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Patterns of Beaver Colonization and Wetland Change in Acadia National Park

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Abstract - The return of *Castor canadensis* (beaver) to areas of their former range has restored a natural disturbance regime to wetland landscapes in North America. We used aerial photographs to study wetland creation and modification by beaver in Acadia National Park, ME, during a period of beaver population expansion (1944–1997). We quantified the change in the number of available ponded wetlands in the landscape during the study period and documented an 89% increase in ponded wetlands between 1944 and 1997. Spatial and temporal patterns of beaver colonization and changes in wetland vegetation and hydrology were recorded at six time periods (1944, 1953, 1970, 1979, 1985, and 1997) for 33 beaver-created wetlands for which we had current amphibian assemblage data. Beaver colonization generally converted forested wetlands and riparian areas to open water and emergent wetlands, resulting in significant increases in the percentage of open water and emergent wetland habitat and a decrease in the percentage of forested wetland area at the study sites. Temporal colonization of beaver wetlands initially favored large sites occurring lower in the watersheds; sites that were impounded later were generally smaller, higher in the watershed, and more likely to be abandoned by the end of our study. Our results suggest that beaver have not only increased the number of available breeding sites in the landscape for pond-breeding amphibians, but also the resulting mosaic of active and abandoned beaver wetlands is likely to provide suitable breeding habitat for a diversity of species.

Introduction

Castor canadensis Kuhl (beaver) were historically widespread and abundant throughout North America, but were locally extirpated in many areas due to trapping (Jenkins and Busher 1979, Naiman et al. 1988, Ruedemann and Schoonmaker 1938). With reduced trapping during the 20th century, beaver returned or were reintroduced to many areas within their former range and actively recolonized available habitat (Johnston and Naiman 1990a, Lisle 1994, Naiman et al. 1988). Beaver are ecosystem engineers, impounding streams to create and modify wetlands (Jones et. al 1994). Beaver dams retain sediments, modify nutrient flow, and convert riparian areas to non-linear wetlands; the results of these changes in the landscape affect geomorphology and can persist for centuries in the absence of beaver (Ives 1942, Naiman et al. 1986, Ruedemann and Schoonmaker 1938). In the presence of beaver, a shifting mosaic of wetlands is created in the landscape, which changes temporally due to colonization and abandonment of individual wetland

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patches by beaver in response to natural disturbances (e.g., fire), food resources, disease, and predation (Naiman et al. 1988, Remillard et al. 1987). The diversity of wetland habitat in beaver-modified landscapes is important for both game and non-game wildlife including fish, bird, amphibian, reptile, mammal, and aquatic invertebrate species (Brown et al. 1996, Dubuc et al. 1990, McCall et al. 1996, McDowell and Naiman 1986, Metts et al. 2001, Russell et al. 1999, Snodgrass and Meffe 1998, Suzuki and McComb 2004).

Long-term investigations of beaver colonization and landscape changes due to beaver activity are made possible by interpreting historical aerial photographs (Howard and Larson 1985, Johnston and Naiman 1990a, Lisle 1994, Remillard et al. 1987). We used aerial photographs to study wetland creation and modification by beaver at Acadia National Park (ANP), Mount Desert Island (MDI), ME between 1944 and 1997, a period of beaver population expansion following reintroduction in 1921, and including a major fire event in 1947 (Muller-Schwarze 1979). The goal of our research was to investigate how the overall landscape, and individual beaver-influenced wetland sites, changed during this time period, and what implications these changes could have for pond-breeding amphibian species. Our objectives were: (1) to quantify the change in the number of ponded wetlands in the landscape and (2) to quantify patterns of beaver colonization and wetland change (hydrology and vegetation structure) in beaver-modified wetlands with current amphibian assemblage data.

