Ecology, 71(4), 1990, pp. 1617–1621

AQUATIC PATCH CREATION IN RELATION TO BEAVER POPULATION TRENDS[1]

CAROL A. JOHNSTON AND ROBERT J. NAIMAN[2]
Natural Resources Research Institute, University of Minnesota, Duluth, Minnesota 55811 USA

Abstract. The creation of aquatic patches by beaver (*Castor canadensis*) in the boreal forest of northern Minnesota, USA, was studied to determine how the population dynamics of a disturbance-causing animal are linked to rates of patch formation and growth over a period of population expansion and stabilization. Using six series of aerial photographs taken between 1940 and 1986, we determined the size and growth rates of individual patches, and the numbers, area, density, and establishment rate of the patch population. The rate of patch formation was much higher during the first two decades of colonization than during the subsequent two decades. The average area of all pond sites, which included both filled and drained ponds, remained at ≈4 ha throughout the time period, but the average area of new ponds decreased significantly over time. Ponds established by 1961 constituted 75% of the total number and 90% of the total pond-site area as of 1986. When pond sites of similar age but different pond cohort (i.e., decade of establishment) were compared, the average area per pond site was always significantly larger for the earlier cohort.

Although the rate of pond creation paralleled the increase in number of beaver colonies between 1961 and 1986, the rate of new pond creation prior to 1961 greatly exceeded the increase in number of beaver colonies. We conclude that the rate of patch formation after the first two decades of beaver colonization was constrained by geomorphology, which limited the availability of sites at which a beaver dam could impound a large area of water.

Key words: beaver; boreal forest; Castor canadensis; *dam; geographic information system; geomorphology; habitat availability; landscape ecology; Minnesota; patch dynamics; pond; population.*

INTRODUCTION

Physical and biological disturbances in the landscape produce patches, defined by Pickett and White (1985) as discrete communities embedded in an area of dissimilar community structure or composition. While much is known about the response of animals to environmental patchiness (Wiens 1976, Paine and Levin 1981), there are few quantitative studies of how animals influence patch formation, particularly at the landscape scale (Forman and Godron 1986). The rate and extent of patch formation by animals depends on many factors, including the mode of disturbance, area affected per individual, species mobility, population size, and the susceptibility of the environment to the disturbance. Even though the effect per individual may be small, the cumulative effect of an animal population may be large (Blais 1954). Therefore, it is important to understand how the population dynamics of a disturbance-causing animal are linked to rates of patch formation and ontogeny.

The creation of aquatic patches in the boreal forest by beaver (*Castor canadensis*) provides an excellent means of studying these relationships because it is a biotically controlled disturbance, which manifests itself by the creation of ponds. Patches created by beaver dams are large enough and contrast sufficiently with the surrounding landscape to make them readily observable on aerial photos (Howard and Larson 1985, Johnston and Naiman 1990). That makes it possible to study patch dynamics over the half-century of airphoto record, a much longer time period than most long-term ecological research.

We have studied patch creation by beaver in northern Minnesota between 1940 and 1986, a period of beaver population expansion (Naiman et al. 1988). Beaver density at our study site is currently ≈1 colony/km² (Broschart et al. 1989), in contrast with conditions at the turn of the century, when beaver populations were very low due to trapping and habitat destruction (Minnesota Department of Natural Resources, *unpublished manuscript*). The goal of our research was to determine how beaver pond patches are related to beaver densities over a period of beaver population expansion and stabilization. Specific objectives were:

1) To determine the spatial characteristics of individual patches (size, growth rate) and the patch population (numbers, area, density, establishment rate);

2) To relate patch size and growth to patch age;

3) To relate beaver population dynamics to the rate of patch establishment;

4) To determine how patch population dynamics are

[1] Manuscript received 21 November 1988; revised 20 October 1989; accepted 30 October 1989.

[2] Present address: Center for Streamside Studies, AR-10, University of Washington, Seattle, Washington 98195 USA.

TABLE 1. Characteristics of beaver pond sites on the Kabetogama Peninsula, Minnesota, USA, 1940–1986. Within a row, values sharing the same lowercase letter are not significantly different (ANOVA, $P < .05$).

