

# The hydrogeomorphological effects of beaver dam-building activity

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**Abstract:** A characteristic of beaver ecology is their ability to build dams and, thus, to modify the landscape to increase its suitability for their occupation. This ability gives beaver great significance as a geomorphic agent. In order to review the hydrogeomorphological effects of beaver dam-building activity, this article places a context on the likely distribution and magnitude of beaver activity by considering the spatial and temporal variability of distributions of beaver and the habitat characteristics which might favour the establishment of substantial beaver populations. A description is then given of the nature and potential dimensions of instream structures built by beaver and the environmental conditions under which dam building has been observed to occur. The hydrogeomorphological impact of dam building is then appraised both locally and at the landscape scale, illustrating the very significant process modification caused by beaver. While the European beaver, *Castor fiber*, is the main focus of this review, it necessarily draws extensively on the much larger literature concerning the North American beaver (*Castor canadensis*).

**Key words:** *Castor fiber*, *Castor canadensis*, beaver dams, beaver meadows, beaver ponds, riparian hydrology, river channel change, sediment storage.

## I Introduction

The research presented in this article was originally commissioned by Scottish Natural Heritage because, under Article 22 of the EC Habitats Directive (EC/92/43), the UK government is required to consider the reintroduction of certain species which are threatened in mainland Europe and have become extinct in the UK. The European beaver (*Castor fiber*) is one of these species. It became extinct in Scotland approximately 300 years ago.

A characteristic of beaver ecology is their ability to build dams and, thus, to modify the landscape to increase its suitability for their occupation. This ability to modify their habitat gives beaver enormous significance as geomorphic agents and has caused them to be described as 'ecosystem engineers' (Gurney and Lawton, 1996). Their consequent direct and significant control on ecosystem structure and dynamics has also led them to be considered a 'keystone species' (Naiman *et al.*, 1986). It is important to recognize these

effects prior to any reintroduction in order to make an informed decision on the feasibility and desirability of restoring this native species to the current landscape.

Although this article primarily reviews the hydrogeomorphological influence of the European beaver (*C. fiber*) as a result of dam-building activities, extensive reference is also made to the more substantial literature on the North American beaver (*C. canadensis*). There are great similarities in the way the two species impact upon the environment, although *C. fiber* is believed to undertake more restricted building activity than *C. canadensis* (Collen, 1995).

This article places a context on the likely distribution and magnitude of beaver activity by considering the spatial and temporal distributions of beaver, including the potential densities of beaver and the density of beaver colonies, and the habitat characteristics which might favour the establishment of substantial beaver populations. A description is then given of the nature and potential dimensions of instream structures built by beaver and the environmental conditions under which dam building has been observed to occur. The environmental impact of dam building is then appraised both locally and at the landscape scale along the river continuum. From the review of these topics, the limitations in the available information and thus requirements for future research are highlighted, and an assessment is made of the hydrogeomorphological impact that is likely to ensue following the introduction of *C. fiber* to an area.

## II Spatial and temporal distributions

### 1 Colonization

*C. canadensis* can rapidly spread into suitable habitats as the population increases. Johnston and Naiman (1990) estimated that it would be possible for *C. canadensis* to colonize as far as 736 km from its initial nucleus over a 46-year period. In the absence of natural predators and competitors, *C. canadensis* has colonized areas of Tierra del Fuego to densities of 0.2–5.8 colonies/km of river in 40 years (Lizarralde, 1993). However, colonization by *C. fiber* after reintroduction appears to be slower. MacDonald *et al.* (1995) review the success of reintroduction of *C. fiber* into various European countries. Annual population increases from these introductions have ranged from close to 0% (The Netherlands) to as high as 34% annually (over six years, Peene Valley, Germany), but levels of approximately 15–20% appear to be typical. A useful comparison can be made between *C. fiber* and *C. canadensis* in Finland, where both species have been introduced. In 1935, 19 *C. fiber* were introduced from Norway, and 7 *C. canadensis* were introduced from the USA in 1937 (Lahti and Helminen, 1974). By 1990, the former had increased to about 800 whereas the latter had resulted in an increase to 3300–5200 (MacDonald *et al.*, 1995). In part this may reflect the larger litter size of *C. canadensis* (Lahti and Helminen, 1974). Whatever the cause, *C. canadensis* was usually found to dominate or displace *C. fiber* at locations where they were both introduced (Lahti and Helminen, 1974; Ermala *et al.*, 1989).