Methods

Study area

Mount Desert Island is located along the central coast of Maine (44º20'N, 68º15'W), and is connected to the mainland by a causeway. Acadia National Park covers nearly half of the 281-km^2 area of the island (Patterson et al. 1983). The study area is in the transition zone between spruce-fir forests to the north and east and northeastern hardwood forests to the south and west (Davis 1966). Coniferous forests are dominated by *Picea glauca* (Moench) Voss (white spruce), *Picea rubens* Sarg. (red spruce) and *Abies balsamea* L. (balsam fir). Deciduous forests are characterized by *Betula* spp. (birch), *Populus* spp. (aspen), *Acer* spp. (maple), *Fagus grandifolia* Ehrh. (American beech), and *Quercus rubra* L. (red oak). Mixed coniferous/ deciduous forests are common. The climate is moist (mean annual precipitation of 106 cm) and cool (-8.2 ˚C mean annual winter temperature and 17.8 ˚C mean annual summer temperature; National Oceanic and Atmospheric Administration [2002])

The terrain is a rugged, glacially carved landscape consisting of alternating north–south oriented ridges and u-shaped valleys. Watersheds are generally short in length (< 5 km from headwaters to ocean) and range in elevation from sea level to 466 m. The study area contains approximately 12,840 hectares (20% by area) of wetland, with freshwater wetlands comprising 42% of the total wetland area and over 40% of the 9000 wetland units represented by National Wetlands Inventory (NWI) maps (Calhoun et al. 1994).

Beaver are documented agents of freshwater wetland creation and modification on MDI (Calhoun et al. 1994, Muller-Schwarze 1979). Beaver, although historically present, were extirpated from MDI in the 19th century through trapping (Bailey 1925). Reintroductions began with four individuals in 1921, and population numbers likely remained low prior to an extensive fire that burned 6800 ha on the eastern side of the island in 1947 (Bailey 1925, Baird 1964, Patterson et al. 1983). The post-fire change in forest composition, particularly the dominance of early successional species preferred by beaver, such as aspen and birch, created favorable conditions for beaver population expansion (Fryxell and Doucet 1993, Jenkins 1979, Johnston and Naiman 1990b). The beaver population reached a peak in the late 1970s (approximately 300 individuals), with over 95% of the population inhabiting the eastern side of the island (Muller-Schwarze 1979), and has since decreased. Recent surveys estimate that the beaver population has stabilized at about 100 individuals (B. Connery, ANP, pers. comm.). The long-term effect of the 1947 fire on forest composition is still evident, as stands of aspen and birch trees are common on the eastern side of the island (Fig. 1).

Quantifying overall landscape change

The time period studied (1944–1997) begins with aerial photographs taken before the 1947 fire, extends through the subsequent expansion of the beaver population, and ends with a recent set (1997) that closely represents present conditions (Table 1). To estimate the change in the suitability of the landscape for pond-breeding amphibian species, we counted and compared the number of flooded wetlands—both open water ponds and wetlands with visible standing water—in 1944 and 1997. The area in which wetlands were counted covers the entire large eastern unit of ANP and adjacent areas, including both burned and unburned areas (Fig. 1). All wetlands that were visibly flooded, and would therefore provide potential breeding sites for pond-breeding amphibians, were counted in the 1944 photographs. Counts were repeated for the same area in the 1997 photographs. The difference between these two numbers was used as an index of wetland landscape change over the observed time period.

Quantifying beaver colonization and wetland change at selected sites

The locations of 33 beaver-modified wetland sites with current amphibian species-assemblage data were identified in aerial photographs for each of

Table 1. Aerial photographs used to determine beaver colonization patterns in Acadia National Park, Mount Desert Island, ME.

Year (month)	Scale	Film type	Commissioning agency
1944 (May)	1:15,000	Black and white	National Oceanic Service
1953 (May)	1:833	Black and white	US Navy
1970 (Sept.)	1:20,000	Black and white	USGeological Survey
1979 (Aug)	1:9,000	Color infrared	J.W. Sewall Co.
1985 (Apr.)	1:9,000	Black and white	US Fish and Wildlife Service
1997 (May)	1:15,840	Color infrared	J.W. Sewall Co.

six time periods (Table 1). We considered only wetlands that were primary beaver colony sites, defined as those with evidence of past or present lodge construction. We used field surveys in 2000 to match observed wetland vegetation classes with aerial photograph vegetation signatures (colors and textures that vary with vegetation type) in the 1997 photos. We stereoscopically interpreted photographs (3x magnification) to determine the proportion of each wetland vegetation class at each site as defined by Cowardin et al.