	1940	1948	1961	1972	1981	1986
A. Total number of pond sites	71	231	595	688	741	835
B. Area per pond site (ha, $\bar{X} \pm 1$ SE)	3.7 ± 0.63^a	4.7 ± 0.39^a	4.4 ± 0.23^a	4.3 ± 0.21^a	4.3 ± 0.21^a	4.3 ± 0.20^a
C. Number of new ponds	71	160	364	93	53	94
D. Area per new pond (ha, $\bar{X} \pm 1$ SE)	3.7 ± 0.63^a	3.9 ± 0.39^a	3.2 ± 0.21^a	1.6 ± 0.22^b	1.3 ± 0.16^b	1.2 ± 0.17^b
E. Maximum number of beaver colonies*	...	...	234	278	398	398
F. Pond sites per colony (A ÷ E)	...	...	2.5	2.5	1.9	2.1
G. Pond site area/colony (B ÷ E)	...	...	11.3	11.0	8.4	9.4
H. Annual precipitation (cm, $\bar{X} \pm 1$ SE)	...	67.7 ± 4.5^a	62.0 ± 3.0^a	65.1 ± 2.5^a	62.2 ± 4.0^a	62.7 ± 3.2^a

* Since previous air photo date.

related to other environmental changes affecting water supply to ponds (i.e., precipitation); and

5) To determine how patch population dynamics change as the carrying capacity of the landscape is approached.

METHODS

The 294-km² Kabetogama Peninsula of Voyageurs National Park (48°34′ N, 93°23′ W), was chosen for study. Upland vegetation on the peninsula is boreal forest, dominated by trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*). Mean annual temperature is 2.4°C, and mean annual precipitation (1940–1986) is 63 cm (NOAA 1986). Typical of the Precambrian shield, the area is topographically complex, with a maximum relief of 90 m.

Aerial photographs taken in 1940, 1948, 1961, 1972, 1981, and 1986 were used to map all beaver pond sites within the study area (Naiman et al. 1988: Figs. 4 and 5). The pond sites included all areas with vegetation altered by the past or present ponding of water by beaver, and ranged from ponds to beaver meadows, which are formerly inundated areas that have revegetated to grass and sedge meadows. Although all pond sites supported beaver colonies at one time, current beaver occupancy was not required for inclusion in this study.

The aerial photos were viewed under stereoscopic magnification (3×) to locate and delineate beaver pond sites for each photo date, using criteria given by Howard and Larson (1985) and Johnston and Naiman (1990). Pond sites were classified as "new" for a given date of photography if they did not appear on previous photos of the same area; other pond sites were classified as "old" even if the impounded area was originally smaller. The mapped data were entered into a Geographic Information System (GIS), which was used to measure individual and cumulative pond-site area for each aerial photo date (Johnston and Naiman 1990). Analysis of variance was used (Tukey-B procedure) to detect differences among photo dates in average area of all pond sites and new ponds.

To determine if pond cohort, the date of photography on which impoundments first appeared, influenced pond growth rate, mean pond area was regressed against the natural logarithm of pond age for each of the 1940, 1948, 1961, and 1972 age classes. The SAS General Linear Models (GLM) procedure (SAS Institute 1988) was used to analyze homogeneity of slopes among the growth curves for the 1940–1972 age classes, and a Kruskal-Wallis one-way ANOVA was used to compare mean area of like-aged ponds by pond cohort group.

Beaver population data collected for the Kabetogama Peninsula since 1958 by the Minnesota Department of Natural Resources (Broschart et al. 1989) were regressed against time to calculate overall rates of population increase between 1961 and 1986. The rate of beaver population increase for the period between 1940 and 1961 was estimated by assuming a linear increase from no beaver in 1936, a year when extensive fires burned the peninsula, to the 234 beaver colonies reported in 1961. These assumptions were adopted to generate the maximum plausible rate of beaver population increase over the time period represented by the aerial photos. The SAS GLM procedure (SAS Institute 1988) was used to determine if the number of pond sites paralleled beaver population size over time for 1940–1961 and 1961–1986. Analysis of variance was used to detect differences among the five time periods in average annual precipitation, based on records from the International Falls weather station 25 km west of the study site (NOAA 1986). Chi-square tests were used to compare the number and area of pond sites per beaver colony over the period of beaver population record. SPSS/PC+ (Norusis 1988) and SAS (SAS Institute 1988) were used to perform all statistical analyses.