### 2 Colony size

Beavers normally live as a family unit or colony, consisting of two parental adults, the yearlings born the previous year and the young of the year. A beaver colony is defined as 'a group of beaver occupying a pond or stretch of stream, using a common food supply

**Table 1** Beaver colony sizes reported in the literature

Source	Location	Colony size (individuals)
<i>C. canadensis</i>		
Collen (1995)		
quoting Hodgdon and Hunt (1953)	Maine	4.3
quoting Payne (1982)	Newfoundland	5.3
quoting Novak (1977)	Ontario	7.6
Hill (1982)	North America	2.7–6.2 (recorded averages)
MacDonald and Barrett (1993)	Europe	3–9
<i>C. fiber</i>		
Curry-Lindahl (1967)	Sweden	
	Ångermanland	5
	Värmland	3.2
	Jämtland	3.1
MacDonald and Barrett (1993)	Europe	5–61
Collen (1995)		
quoting Myrberget (1967)	Sweden	4.9
Zurowski and Kasperczyk (1986)	Poland	3.7
quoting Palionene (1975)	Lithuania	4
quoting Golodusko (1975)	Byelorussia	4.4
quoting Tamuch and Tolkarev (1976)	Polesie	3.4

and maintaining a common dam or dams' (Bradt, 1938, cited in Hill, 1982: 262). Various average colony sizes have been reported (Table 1), with colonies of *C. fiber* being thought to be a little smaller than those of *C. canadensis*.

### 3 Colony density

The density of colonies varies with the quality of the habitat and the degree to which colonization of an area has stabilized (Table 2). Semyonoff (1951, cited in Collen, 1995) suggested that in Russia, 1.5, 0.5 and 0.1 colonies per km might be expected in *good*, *quite good* and *mediocre* beaver habitat, respectively. Hartman (1994a) reports on *C. fiber* colonization of the Värmland and Västernorrland Provinces of Sweden. In two study areas populations built to maximum densities of 0.25 and 0.2 colonies per km<sup>2</sup>. The number or density of colonies in an area is an important factor in governing the potential number of dams that may be constructed.

### 4 Habitat suitability

Hill (1982: 262) notes that *C. canadensis* 'occur commonly in large rivers, impoundments, and large lakes with relatively constant water levels, in protected areas of large lakes that have extensive wave action, streams, tributaries and small seepages that have adequate flow for damming'. Although proximity to a water body is an essential requirement for beaver, the nature of that water body and other properties of the habitat play a role in governing the degree to which beaver might colonize and sustain a population.

**Table 2** Beaver colony density reported in the literature

Source	Location	Density
<i>C. canadensis</i>		
Boyce (1983)	Alaska	0.63/km (mean nearest neighbour)
Beier and Barrett (1987)	Truckee R., CA	0.74/km (sites < 2% slope)
Howard and Larson (1985)	Massachusetts	0.83/km
quoting Collins (1976)	Wyoming	0.9/km
quoting Nordstrom (1972)	New Brunswick	1.25/km
Johnston and Naiman (1987)	Minnesota	1.0/km <sup>2</sup>
Lizarralde (1993)	Tierra del Fuego	0.2–5.8/km
McCall <i>et al.</i> (1996)	Maine	0.32/km <sup>2</sup> (no trapping)
Robel and Fox (1993)	Kansas	0.08–1.4/km (rivers) 0.0–0.25/km (reservoirs)
<i>C. fiber</i>		
Hartman (1996)	Sweden (R. Sverkestaån)	1.0/km
Hartman (1994b)	Sweden Värmland and Västernorrland	0.25/km <sup>2</sup> (peak density)
MacDonald <i>et al.</i> (1995)		
quoting Heidecke (1984)	Peene Valley (Germany)	0.26/km
Sidorovich <i>et al.</i> (1996)	Belarus–Poland	0.29/km (average) 0.0–0.5/km (range)

Note:

Densities are expressed either in km of river or per unit area in km<sup>2</sup>.