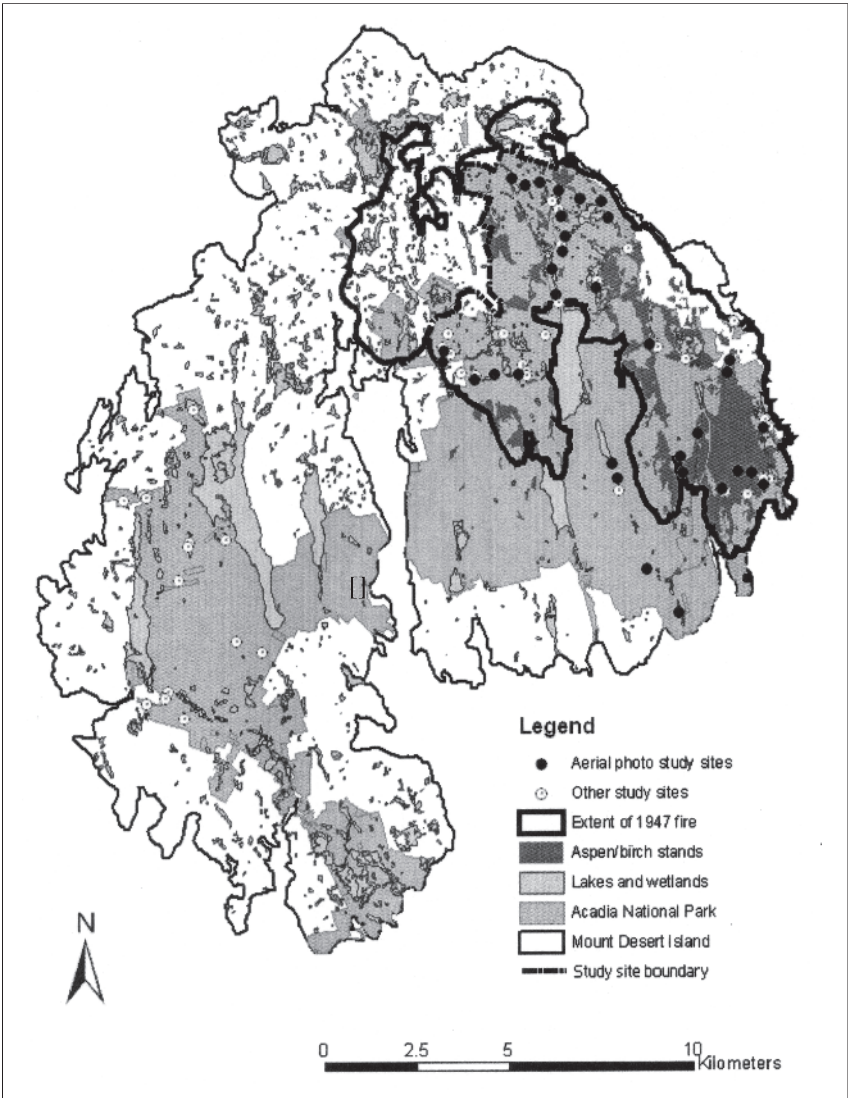

Figure 1. Location of aerial photo study sites in Acadia National Park, ME. The entire area to the south and east of the study site boundary was included in the wetland landscape analysis.

(1979). We used a transparent grid with 2-mm x 2-mm squares to estimate wetland class proportions. Wetland classes were identified simply as open water (OW), emergent (EM), scrub/shrub (SS), or forested (FO). The total proportion of impounded area (area with visible standing water) and the presence of beaver dams and lodges were recorded for each observation. Due to limited access to aerial photographs and differences in photograph scale, proportions, rather than actual areas, were used to quantify trends in beaver wetlands. Independent measurements by a second trained observer on a subset of 10 sites resulted in proportion estimates that were generally (> 80%) within 2% of those of the initial observer, and in no case did estimates vary by more than 5%.

Estimated wetland areas were obtained from geographic information systems (GIS) coverages of NWI maps. We quantified relative watershed position for each site using the ArcGIS distance tool and a GIS watershed layer obtained from ANP. Based on the distance from the base of the watershed, we classified sites as low (< 1/3 distance), medium (1/3–2/3), or high (> 2/3) in the watershed. Mean wetland area was calculated for each watershed position, and a Kruskal-Wallis test was used to compare mean wetland area by watershed position. The mean percentage area covered by open water, emergent, shrub/scrub, and forested wetland and mean percentage impounded area were calculated for all sites in 1944 and in 1997. Significance of changes in wetland composition from 1944–1997 was determined using paired t-tests. We performed all statistical tests using SYSTAT (SYSTAT 10.2.01) with a $p < 0.05$ significance level.