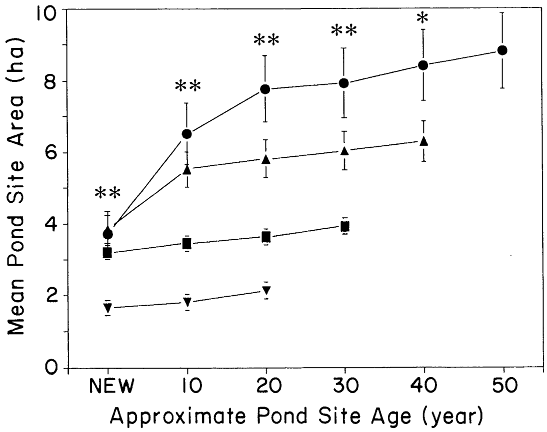

FIG. 1. Average pond-site area, by pond cohort. ● = 1940 pond cohort ($y = 1.27 \ln(x) + 3.72$), ▲ = 1948 pond cohort ($y = 0.63 \ln(x) + 3.85$), ■ = 1961 pond cohort ($y = 0.18 \ln(x) + 3.16$), ▼ = 1972 pond cohort ($y = 0.14 \ln(x) + 1.62$). * and ** indicate significant effects of pond-site age on average pond area (Kruskal-Wallis one-way ANOVA) at .05 and .01 significance levels.

RESULTS

Patch characteristics

All sites that had been impounded by beaver during the 46-yr period were still clearly distinguishable on the 1986 photos. Although some areas had been briefly abandoned, they were either reflooded by new beaver occupants or had been altered to such an extent as to retard secondary succession. Therefore, there was no patch extinction over the time period studied.

The number of pond sites increased dramatically over the half-century study period, so that the 1986 maximum of 835 pond sites was over an order of magnitude greater than the number in 1940 (Table 1). Pond sites ranged from <1 to 45 ha, those of 1–2 ha being most frequent. Although the average pond-site area remained at ≈4.3 ha throughout the 46-yr period ($F = 0.379$, df = 5, $P = .864$), the average area of new ponds decreased significantly over time (Table 1). New ponds established in 1940, 1948, or 1961 were significantly larger ($F = 8.854$, df = 5, $P < .0001$) than new ponds established in 1972, 1981, or 1986, so that the average area of a pond established in 1986 (1.2 ha) was only one-third the average area of a new pond in 1948.

The pattern and magnitude of pond growth varied according to the decade in which the pond was initiated (i.e., its cohort). There were significant differences across cohorts in average area of like-aged pond sites (i.e., 10, 20, 30, or 40 yr of age) (Fig. 1). The regression of the growth curve for the 1940 pond cohort was also significantly different than those for all subsequent cohorts. Therefore, not only were 1940-cohort-class ponds significantly larger to begin with than ponds initiated in 1972 or later, they also grew at a faster rate once established, doubling in average area after only two decades (Fig. 1). The 1948 pond cohort also grew rapidly during the first decade after establishment (43% increase in average pond-site area), but there were no significant differences among the growth curves for the 1948, 1961, and 1972 age classes. Since 1961, average pond-site area increases in all age classes were linear and small, ranging from 0.1 to 0.8 ha/decade.

The combination of high rates of pond creation, larger initial pond area, and rapid growth made the 1940, 1948, and 1961 pond cohorts the most spatially influential (Fig. 2). As of 1986, these cohorts constituted 75% of the total number of pond sites and 90% of the total area impounded. The establishment of new ponds was the primary cause of increased cumulative pond-site area prior to 1961 (70% of the total increase), the rest being due to the enlargement of existing ponds. The proportions were reversed after 1972. Therefore, ponds constructed by beaver during their first few decades of occupancy have the greatest impact on the landscape.

Pond establishment relative to changes in beaver population

Although beaver were continuously creating new ponds throughout the time period studied, there were significant differences among time periods in the rate of new-pond creation (Table 2). The rate was highest between 1940 and 1961, when new ponds were being created at an average rate of 25 ponds/yr, but declined to 10 ponds/yr between 1961 and 1986. The rate of increase in cumulative pond-site area followed a similar trend (Fig. 2).