*a River flow and lake-level regime:* The discharge/water-level regime is important to beaver, who will build dams to stabilize water levels when necessary. The introduction of modifications to the water-level regime of a river or lake can lead to major impacts on beaver. For example, Wolff *et al.* (1989) show how flow augmentation to improve the quantity and reliability of the flow in an ephemeral stream in Wyoming led to a threefold increase in the number of beaver and a doubling of the total impounded area of beaver ponds within two years. Curry-Lindahl (1967) noted the catastrophic impact of rapidly varying winter flows associated with hydropower generation on the local beaver population. Martin (1977) considered a variety of impacts of human-modified stream-flows on beaver, including the potential of increased winter flows to wash away food caches, and the potential of low flows in autumn to stimulate dam building. Smith and Peterson (1991) also noticed alterations in beaver behaviour consequent upon winter drawdown in lake levels. The beaver spent less time in their lodges, were unable fully to use stored food and spent more time foraging than beaver on reservoirs that were not subject to winter drawdown. As a result, Smith and Peterson recommended that total annual water-level fluctuation should not exceed 1.5 m, whereas winter drawdown should not exceed 0.7 m.

*b River channel characteristics:* Streams containing steep, rocky or bedrock bottoms are less favoured by beaver, possibly as a result of the destructiveness of high water conditions in such streams (Hill, 1982, citing Retzen *et al.*, 1956). Hacker and Conblentz (1993) identified soft soils as one of six habitat factors associated with beaver recolonization of clearcut areas in Oregon. The materials that constitute the bank and bed of the

water course are important because they affect whether and where beaver can construct burrows and lodges, whether it is possible to construct dams to regulate water levels, and the degree to which dam and canal construction will give access to substantial new areas and sources of food. This is another reason why beaver may not favour streams flowing on bedrock or with a very coarse, rocky bed. Boyce (1983), studying *C. canadensis* in Alaska, found the highest densities of beaver colonies in areas where a high proportion of the area used by the colonies contained sand or gravel bars. He attributed the importance of this to its association with a dynamic fluvial environment where diversity in bed topography and deposited sediment calibre provides deep pools and oxbows, and sources of fine clay sediments for dam and lodge construction, and where the riparian zone is patchy, offering a range of vegetation types reflecting different stages in vegetation colonization. Boyce (1983) does not indicate precisely where beaver establish colonies or locate dams and lodges in this environment but comments that oxbows are frequent. Beaver colonies have been noted frequently to establish around oxbows and other floodplain water bodies adjacent to large river channels (e.g., Townsend and Butler, 1996).