Results

Landscape change

The total number of visibly flooded wetland units in the study area increased by 89%, from 73 in 1944 to 138 in 1997. In parallel, evidence of beaver activity, in the form of dams and lodges, was limited in 1944, but was abundant throughout the study area in the 1997 photographs.

Beaver colonization and wetland change

Of the 33 wetlands studied, 27% ($n = 9$) existed as ponds or contained some standing water in 1944. Only 2 of these showed evidence of beaver activity: one site had a beaver lodge and appeared to be an active beaver colony, while the other site was an abandoned beaver wetland. The remaining 7 sites contained natural or human-created ponds without interpretable evidence of past or current beaver colonization.

Widespread colonization of the landscape after the 1947 fire was not immediate; only 3 study sites, all within 1 km of previously existing beaver colonies, were newly colonized by 1953. Temporal increases in the number of wetlands newly colonized by beaver paralleled the increase in the beaver population to its peak in 1979. Additional colonization after 1979 was minimal, suggesting that much of the available habitat in the landscape had been exploited (Fig. 2).

In the first half of the study period (1944–1970), beaver primarily colonized previously ponded sites and unflooded wetlands in the low and middle watershed categories (Fig. 3). By 1970, 6 of the previously ponded sites were colonized (including the two that showed signs of beaver activity in 1944), and the additional 3 previously ponded sites were colonized by 1979. All sites in the lowest watershed category and 77% of the mid-watershed sites had been colonized by 1970, and colonization of high watershed position sites was increasing. Sites colonized after 1970 were primarily located high in the watershed, with limited new colonization of mid-watershed sites (Fig. 3).

The mean area (ha ± SE) of beaver sites in the lowest watershed category was significantly larger than for sites found higher in the watershed (low = 4.94 ± 1.19, medium = 1.26 ± 0.37, high = 1.26 ± 0.33; Kruskal-Wallis test statistic = 8.33, 2 df, $p = 0.016$). Mean area of impounded wetlands showed a decreasing trend with both time and higher watershed position. Mean area (ha ± SE) of sites colonized at each time period since the previous photos was: 1953, 2.02 ± 1.28; 1970, 2.16 ± 0.59; 1979, 1.43 ± 0.30; 1985, 0.37 ± 0.24. The large variability in the area of sites colonized by 1953 was influenced by a small sample size ($n = 3$) and one small site. Mean area of newly colonized wetlands is not provided for 1944 and 1997; these years had a single newly colonized wetland. Abandonment of sites by beaver was related to watershed position, with the greatest proportion of sites aban-

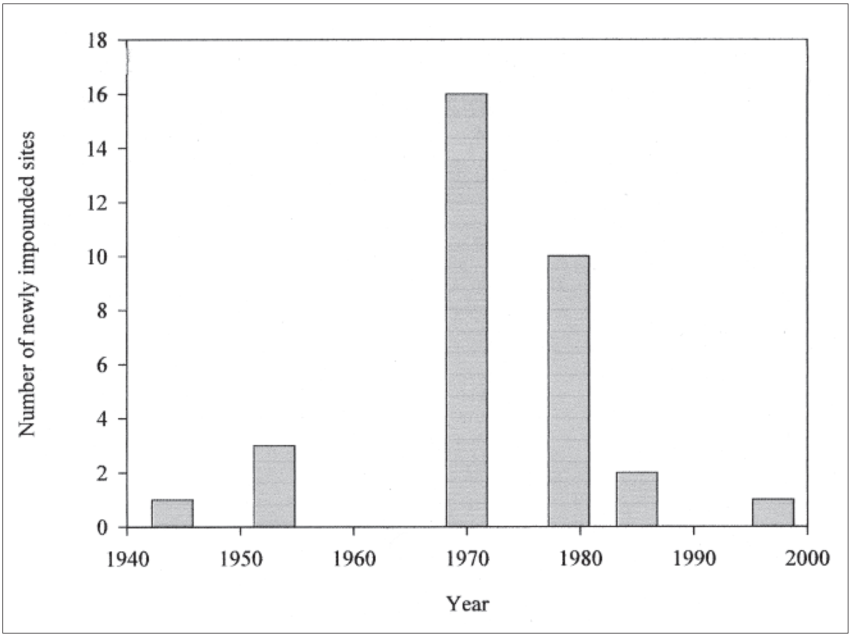

Figure 2. Number of newly impounded study sites observed at each aerial photo interval. Newly impounded sites are those colonized since the previous photo series. Aerial photo years are 1944, 1953, 1970, 1979, 1985, and 1997.

doned by 2000 found in the highest watershed category (low = 25%, medium = 31%, high = 63%). When compared to the lower two categories, sites in the highest watershed category showed a strong trend toward being abandoned by the end of the study period ($\chi^2 = 3.640$, 1 df, $p = 0.056$). Abandoned sites were significantly smaller in area than active sites ($t = -2.809$, df = 31, $p = 0.009$). The probability that a site would be abandoned by 2000 increased the later the site was initially colonized (Fig. 4). All sites colonized after 1979 were abandoned before 2000.

