and slope ($y = 0.0204x - 0.266$). These regressions indicate that

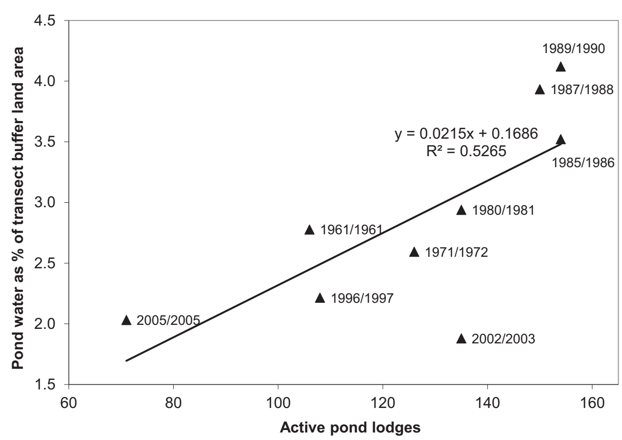

Figure 5. Pond water area as a percentage of the landscape in relation to the number of active beaver colonies counted on transect surveys in Voyageurs National Park, Minnesota, 1961–2005. Labels adjacent to symbols are transect survey year/impoundment map year.

an increase of 100 active colonies would result in a 2.15% increase in pond water area, equivalent to 5.4 km^2 of water within the 250-km^2 study region. There was no significant regression between other cover types and number of active beaver colonies at the peninsula scale.

Modeling Active Beaver Sites

The pruned classification tree model of beaver activity at the site scale based on data from the 2000 lodge map and the 2003 beaver impoundment map retained only 2 variables: pond area per site and pond plus marsh area per site. The first split in the tree classified as inactive those sites with very small pond areas (<0.255 ha; Fig. 6). The remaining sites were further divided into those with pond plus marsh area greater than or equal to 2.633 ha (= active) and those with smaller areas of pond plus marsh (= inactive). This simple model, having only 3 terminal nodes, had an overall accuracy of 78% (Table 2).

Classification trees developed using the 1984 and 2006 lodge maps had 4 terminal nodes, and overall accuracies of 79% and 82%, respectively (Fig. 6). Both the 1984 and 2006 CART models used pond or pond plus marsh area to set classification thresholds for the first and second splits, with larger pond and marsh areas indicating active beaver colonies. The third split in the 1984 and 2006 CART models was based upon woody deciduous cover. In 2006, the 129 sites with pond areas between 0.84 and 2.33 ha were split into 2 groups with woody deciduous cover of $\geq$0.076 ha (active) or <0.076 ha (inactive; Fig. 6). Examination of the 28 sites that were correctly identified using this criterion showed that all had areas of seasonally flooded deciduous shrubs (PSS1E), usually positioned upstream of any open water. The 1984 sites deemed active by virtue of their woody deciduous cover were also associated with seasonally flooded deciduous shrubs. Speckled alder (*Alnus incana*) typifies this cover type.

Error analyses of the 3 site-scale models revealed that they were far better at identifying inactive sites than active sites, however. For the 2000 lodge map model, 93% of the sites known to be inactive based on the field data were correctly