*c Food availability:* *C. canadensis* is selective in its choice of woody plants (e.g., Busher, 1996), often showing a strong preference for aspen over all other species, and also preferentially utilizing willow, alder, maple and ash species. Smaller woody stems (<4 cm diameter) are preferred (Basey and Jenkins, 1995; Barnes and Mallik, 1996), and the size of pieces cut decreases with increasing distance from water (Jenkins, 1980). Similarly, vegetation as a food source for *C. fiber* is suggested by Stocker (1983) to be a crucial issue in attempts at reintroduction. In Finland, *C. fiber* use any of the available hardwood species, but show a clear preference for aspen (*Populus tremula*) and birches (*Betula pubescens* and *B. verrucosa*). Debarking of conifers is rare (Lahti and Helminen, 1974). Beaver diet varies seasonally (Lahti and Helminen, 1974; Svendsen, 1980; Roberts and Arner, 1984). Both *C. canadensis* and *C. fiber* consume woody vegetation, grass and forbs, and aquatic vegetation. They depend largely on woody food sources in winter, but can spend up to 90% of feeding time consuming grass, forbs and aquatic vegetation in summer. Barnes and Dibble (1988) illustrate the impact of beaver in west central Wisconsin on forest succession. The beaver greatly reduced tree density and were selective in their choice of woody plants. As a result, a major reduction was predicted in future populations of ash, hickory and hackberry in areas of beaver activity, and a corresponding increase in the density of basswood, elm, and possibly silver maple and prickly ash. Doucet and Fryxell (1993) undertook experimental investigations of food preference by *C. canadensis* for five forage species, and found a clear order of preference as follows: aspen (*Populus tremula*), white water lily (*Nymphaea odorata*), raspberry (*Rubus idaeus*), speckled alder (*Alnus rugosa*), and red maple (*Acer rubrum*). In Sweden, *C. fiber* mainly feed on fresh bark as well as shoots, buds, twigs and leaves, of deciduous trees, particularly aspen (*Populus tremula*), birch (*Betula pubescens*) and salix species (*Salix caprea*, *S. aurita*, *S. cinerea*, *S. glauca*, *S. lapponum*, *S. pentandra*). They also eat roots stems and leaves of many grasses and flowering plants (Curry-Lindahl, 1967). Thus availability of preferred vegetation is likely to be an important criterion in habitat selection. Since the maximum distance that beaver will travel from water to obtain food is thought to be approximately 100 m and beaver commonly browse within 10 m (Howard and Larson, 1985; Nolet *et al.*, 1994), the proximity of preferred food to water courses is particularly important. However, beaver can change such proximity by impounding ponds and

constructing canals. The resultant change in the position of the water shoreline can extend considerably the access of beaver to food in areas of low relief.

*d Important combinations of factors in habitat selection:* A number of researchers have undertaken multivariate analyses of habitat characteristics in order to identify those which best discriminate areas that are likely to be colonized or used by beaver.

Howard and Larson (1985) used principal components regression to assess the relationship of habitat variables to beaver (*C. canadensis*) colony site longevity (revealed from air photograph analysis), and linear discriminant analysis to assess the relationship of 14 habitat variables to colony site longevity. Of these 14 variables, 7 appeared significantly to affect colony site longevity: watershed size, stream width, stream gradient, soil drainage class, percentage hardwood vegetation within 100 m and 200 m, and percentage abandoned fields within 100 m. Within the restrictions of the sampled range of habitat characteristics which included only relatively narrow streams (<8 m wide) and relatively small watersheds (<750 ha), these analyses were interpreted to reveal that the best beaver habitat was associated with relatively wider streams with low gradient and poor soil drainage.

Beier and Barrett (1987) used stepwise logistic regression in a series of pairwise contrasts to identify variables influencing habitat use by beaver (*C. canadensis*). They classified 214 stream reaches of approximately 700 m length into four groups: 1) at least one active colony present; 2) sign of at least one abandoned colony; 3) sign of past/present beaver usage but not a colony; and 4) no sign of past/present beaver usage. Six physical and 11 vegetation variables were estimated for each reach. Three physical variables (stream gradient, stream depth and stream width) were found to be the most important factors. Low stream gradients were thought to be important because they allow beaver to increase greatly their safe foraging area by dam building, to establish a food transportation system and, as a result of the lower energy environment, to reduce the potential for damage to dams, lodges and food caches. Deeper and wider streams offer a higher volume of river channel and so were thought to offer more cover, sites for food caches and a more reliable source of water for impoundments. Mean values of river channel gradient ( $s$ , in %), width ( $w$ , in m), depth ( $d$ , in m) and the associated sample size ( $n$ ) of reaches according to beaver occupancy class were as follows: class (1)  $s = 1.16$ ,  $w = 8.1$ ,  $d = 2.44$ ,  $n = 53$ ; class (2)  $s = 4.22$ ,  $w = 5.9$ ,  $d = 2.13$ ,  $n = 45$ ; class (3)  $s = 5.75$ ,  $w = 4.9$ ,  $d = 1.85$ ,  $n = 44$ ; (4)  $s = 12.53$ ,  $w = 1.4$ ,  $d = 0.85$ ,  $n = 72$ . Sites abandoned by beaver were related to two types of reach. The first type consisted of reaches that were similar to those with active colonies but with relatively low food availability. These may be reoccupied when the vegetation recovers. The second type were similar to the uncolonized reaches and were probably only occupied for a short period prior to abandonment.