The creation of beaver flowages between 1944 and 1997 increased the percentage of impounded wetland area and resulted in a general conversion of forested wetlands to earlier stages of wetland succession, particularly open water and herbaceous wetlands. Mean percent-impounded area at study wetlands increased significantly from 10% in 1944 to 61% in 1997 (paired t-test, $t = -8.244$, df = 32, $p < 0.001$; Fig. 5). The change in hydrology, as indicated by an increase in impounded area, was accompanied by significant increases in mean percentage of open water (paired t-test: $t = -6.022$, df = 32, $p < 0.001$) and emergent (paired t-test: $t = -4.545$,

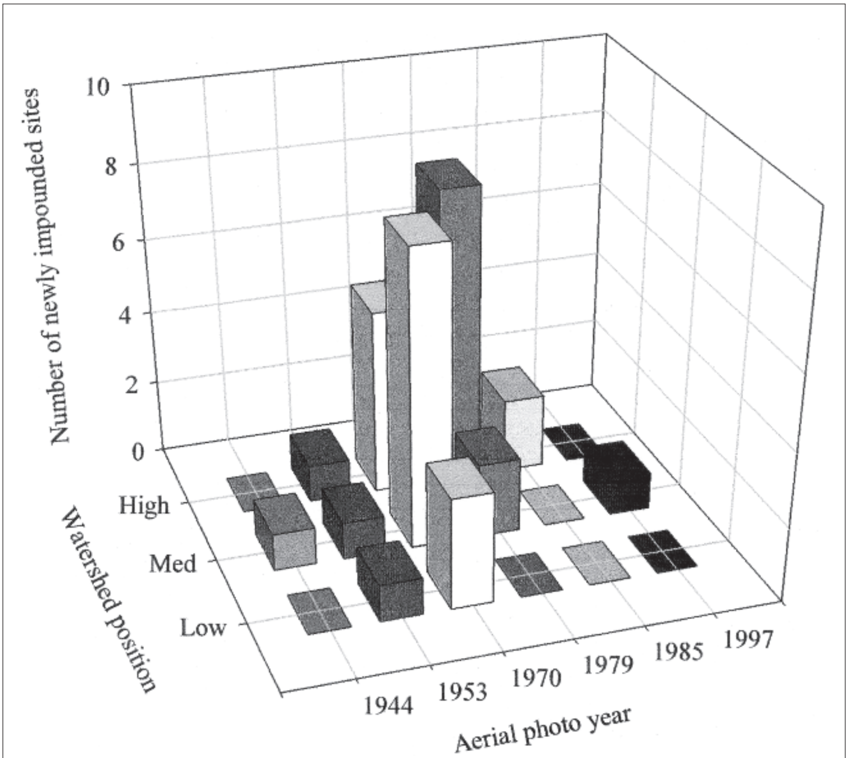

Figure 3. Number of newly colonized sites in each watershed position at each aerial photograph interval. Beaver colonization shows a trend from early colonization of sites low in the watershed to later colonization of sites high in the watershed.

df = 32, $p < 0.001$) wetland classes and a decrease (paired t-test: $t = 8.590$, df = 32, $p < 0.001$) in the mean percentage of site area dominated by forested wetland classes (Fig. 5). The mean percentage of shrub/scrub wetland classes did not change significantly (paired t-test: $t = 0.406$, df = 32, $p = 0.688$). All wetlands that were abandoned by beaver during the study period retained open water and herbaceous wetland components through 1997.

