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Signatures of self-assembly in size distributions of wood members in dam structures of *Castor canadensis*

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ABSTRACT

Beavers (*Castor canadensis*) construct dams on rivers throughout most of their historical range in North America, and their impact on water patterns in the landscape is considerable. Dam formation by beavers involves two processes: (1) intentional construction through the selection and placement of wood and sediment, which facilitates (2) the passive capture and accretion of suspended wood and sediment. The second process is a self-assembly mechanism that the beavers leverage by utilizing energy subsidies of watershed transport processes. The relative proportion of beaver activity to self-assembly processes in dam construction, however, is unknown. Here we show that lotic self-assembly processes account for a substantial portion of the work expended in beaver dam construction. We found through comprehensive measurement of the stick dimensions that the distributions for diameter, length, and volume are log-normal. By noting evidence of teeth markings, we determined that size distributions skewed significantly larger for wood handled by beavers compared to those that were not. Subsequent mass calculations suggest that beavers perform 50%–70% of the work of wood member placement for dam assembly, with riparian self-assembly processes contributing the remainder. Additionally, our results establish a benchmark for assessing the proportion of self-assembly work in similar riparian structures.

1. Introduction

Beavers (*Castor canadensis*) have often been referred to as ecosystem engineers because of the structures they build and the amount of landscape they alter (Finley, 1937; Cullen, 1962; Beakley, 1984; Allred, 1986; Pollock et al., 1995; Wright et al., 2002). Throughout their geographic range, which includes almost all of North America, they build dams and lodges out of wood that they cut by gnawing with their chisel-like teeth. The lodges, which can be several meters wide and tall, are used as residences for family units. Because beavers are active year round, the lodges are especially useful for overwintering. Their dams are constructed on streams and small rivers in order to create ponds that provide protection from terrestrial predators and that facilitate movements and transport of wood to construction sites (Johnson, 1927; Morgan, 1986; Muller-Schwarze, 2003). The beaver ponds can cover many hectares in area and can occur in series along the course of a stream. Through their construction activities beavers affect the riparian forest by tree cutting and flooding, and they create habitats for aquatic organisms found in the ponds (Naiman et al., 1988; Remaillard et al., 1988; Gurnell, 1998; Johnston, 2001; McKinstry et al.,

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2001; Nyssen et al., 2011). Furthermore, after ponds fill with sediments and are abandoned by the beavers, a successional sequence is triggered as the riparian forest grows back on the site (Gese and Shadle, 1943; Gill, 1972; Barnes and Dibble, 1988; Sturtevant, 1998).

Dam construction has been described anecdotally, but quantitative analysis of the design of beaver dams has not been widely reported. Beaver dams can range up to 100 m in length and 5 m in height, depending on the size of the stream that is being dammed (Gurnell, 1998). The sizes of wood members that compose the dam generally relate to browse selection behavior of beavers and the riparian forest composition, with preferred sizes generally found to be between 1 and 5 cm in diameter and up to 3 m in length (Johnston and Naiman, 1990; Barnes and Mallik, 1996, 1997; Haarberg and Rosell, 2006; Janiszewski et al., 2006). Dam structures are maintained by the beavers for a number of years until the pond behind the dam becomes filled with sediments. Although a downed tree trunk can be used as a foundation for a dam, sticks and tree branches of various sizes are usually first laid in place and mud is added to the dam as the building progresses. Several different techniques of dam construction have been identified in terms of orientation of wood depending at least in part on the current velocity of the stream being dammed (Gould and Gould, 2007). When the flow rate is low, wood can be laid across the stream. When water flow rate is higher, however, branches can be anchored in place often with more horizontal and longitudinal orientation. Continued flow processes of the stream leads to accretion of additional wood and sediment material, filling out the overall structure of the dam. While the processes of active construction and passive accretion for dam assembly are well understood, the relative contributions of each process to the dam assembly effort are unknown. Our focus is on characterization of the wood members used in beaver dam construction. We explored through dam deconstruction the mass, number, and sizes of wood members that compose the dam structure. Also, we explore the hypothesis that self-assembly is a major factor in the dam construction. We propose that wood that passively falls into a stream and floats downstream contributes to the structure of the dam without direct handling by beavers. It is well known that woody debris jams can self-assemble in streams resulting from interactions between individual pieces of wood and the stream channel (Keller and Swanson, 1979; Bilby and Likens, 1980; Smock et al., 1989). We explore the self-assembly hypothesis for a beaver dam by classifying wood members by the presence or absence of gnaw-marks at the ends of the sticks. We suggest that wood members without gnaw-markings potentially have contributed to the dam by self-assembly rather than by intentional placement by the beavers, and that this self-assembly accounts for a significant portion of the dam construction process.

2. Methods and analysis

A small beaver dam was identified on the property of the Patuxent Wildlife Research Refuge in central Maryland for deconstruction. This dam was located on a first-order stream that drains a pond used for waterfowl management. The stream was approximately 1.5 m deep upstream and 0.5 m deep downstream from the dam. The physical characteristics of the beaver dam were measured in situ prior to deconstruction. The dam was approximately 6 m long across the stream channel and 1 m wide, with a radius of curvature of approximately 10 m concave in the upstream direction. It consisted of a framework of wood and sloping accumulation of sediment upstream of the dam.

The dam was deconstructed manually and all sticks were collected and retained for measurement. For each stick, measurements were taken of the diameter, to the nearest 0.1 cm, and length, to the nearest 1 cm. The presence or absence of beaver activity was noted for each stick through observing evidence of chewing marks and/or stripping of outer bark. Sticks were grouped into three diameter size classes of <1.0 cm, 1.0–4.5 cm, and >4.5 cm. Sticks in each class were counted, allowed to air-dry in the lab for 2 weeks, and weighed as a class group using a 50-kg linear spring scale.

Histograms were prepared of diameter, length, and nominal volume (calculated for each stick as the cross-sectional area multiplied by the length, assuming a constant circular cross-section along the full length of the stick) for sticks exhibiting beaver activity and no beaver activity. These histograms were compared to probability density functions typically used to describe particle size distributions, including normal, log-normal, log–logistic, and Weibull distributions, with goodness-of-fit determined with a Kolmogorov–Smirnov test. Descriptive statistics for each distribution were determined. Cumulative density functions for each geometric descriptor were prepared, and comparisons between sticks exhibiting beaver activity and no beaver activity were made with a Kolmogorov–Smirnov goodness of fit test. The proportions of beaver activity and no beaver activity sticks were determined for each of the three diameter size classes, each of three length size classes (arbitrarily established at <10 cm, 10–100 cm, and >100 cm), and each of three volume size classes (arbitrarily established at <10 cm^3, 10–1000 cm^3, and >1000 cm^3) and analyzed for trends. The proportion of total stick volume for each of the three diameter size classes was determined and compared to the total stick mass measured for each size class.

3. Results

The structure of the beaver dam is evident in the distribution of stick diameter across size classes, and the distribution illustrates tradeoffs between numbers and mass (Table 1). The total number of sticks was 3675, with a total mass of 178.7 kg and a total estimated stick volume of 583E3 cm^3. The largest number of sticks (51.3%) were in the smallest (<1.0 cm) diameter size class, and the smallest number (2.8%) were in the largest (>4.5 cm) diameter size class. Total stick mass and total estimated stick volume were inversely distributed, with both a majority of mass (50.8%) and estimated volume (60.4%) in the largest diameter size class. Of the total number of sticks, 1682 (45.8% of total) exhibited signs of beaver activity (Table S-1, Supplemental information, Appendix A).