Hartman (1996) evaluated habitat selection by *C. fiber* along a 30 km stretch of the River Sverkestaånin, south central Sweden. The tortuosity of the shoreline and a dominant cover of grasses and forbs provided the strongest discrimination of beaver occupancy (although tortuosity may be directly influenced by beaver and ground cover is also very likely to be a reflection of beaver impact). Thereafter, beaver showed a habitat preference for softer soils, higher cover of deciduous tree species and narrower sections of river. In the study area the river had little variability in gradient or depth, and so these did not impact on habitat selection. Furthermore, river width was generally large (mean = 114 m) because it was affected by lake formations. Thus the preference for narrower sections still implied widths of the order of 40 m.

The results from these studies may appear to conflict to some degree, but this is indicative of the different fluvial environments in which the studies were undertaken, and some general but quite broad conclusions can be drawn about the characteristics of suitable beaver habitat:

- *Food availability.* Easy access to grasses, forbs and hardwood vegetation.
- *Channel dimensions.* Where streams are small and shallow, the larger channels are preferentially selected by beaver, whereas in areas of wide channels, the narrower locations are selected. A preference for channel widths of the order of 8–40 m is identified by the quoted sources.
- *Channel/floodplain gradient.* Lower gradients are preferred (e.g., <2% slope).

MacDonald *et al.* (1995) present criteria for gauging the quality of release sites for *C. fiber*, which further illustrate the broad range of habitat characteristics that suit colonization by beaver. They suggest that the physical–vegetational characteristics of a *good* site are as follows: 2–4 m water depth, 10–100 m river width, <0.3 m.s<sup>-1</sup> flow velocity, bank materials of peat-loam soil, bank height >1.5 m, bank slope <60°, woody species predominantly aspen and willow and <8 cm diameter, and a good herb cover. Even within this *good* category, the range of suitable physical conditions is quite wide, but if conditions from the *fair* category are added, the range becomes enormous (e.g., river depths of 1–6 m, widths of 2–300 m, banks >0.5 m height and <80° slope). Only the requirement for fine bank material seems to be a relatively restrictive requirement. However, beaver do not always construct dams. The building activities of beaver and the environmental conditions under which dam building has been observed to occur are discussed below.

### III Building activities

Beavers can greatly affect their environment by constructing dams, canals and other structures. For example, where *C. canadensis* remain unexploited, these activities can influence as much as 20–40% of the total length of 2nd to 5th-order streams (Naiman *et al.*, 1986), and can involve impressive scales of constructional activity (e.g., Morgan, 1868). Under exploitation, the impact of *C. canadensis* is more restricted, whereas *C. fiber* appears to undertake dam building less frequently. In addition to cutting wood to construct dams, wood is also used by both species in lodge construction as well as being a major food source that is often stored under water in caches. Cutting operations are mostly made close to the water course but in some cases they may extend as far as 100 m away (Curry-Lindahl, 1967). However, the construction of dams raises the local water level, so changing the position of the water's edge, which is further modified by the excavation of canals out from the pond margin (Hodgdon and Lancia, 1983).