Discussion

Landscape change

Our results show that beaver population expansion, following their reintroduction in the 1920s and a large fire event in 1947, has resulted in considerable changes to the wetland landscape of MDI. We documented an 89% increase in the number of ponded wetlands in the landscape between the years of 1944 and 1997. The increase in ponded wetlands may in part be the result of new wetland creation by beaver, but detailed observations of individual wetlands reveal that there was also a significant conversion of existing

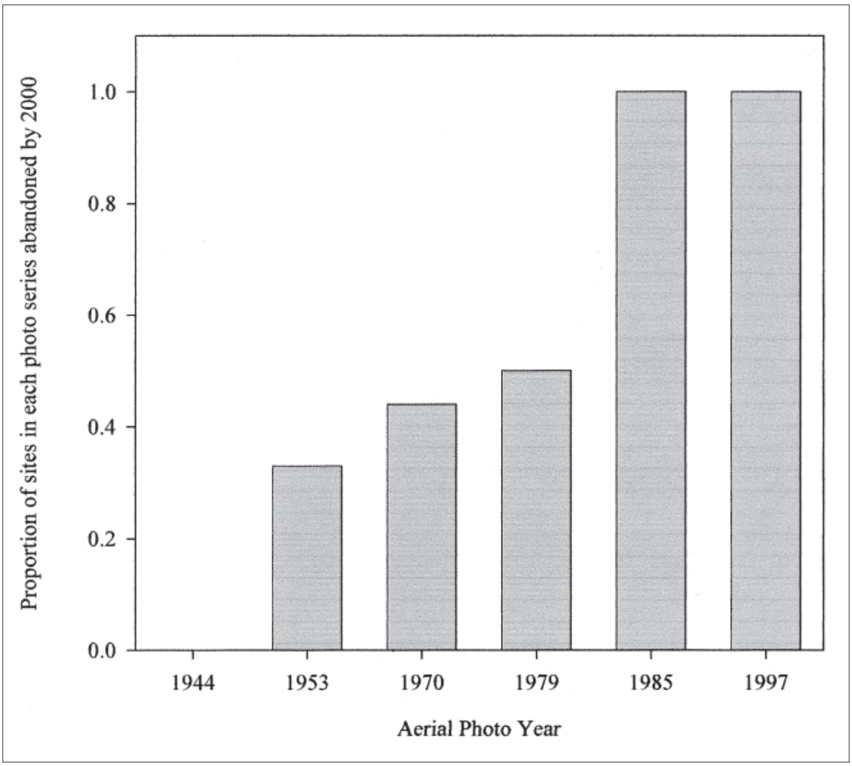

Figure 4. Proportion of sites in each photo series currently abandoned. The likelihood of abandonment increases the later a site was initially colonized. Abandonment was determined by field surveys in 2000.

forested wetlands to open water and emergent wetlands as a result of changes in hydrology due to beaver impoundments.

Beaver colonization patterns

Beaver colonized pre-existing ponds early in the study period. Although beaver are most known for foraging on the inner bark of small-diameter, early successional tree species, beaver also forage preferentially on aquatic macrophytes, particularly during the summer months (Bradt 1938, Svendsen 1980). In large wetlands with abundant resources, a beaver colony may be sustained almost exclusively by resources found within the pond (Howard and Larson 1985). Colonization of these sites represents less effort in dam construction and a food supply with a greater longevity, particularly in the absence of abundant preferred tree species.

Lisle (1994) traced beaver colonization patterns in a watershed in Maine and concluded that the long-term absence of beaver in the watershed allowed for succession of wetlands to a shrub or forested state. Rather than creating new wetlands, beaver recolonization from 1939–1991 at this site resulted in