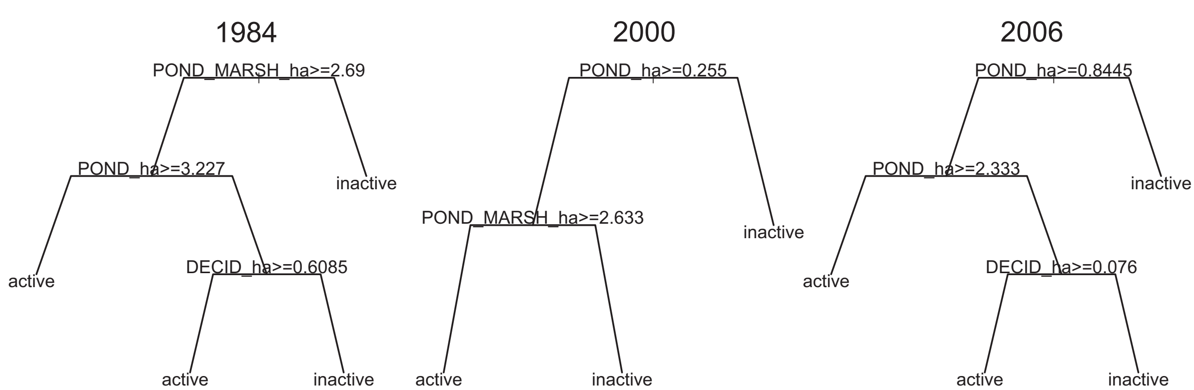

Figure 6. Classification trees for distinguishing activity of beaver pond sites in Voyageurs National Park, Minnesota based on associated cover types, derived from 1984, 2000, and 2006 lodge maps and their corresponding impoundment maps. Sites meeting the decision criterion go to the left split, whereas those not meeting the criterion go to the right. DECID_ha, area of beaver-impounded deciduous woody vegetation in hectares; POND_ha, beaver pond water area in hectares; POND_MARSH_ha, area of beaver-impounded marsh and pond area in hectares.

Table 2. Error analysis comparing field observations with classification tree models (Fig. 6) derived from 1984, 2000, and 2006 lodge maps and their corresponding impoundment maps. Numbers along the table diagonal with an asterisk are correctly classified. User's accuracy is the probability that a site modeled as a particular class really was that class according to the lodge map; producer's accuracy is the probability that a particular class identified on the lodge map was correctly modeled as such. Overall accuracy was 78.9%, 77.9%, and 81.6% for the 1984, 2000, and 2006 models, respectively.

Model	Field data			
	Active	Inactive	Total	User's accuracy
1984 (4 terminal nodes)				
Active	73*	21	94	77.7%
Inactive	134	506*	640	79.1%
Total	207	527		
Producer's accuracy	35.3%	96.0%		
2000 (3 terminal nodes)				
Active	75*	35	110	68.2%
Inactive	127	497*	624	79.6%
Total	202	532		
Producer's accuracy	37.1%	93.4%		
2006 (4 terminal nodes)				
Active	65*	29	94	69.1%
Inactive	106	534*	640	83.4%
Total	171	563		
Producer's accuracy	38.0%	94.8%		

classified by the CART model, but only 37% of the sites known to be active were correctly identified (producer's accuracy; Table 2). The user's accuracy for active ponds (i.e., the probability that a site modeled as active really was active in the field) was 68%. Thus, a site with pond plus marsh area $\geq$2.633 ha was quite likely to be active, but some active sites had other water and vegetation cover characteristics that were unaccounted for by this model.

When the simplest CART model (2000 lodge map 3-terminal node model) was applied to the data from the 1984 and 2006 lodge maps, overall accuracy was 78–79%, and producer's accuracy for active sites improved to 50% and 40%, respectively. Thus, this simpler model may be preferable for applications where the objective is to maximize identification of active sites.

DISCUSSION

This study and its predecessor (Broschart et al. 1989) are unique in combining the evidence of beaver works with independently collected beaver population data. Many authors have documented trends in wetland creation and modification by beavers (Syphard and Garcia 2001, Cunningham et al. 2006, Hood and Bayley 2008, Little et al. 2012) and others have studied long-term beaver population trends (Bergerud and Miller 1977, Fryxell 2001), but studies of the former as a function of the latter are lacking. The VNP population data allowed us to confirm beaver activity rather than merely assuming activity based on the appearance of beaver works.

This research demonstrates that the area of open water and marsh in beaver ponds is a good but not perfect indicator of beaver colony activity at both site and landscape scales. This relationship is intuitive given that beaver dams impound water, and dam maintenance is required for long-term water retention. Dams that burst catastrophically experience a sudden loss of pond area and are generally abandoned by their beaver colonies, at least temporarily. Ponds become abandoned for a variety of reasons including death of 1 or both of the adult pair (Svendsen 1989) or movement of the colony to another pond due to changes in food abundance or other habitat characteristics (Fryxell 2001, Cunningham et al. 2006). Dams that remain intact upon abandonment may retain water for a number of years, however, and would be modeled as false positives (i.e., predicted activity but actual inactivity).