#### 1 Dams

Dams consist of tree trunks, branches, twigs, earth, mud and sometimes stones. Beaver require their shelter (lodge or burrow) to have access points which are under water, and so dams are constructed where necessary to achieve this, with building activity being timed according to necessary adjustments in the water level (Richard, 1983). Several

dams can be built by the same colony to control the ponded water level in relation to the lodge or burrow entrances. The length and height of dams vary with the topography. Early descriptions of the number and dimensions of dams built by *C. canadensis* in relatively undisturbed conditions in North America (e.g., Morgan, 1868; Dugmore, 1914; Warren, 1927) indicate some enormous structures several hundred metres long and several metres high. However, the large majority were suggested by Dugmore (1914) to be less than 1.5 m high. This typical height of beaver dam is supported by Townsend's (1953) observations in Montana, where dams varied in size from small canal dams approximately 0.5 m long up to dams of 13 m in length and reaching heights of up to 1.5 m. Recently, Butler (1995) has suggested typical dam sizes of 15–70 m long and 1–2 m wide, although he does not indicate whether the longer dams are constructed to span channels of that width. These North American sources also illustrate that although many of the dams are watertight structures, if not well maintained they become leaky, and on some larger rivers they only extended part-way across the channel.

It is thought that *C. fiber* build dams less frequently than *C. canadensis* and that usually they build rather smaller structures. For example, dams built by *C. fiber* in Sweden rarely exceed 15 m in length, are typically 1 m in height (Curry-Lindahl, 1967), and are usually only built in shallow waters less than 10 m wide (Hartman, 1994a). In Poland, Zurowski and Kasperczyk (1986) found that of 257 beaver sites in the Suwalki Lakeland, only 50 had dams. Medwecka-Kornas and Hawro (1993) describe 12 dams in the Saspowka brook, Poland, ranging from 2.5–24 m in length (average 8.5 m) and 0.4–1.7 m in height (average 0.8 m). Zurowski (1992) found that of 62 sites of beaver colonies in the Masurian and Brodnica Lakelands, 17 had dams, with more than one dam occurring in many sites. Furthermore, all the dams were located on small rivers or drainage ditches and appeared to be constructed primarily to provide access to new food areas. Zurowski (1992) tried to evaluate the stimuli which are supposed to trigger dam building. Although the sound of running water has been suggested to be an important stimulus for dam building by both *C. canadensis* (e.g., Hodgdon and Lancia, 1983) and *C. fiber* (e.g., Richard, 1983), Zurowski (1992) concluded that this was of secondary importance to the stimulus of improving safety and access to food at particular sites.

Richard (1955) described dams constructed by *C. fiber* in France. They consisted of pieces of wood, typically 1–2 m long and sometimes stones, which were then sealed with mud on the upstream face. Woo and Waddington (1990) classified dams constructed by *C. canadensis* in subarctic northern Ontario according to their construction materials. They identified two types of construction materials for active dams: stones, new branches, fresh mud; and no stones, fresh branches and mud. Four types of construction material were described for old dams: stones, old branches, mud and debris; no stones, old branches, mud and debris; no stones, old branches, some remaining mud and debris; only branches remaining. Two types of construction materials were associated with relict dams: only branches remaining; most of branches gone, only half of original structure remains. They also identified four types of dam according to their flow control: overflow (broadly distributed overtopping of the dam crest), gapflow (concentrated spillage over one or more low points in the dam crest), throughflow (seepage through the dam face) and underflow (leakage from the base of the dam). The occurrence of these four flow types is correlated with increasing age and deteriorating state of repair of the dam.

Richard (1955) classified dams constructed by *C. fiber* on the upper course of the River Tave, France, according to their structure. Here dams attained 8–10 m in length and were