Because of the lack of patch extinction, the number of pond sites on the aerial photos reflects the maximum extent of beaver colonization since the previous airphoto date. Therefore, the number of pond sites was divided by the maximum number of beaver colonies during the time period to determine average area and number of pond sites per beaver colony (Table 1). Pond-site area per beaver colony did not change significantly ($\chi^2 = 0.285$, df = 3, $P = .963$) over the study period, averaging 10 ha/colony. The number of pond sites (both occupied and abandoned) per colony also did not change significantly over time, remaining at ≈2.2 ponds per colony ($\chi^2 = 0.704$, df = 3, $P = .872$).

The number of beaver colonies on the Kabetogama Peninsula increased by 8.9 colonies/yr between 1960 and 1986 (Table 2). There was no significant difference between the regressions of beaver population and number of pond sites over that time period, indicating that the increase in number of pond sites after 1961 can be explained by the increase in number of beaver colonies.

The rate of beaver population increase estimated for 1940–1961 was similar to the rate recorded after 1961: 9.4 colonies/yr. The rate of increase in number of pond sites between 1940 and 1961, however, greatly exceeded the estimated increase in beaver population, the slopes of the two regressions being significantly

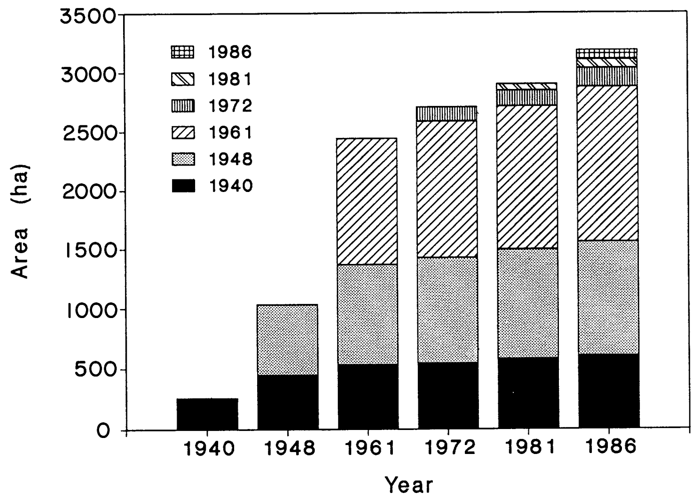

FIG. 2. Cumulative pond area, by age class.

different ($F = 28.06$, $P = .034$). Furthermore, other plausible assumptions about initial number of beaver colonies (e.g., >0 colonies in 1936) or rate of population increase (e.g., exponential rather than linear increase to the 1961 population value) would have *increased* the difference between the slopes of the two lines. In any case, it is clear that the rate of beaver pond building was much higher between 1940 and 1961 than would be predicted by the trend of population increase alone.

DISCUSSION

Although the area disturbed by an individual beaver pond is small in relation to catastrophic disturbances such as fire and hurricanes, the cumulative disturbance of many beaver ponds over time results in extensive alteration. Factors that contribute to the widespread extent of this disturbance include beaver population dynamics, beaver mobility, and patch longevity.

Our data from the Kabetogama Peninsula demonstrate that beaver can quickly create new patches through their dam-building activities, rapidly spreading into suitable habitats as their population increases. This is due in part to beaver biology and behavior (Jenkins and Busher 1979). Young beaver leave their parent colony at ≈2 yr of age in search of new habitat, usually dispersing within a 16-km radius of their natal pond. Given this dispersal radius and an average annual litter size of 3–4 kits/yr, it would be possible for beaver to colonize areas as far as 736 km from an initial nucleus over a 46-yr period. Since all land on the Kabetogama Peninsula is within 5 km of one of the three major lakes which surround it, distance did not affect the susceptibility of this landscape to beaver disturbance.

The pond growth curves (Fig. 1) show that beaver selected first those areas that created the largest ponds with the greatest potential for expansion. As more and more of the potentially floodable sites were occupied, new pond creation decreased and was limited to less desirable sites (i.e., sites where only small ponds could be established). The cumulative area of ponds established after 1961 was very small in comparison to that of ponds created during the first 20 yr of colonization (Fig. 2).