Active beaver sites that are not associated with large expanses of water are more difficult to detect from cover maps. Some of these may be beaver-impounded bogs, where vegetation changes are subtle and open water areas are small (Rebertus 1986, Ray et al. 2001). Experimental flooding of a treed bog complex in northeastern Ontario showed that shallow flooding of bog vegetation led to quick re-establishment of open bog vegetation upon the floatation of peat mats, such that there was little loss of total biomass despite the gain in water volume (Asada et al. 2005). The incomplete detection of active beaver sites using the CART models (i.e., producer's accuracy of 35–38%) is a tribute to the beaver's habitat versatility; beavers typically generate their own pond habitat but can adapt to existing aquatic environments in boreal landscapes.

Land cover changes caused during the early stages of beaver expansion during recolonization may differ from those that occur later, after the most suitable habitats have been occupied. Thus, the models we developed using aerial surveys conducted through 2005 differed from those previously developed using only pre-1986 data (Broschart et al. 1989) because of changes in the proportion of marsh and meadow over time. These 2 cover types were very responsive to beaver activity during the initial expansion period, but open water became a better indicator over time.

The finding that frequency of beaver residency increased with the size of a pond site is consistent with earlier findings that VNP beavers impounded first those sites that would create the largest ponds with the greatest potential for growth (Johnston and Naiman 1990*a*). A larger pond site would provide a greater supply of aquatic plants and a larger pond perimeter would provide greater access to woody plants, food items which are essential components of the beaver diet and survival (Severud et al. 2013). Pond site area was not chosen as a criterion in any of the CART models, however, possibly because larger pond sites may also be older, with depleted woody forage availability. Alternatively, the largest pond sites may be impounded bogs that supply poor beaver forage, such as conifers and ericaceous shrubs.

Beaver densities at VNP, which peaked at 1.4 colonies/km^2 in the 1980s, are higher than most densities reported in the literature (Bergerud and Miller 1977, Jarema et al. 2009). The VNP colony densities were also 2–3 times greater than densities observed elsewhere in northern Minnesota using the same aerial cache counting method (Berg 2000). The high densities observed at VNP were probably due to the lack of exploitation (trapping ceased in 1975), the presence of highly suitable beaver habitat, and a bedrock-controlled topography with many ridges and valleys that are conducive to pond building. The cause of the recent decline in active colony density was not studied but may be depletion of food resources due to selective foraging by beavers, similar to that experienced in Algonquin Provincial Park in eastern Ontario (Fryxell 2001). Gray wolves (*Canis lupus*) are the primary predator of beavers in this landscape and changes in wolf predation rates on beavers may be linked to beaver abundance (Romanski 2010). Tularemia also contributed to a regional beaver die-off in the 1950s (Stenlund 1953), before population data were collected for this study, but there have been no recent large-scale disease outbreaks in our study area since that time.

Verification of the spatial footprint of the aerial transects helped increase the transferability of these results by expressing colony densities per unit area, allowing comparison with beaver studies elsewhere in North America. Data expressed as counts/length of survey transect are less useful, especially when ground transects follow features conducive to beaver occupation (e.g., streambeds) that might bias the results. When combined with average pond site area, colony densities can be used to estimate cumulative beaver impact on the landscape.

We believe the beaver transect data to be of high quality because they were collected using the same protocols, often by the same observers, year after year. Weather, precipitation, and other observation conditions were recorded as excellent for most years of the survey. However, any field data are subject to errors and omissions. We assumed 100% detection of active beaver colonies for the lodge maps and transect surveys and the 1:1 correspondence of lodge counts of our 2 independent data sets for 1984 and 2000 appear to confirm this. However, other studies have reported that aerial census can miss as many as 30% of beaver food caches (Payne 1981, Brown and Parsons 1982, Swenson et al. 1983). Flight lines were followed closely based on topographic features and north-south compass headings, and in later years also used GPS. However, the footprint of the transects may have varied slightly from year to year as survey conditions varied. Some inter-annual population increases seem suspiciously large, such as the 80% increase between 1969 and 1970 and the 61% increase between 1999 and 2000. Also, there was occasionally temporal mismatch between the beaver impoundment maps and the beaver counts, which could not be avoided when using historical aerial photos and field data. Despite these issues, long-term population datasets collected over such a large area are rare, and we believe that they provide insights that cannot be gained from short-term data.