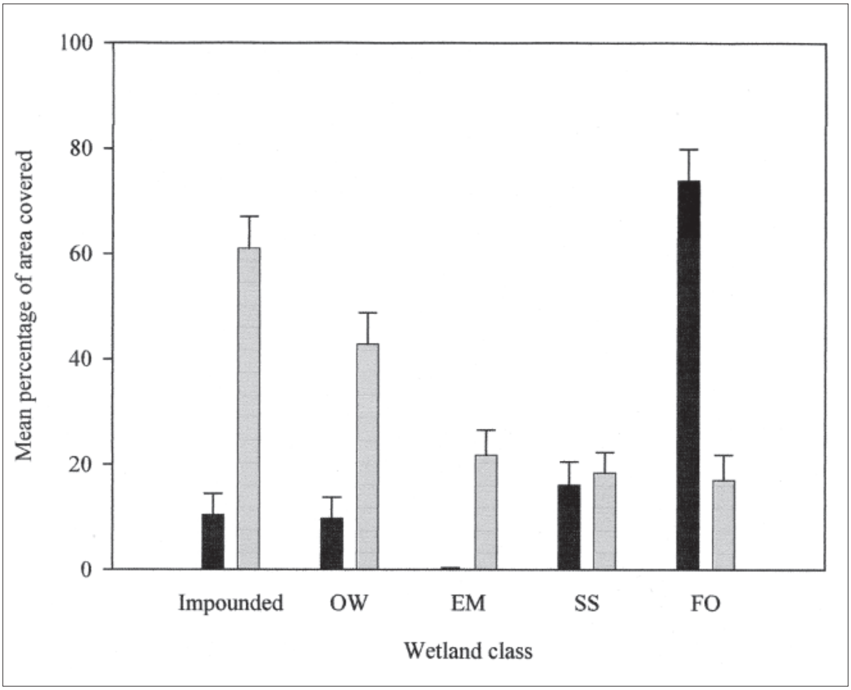

Figure 5. Change in mean percentage area of wetland impounded and wetland class composition in study sites from 1944 (black bars) to 1997 (gray bars). Impounded area refers to the total area with visible standing water regardless of wetland class. OW = open water, EM = emergent vegetation, SS = scrub/shrub, FO = forested. Mean impounded area, mean open water, and emergent wetland area increased significantly from 1944–1997. Mean area covered by forested wetland classes decreased significantly.

a conversion of forested and shrub wetlands to open water and herbaceous wetlands. Our results corroborate those findings, indicating that beaver were recolonizing wetlands that were likely historically created and/or modified by beaver. At least 42% of newly created beaver flowages in our study were colonized from obvious existing wetland basins. These basins were flat areas in otherwise steep watersheds where sediments had been previously deposited, and were likely the direct result of beaver activity prior to their local extinction. Many of the additional riparian areas that were impounded may have been forested wetland basins as well; however, we were unable to distinguish distinct basins from the aerial photographs due to small size and/or dense tree cover at these sites.

Beaver in ANP showed patterns of colonization from 1944–1997 similar to those reported previously in Maine from 1939–1991 (Lisle 1994) and in Minnesota from 1940–1986 (Johnston and Naiman 1990a); in all studies, large sites were impounded earlier in the study period. Lisle (1994) also described a pattern of colonization that was related to the perimeter/dam ratio; sites in which a small dam could impound a large amount of water were colonized first. Large sites provide convenient access to a greater area of potential food, both within and outside of the wetland. These patterns of colonization indicate a selection for higher quality sites initially and smaller, less-desirable sites either when food resources are exploited at more desirable sites or when populations expand to the point where only marginal habitat is available (Howard and Larson 1985, Johnston and Naiman 1990a).

Johnston and Naiman (1990a) concluded that a reduced rate of new site colonization over time was constrained by geomorphology rather than by a decrease in beaver population. Presumably, in this case, beaver had exhausted potential sites in the landscape. The mountainous topography of MDI, with steep, high gradient watersheds, limits suitable sites for potential beaver colonization (Baird 1964); our data suggest that beaver population expansion on MDI was also constrained by geomorphology. Very few sites were colonized after 1979, despite the fact that beaver populations were deemed to be at or near their carrying capacity (Muller-Schwarze 1979). The estimated rate of beaver population growth from 1964–1978 was 2.4%, suggesting that populations were stabilizing, most likely due to the decreasing availability of suitable habitat. Estimates of beaver-colonized sites in 1979 deemed 19% of sites as optimal, 27% as adequate, 42% as marginal, and 11% as sub-optimal based on available food supplies (Muller-Schwarze 1979). With greater than 50% of the sites classified as marginal or sub-optimal, it is no surprise that we found smaller sites that were colonized later were more likely to be abandoned. Our study-site sample seems representative of the reported distribution of available habitat quality, since close to 50% (16/33) of our study sites were abandoned by 1997.