Swanson et al. (1988) have shown that landscape geomorphology can affect ecosystem development and change. We believe that the observed decrease in rate of beaver pond creation after 1961 is due to the attainment of a threshold controlled by the geomorphology of the Kabetogama Peninsula. Prior to 1961 there were many sites at which a beaver dam could impound a large area of water, but after 1961 few such sites remained. Because beaver impoundments are restricted to sites where a low dam can retard the flow of water sufficiently to create a pond, there is a limit to the area which can potentially be affected by beaver. Once this limit is attained, the area affected tends to

TABLE 2. Regressions for increase in number of beaver colonies and pond sites (y), 1940–1961 and 1961–1986. x = time (yr) since the beginning of the period. Methods for estimating beaver population increase from 1940–1961 are described in Methods. ** = significant at $P < .01$.

	Beaver population	n	R^2	Pond sites	n	R^2
1940–1961	$y = 9.4x + 37$	...	...	$y = 25.2x + 55$	3	0.993**
1961–1986	$y = 8.9x + 131$	22	0.648**	$y = 9.8x + 571$	4	0.969**

remain constant, due to the extreme longevity of beaver impoundment patches.

Although there are other plausible hypotheses for the decline in rate of beaver pond creation after 1961, the available evidence argues against them. A decrease in the rate of beaver population growth could have caused the decrease in rate of pond creation after 1961, but population data do not support this (Table 2). Changes in precipitation could have caused a change in rate of pond creation, but there were no significant differences in precipitation among the five time periods studied (Table 1). Depletion of forage reserves at existing ponds could have been a stimulus for new pond creation by beaver, but this would have resulted in an *increase* in pond creation over time as the population increased and food became more scarce.

The Kabetogama Peninsula may be entering a new phase of beaver pond establishment and ontogeny. The beaver population appears to have peaked at 398 colonies in 1981, in contrast to the increasing population trend of the past half-century. All colony counts have been lower since 1981, including those for 1987 ($n = 334$) and 1988 ($n = 330$), and beaver colony densities at Voyageurs are already much higher than other values in the literature (Broschart et al. 1989). We predict that new pond establishment will cease once beaver have impounded all the marginally floodable areas. At that threshold of peak impoundment density, continued disturbance by beaver will be restricted to previously disturbed areas, and the ability of the landscape to sustain the beaver population will depend on forage availability.

Acknowledgments

John Bonde, Michael Broschart, Mark Springan, and Mark Stensaas were involved with various aspects of air-photo interpretation, data entry, and GIS analysis. Greg Grunwald did the statistical analyses. Research support came from the National Science Foundation (grants #BSR-8516284 and BSR-8817665). We thank John Pastor for constructive comments on early drafts of this manuscript. This is contribution Number 50 of the Center for Water and the Environment and Number 7 of the NRRI GIS Laboratory.

Literature Cited

Blais, J. R. 1954. The recurrence of spruce budworm infestations in the past century in the Lac Seul area of northwestern Ontario. Ecology **35**:62–71.

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.

Forman, R. T. T., and M. Godron. 1986. Landscape ecology. John Wiley & Sons, New York, New York, USA.

Howard, R. J., and J. S. Larson. 1985. A stream habitat classification system for beaver. Journal of Wildlife Management **49**:19–25.

Jenkins, S. H., and P. E. Busher. 1979. *Castor canadensis.* Mammalian Species **120**:1–8.

Johnston, C. A., and R. J. Naiman. 1990. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landscape Ecology **4**:5–19.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience **38**:753–762.

NOAA (National Oceanic and Atmospheric Administration). 1986. Local climatological data, International Falls, Minnesota. National Climate Data Center, Asheville, North Carolina, USA.

Norusis, M. J. 1988. SPSS/PC+ version 2.0 for the IBM PC/XT/AT. SPSS, Chicago, Illinois, USA.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **51**:145–178.

Pickett, S. T. A., and P. S. White (editors). 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.

SAS Institute. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute, Cary, North Carolina, USA.

Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. BioScience **38**:92–98.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics **7**: 81–120.