MANAGEMENT IMPLICATIONS

A method to quantitatively relate beaver works with the density of active beaver colonies could benefit beaver management, particularly in areas lacking beaver population data. This research confirms that water impoundment by beaver dams generates predictable vegetation changes that can reliably be used as an indicator of beaver population at the landscape scale, but that beaver works are less reliable predictors of beaver colony presence–absence at the site scale. The size thresholds in the CART models developed for VNP may differ at other sites, but managers could adapt those thresholds using typical beaver pond sizes for local conditions. Aerial photo tools to implement this approach are now widely available. Although this research commissioned aerial photo flights or purchased archival prints, the free software Google Earth has a tool to show historical digital imagery that typically begins with 1990s United States Geological Survey orthophotos. Managers could easily view changes in beaver impoundments since the 1990s using this slider bar tool. Information on beaver–impoundment relationships could be used to measure and monitor beaver populations and their resultant influence on water storage capacity, biodiversity, fish passage, and other relevant natural resource management concerns.

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LITERATURE CITED

Asada, T., B. G. Warner, and S. L. Schiff. 2005. Effects of shallow flooding on vegetation and carbon pools in boreal peatlands. Applied Vegetation Science 8:199–208.

Berg, W. E. 2000. 2000 aerial beaver lodge survey. Forest Wildlife Populations and Research Group, Minnesota Department of Natural Resources, Grand Rapids, Minnesota, USA.

Bergerud, A. T., and D. R. Miller. 1977. Population dynamics of Newfoundland beaver. Canadian Journal of Zoology-Revue Canadienne De Zoologie 55:1480–1492.

Broschart, M. R., C. A. Johnston, and R. J. Naiman. 1989. Prediction of beaver colony density using impounded habitat variables. Journal of Wildlife Management 53:929–934.

Brown, M. K., and G. P. Parsons. 1982. Reliability of fall aerial censuses for locating active beaver colonies in New York. New York Fish & Game Journal 29:204–206.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the Unit ed States. Report FWS/OBS 79/31. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Cunningham, J. M., A. J. K. Calhoun, and W. E. Glanz. 2006. Patterns of beaver colonization and wetland change in Acadia National Park. Northeastern Naturalist 13:583–596.

Dickinson, N. R. 1971. Aerial photographs as an aid in beaver management. New York Fish & Game Journal 18:57–61.

Faber-Langendoen, D., N. Aaseng, K. Hop, M. Lew-Smith, and J. Drake. 2007. Vegetation classification, mapping, and monitoring at Voyageurs National Park, Minnesota: an application of the U.S. National Vegetation Classification. Applied Vegetation Science 10:361–374.