Beaver activity showed a general trend from early colonization of larger sites low in the watershed to smaller sites high in the watershed. Small sites high in the watershed would not only provide less access to food resources, resulting in decreased longevity, but would also prove more difficult for beaver to maintain adequate water levels for protection and storage of winter food supplies (Howard and Larson 1985). Watersheds in ANP are generally short and steep with many ephemeral and intermittent streams in the higher reaches, which would provide limited additional inflow after the spring rains and snowmelt runoff (Baird 1964; J.M. Cunningham, pers. observ.). Lisle (1994) observed that some drainages were not colonized in a stair-step fashion; dispersal occurred in both an upstream and downstream direction. Because the area measurements of mid-watershed and high watershed sites were not significantly different in our study, it is likely that some of our watersheds were colonized in a non-linear fashion; however, there was still a clear trend toward upstream movement of colonization over time. High watershed sites were also much more likely to be abandoned, indicating that they were less suitable sites.

Implications for pond-breeding amphibians

Beaver-colonization and wetland-change patterns have implications for potential habitat for pond-breeding amphibian species. The number of ponded wetlands in the study area today is 89% greater than at the start of the study period, and this increase is directly linked to the return of beaver to the landscape. Beaver created flooded wetland patches in the landscape and maintained these patches to the potential benefit of pond-breeding amphibian species. Beaver colonization not only increases the number of ponded wetland patches in the landscape, but also decreases inter-wetland distance (Lisle 1994). Assuming that beaver-created or modified wetlands provide suitable habitat, increased habitat availability and connectivity should benefit all pond-breeding amphibian species. Cunningham (2003) found that beaver activity and connectivity of wetlands were useful predictors of high species richness for pond-breeding amphibians in ANP. Increased amphibian species richness in beaver wetlands is likely a direct result of beaver creating suitable habitat, and may be enhanced further by the increased connectivity of these sites in the landscape.

The rapid expansion of the beaver population in ANP in response to abundant food and habitat resources has resulted in a spatial and temporal mosaic of wetlands that was not available for amphibian breeding prior to beaver recolonization. This mosaic is the result of a beaver population that grew to its limit spatially, exploited marginal habitats, and has since decreased to a population that is likely to be more sustainable. Temporal changes in abandoned beaver wetlands and wetlands that are infrequently disturbed by beaver further increase wetland heterogeneity in the landscape.

Wetland heterogeneity in the landscape, particularly in regard to hydroperiod, is important to provide a range of possible sites for pond-breeding amphibian species with differing habitat requirements. Cunningham (2003) showed that beaver have created favorable breeding habitat in ANP, both for species that require permanent wetlands and for those that may benefit from periodic drying. For example, *Rana catesbeiana* Shaw (Bullfrog) at wetland study sites in ANP was found to breed only within large, permanent, deep ponds with fish, which were created or modified and maintained by beaver. The permanent hydroperiod of these sites is necessary to support the 2–3 year larval period of Bullfrogs. Abandoned beaver study sites in ANP maintained a fishless pond environment, due to a high watershed position and periodic drying, which favored *Rana sylvatica* LeConte (Wood Frog) breeding. Wood Frogs and Bullfrogs never bred in the same wetlands due to their differing requirements for successful breeding; however, the presence of beaver in the landscape has increased the overall availability of habitat for both of these species

Conclusions

The return of beaver to Acadia National Park has re-established a natural disturbance regime that contributes to increased landscape heterogeneity. Rapid, widespread colonization of the landscape by beaver was made possible by a fire disturbance that increased the availability of preferred early successional tree species. Wetland succession in beaver-disturbed landscapes follows non-linear, multidirectional pathways due to varying levels of beaver disturbance (Remillard et al. 1987). Cycles of beaver colonization and abandonment had an estimated return interval of 10–30 years in one study, and although some sites succeeded to shrub/scrub wetlands, in no instance did wetlands progress to a forested state (Remillard et. al 1987). If this is the case in ANP, the current wetland landscape could be maintained for some time. However, if in the absence of large-scale disturbance on the landscape (e.g., fire) beaver populations do not continue to expand and colonize marginal sites, we may see a return of some of these sites to a forested state. The loss of these small, open-canopy sites would reduce the number of suitable Wood Frog breeding sites in the landscape and might also affect populations of other pond-breeding amphibian species (e.g. Cunningham 2003; Halverson et al. 2003; Skelly et al. 1999, 2002). Large sites with permanent beaver colonies and a stable water level and hydroperiod may not be as likely to experience large shifts in amphibian assemblages over time. However, sites that are periodically disturbed by beaver, and therefore are more dynamic, could show substantial changes in amphibian species composition (e.g., Petranka et al. 2004). Further research is needed to understand more fully how amphibian assemblages change in relation to patterns of beaver disturbance over time.

Acknowledgments

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