Fryxell, J. M. 2001. Habitat suitability and source-sink dynamics of beavers. Journal of Animal Ecology 70:310–316.
Hood, G. A., and S. E. Bayley. 2008. Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. Biological Conservation 141:556–567.
Host, G., and P. Meysembourg. 2010. Historic and recent landscape changes in relation to beaver activity in Voyageurs National Park, Minnesota, USA. Final report to National Park Service, Great Lakes Inventory & Monitoring Network/Voyageurs National Park. Natural Resources Research Institute, Duluth, Minnesota, USA.
Hyvönen, T., and P. Nummi. 2008. Habitat dynamics of beaver *Castor canadensis* at two spatial scales. Wildlife Biology 14:302–308.
Jarema, S. I., J. Samson, B. J. McGill, and M. M. Humphries. 2009. Variation in abundance across a species' range predicts climate change responses in the range interior will exceed those at the edge: a case study with North American beaver. Global Change Biology 15: 508–522.
Johnston, C. A. 1994. Ecological engineering of wetlands by beavers. Pages 379–384 *in* W. J. Mitsch, editor. Global wetlands: old world and new. Elsevier Science, Amsterdam, The Netherlands.
Johnston, C. A. 2012. Beaver wetlands. Pages 161–171 *in* D. P. Batzer, and A. Baldwin, editors. Wetland habitats of North America: ecology and conservation concerns. University of California Press, Berkeley, USA.
Johnston, C. A., and R. J. Naiman. 1990*a*. Aquatic patch creation in relation to beaver population trends. Ecology 71:1617–1621.
Johnston, C. A., and R. J. Naiman. 1990*b*. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landscape Ecology 4:5–19.
Johnston, C. A., and S. K. Windels. 2015. Using beaver works to estimate colony activity in boreal landscapes (online spatial data). CUAHSI Spatial Data Service. Consortium of Universities for the Advancement of Hydrologic Science Inc., Medford, Massachusetts, USA. doi:10.4211/spatialdata-johnstonc01
Little, A. M., G. R. Guntenspergen, and T. F. H. Allen. 2012. Wetland vegetation dynamics in response to beaver (*Castor canadensis*) activity at multiple scales. Ecoscience 19:246–257.
Parsons, G. P., and M. K. Brown. 1978. An assessment of aerial photograph interpretation for recognizing potential beaver colony sites. New York Fish & Game Journal 25:175–177.
Payne, N. F. 1981. Accuracy of aerial censusing for beaver colonies in Newfoundland. Journal of Wildlife Management 45:1014–1016.
R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Ray, A. M., A. J. Rebertus, and H. L. Ray. 2001. Macrophyte succession in Minnesota beaver ponds. Canadian Journal of Botany-Revue Canadienne De Botanique 79:487–499.
Rebertus, A. J. 1986. Bogs as beaver habitat in north-central Minnesota. American Midland Naturalist 116:240–245.
Reddoch, J. M., and A. H. Reddoch. 2005. Consequences of beaver, *Castor canadensis*, flooding on a small shore fen in southwestern Quebec. Canadian Field-Naturalist 119:385–394.
Remillard, M. M., G. K. Gruendling, and D. J. Bogucki. 1987. Disturbance by beaver (*Castor canadensis* Kuhl) and increased landscape heterogeneity. Pages 103–122 *in* M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.
Romanski, M. C. 2010. Estimates of abundance and predation: the population ecology of beaver in Isle Royale National Park. Thesis, Michigan Technological University, Houghton, USA.
Severud, W. J., S. K. Windels, J. L. Belant, and J. G. Bruggink. 2013. The role of forage availability on diet choice and body condition in American beavers (*Castor canadensis*). Mammalian Biology - Zeitschrift für Säugetierkunde 78:87–93.
Stenlund, M. H. 1953. Report of Minnesota beaver die-off, 1951–1952. Journal of Wildlife Management 17:376–377.
Svendsen, G. E. 1989. Pair formation, duration of pair-bonds, and mate replacement in a population of beavers (*Castor canadensis*). Canadian Journal of Zoology 67:336–340.
Swenson, J. E., S. J. Knapp, P. R. Martin, and F. C. Hinz. 1983. Reliability of aerial cache surveys to monitor beaver population trends on prairie rivers in Montana. Journal of Wildlife Management 47:697–703.
Syphard, A. D., and M. W. Garcia. 2001. Human- and beaver-induced wetland changes in the Chickahominy River watershed from 1953 to 1994. Wetlands 21:342–353.
Therneau, T. M., E. Atkinson, and B. Ripley. 2014. Package rpart: recursive partitioning and regression trees. http://cran.r-project.org/web/packages/rpart/rpart.pdf. Accessed 30 Sep 2014.
Wright, J. P., A. S. Flecker, and C. G. Jones. 2003. Local vs. landscape controls on plant species richness in beaver meadows. Ecology 84:3162–3173.

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