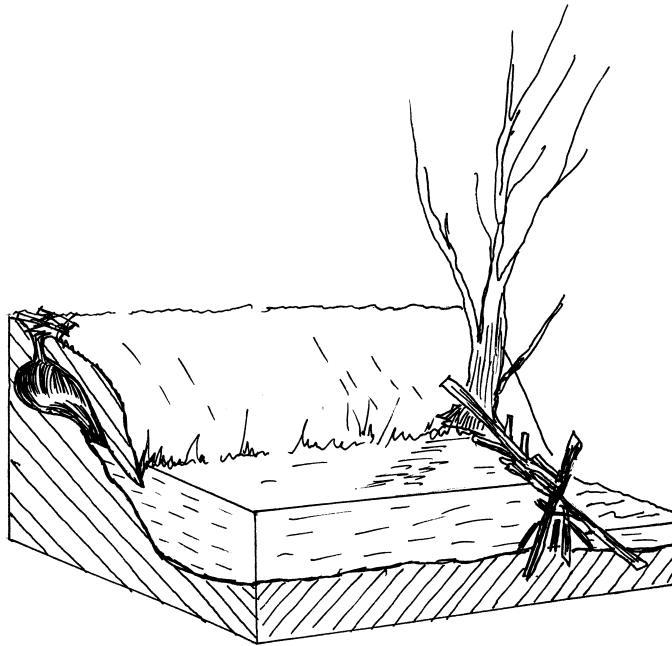
constructed of wood pieces that were aligned across the river, parallel to the banks or near vertically. The near-vertical pieces and those parallel to the bank form the key pieces of the structure, which is then filled out upstream with transverse pieces. Three basic types of structure were identified. Type 1 uses a fallen or inclined tree to give support to the structure, although other vertical pieces of wood may be introduced by the beaver. Type 2 is based upon a structure of vertical key pieces of wood which have been driven into the stream bed. Type 3 is counterbalanced by longitudinally orientated props which support the downstream face of the dam against the upstream water pressure. This third type of structure is combined with type 2 in constructing the largest dams.

Beaver dams adopt a variety of planforms, but upstream-orientated arc-forms are common. Dams may simply occupy the active river channel, they may extend across low-gradient banks or they may extend across floodplains and/or side channels to create wide ponds. Dams can evolve through time. For example, small within-channel dams can be progressively extended into long channel-floodplain dams as the beaver colony increase the height and build up the dam laterally (Richard, 1967). This illustrates the way in which beaver may develop long dams and large ponds on floodplains, even though the width of dammed channel is relatively small.

Once a dam is constructed and a pond is created in a low-gradient area, the zone of floodplain accessible to beaver can be further extended by canal construction. Canals constructed by *C. canadensis* can vary in length from <1 m to >100 m, in width from 0.35 m to 1 m, and are typically over 0.5 m deep. Canals are used as routeways and also to transport timber to the beaver pond.

## 2 Burrows, lodges and caches

Figure 1 illustrates a typical arrangement of dam, burrow and below-water burrow entrance. However, local physical conditions do not always permit such an arrangement and, as a result, beaver can construct a wide variety of shelters. Erome (1984) produced a typology of beaver shelters constructed in the Rhône basin by *C. fiber*. The typology relates to different combinations of bank slope and profile, suitability for burrowing, bank material cohesiveness, and the potential for the entire burrow entrance to be maintained at or below the water level. Natural holes in the bank are often utilized. When natural holes are not available, beavers excavate their burrows where the bank is high enough and the bank material is sufficiently firm. When these conditions are not met, intermediate structures between burrows and lodges, called bank lodges, are found. Varying amounts of woody material are incorporated either to conceal the burrow entrance, to compensate for the lack of soil cohesiveness or for lack of soil depth. The level of the nest chamber is typically 0.3–0.7 m above the upper edge of the burrow entrance. This difference in level defines an upper limit to desirable water-level fluctuations, particularly to rapid water-level fluctuations that might drown the kits. Nest chambers are typically 0.4–0.5 m in height and so, allowing for sufficient clearance of the top of the riverbank above the ceiling of the nest chamber, bank heights of 1.5–2.0 m above the roof of the burrow entrance are required for successful burrow construction. Where the banks are lower, various forms of bank lodge can be constructed which combine a bank burrow with a woody construction on the bank top. True lodges, made entirely from wood pieces, were found by Erome (1984) to be very rare in the Rhône basin, where they are built only when it is not possible to create the alternative structures. Although beavers will normally construct burrows in preference to lodges



**Figure 1** A typical configuration of dam, burrow and below-water burrow entrance

where the riverbanks are sufficiently high, Zurowski (1992) found that *C. fiber* built many lodges in the Masurian and Brodnica Lakeland of Poland. On average, each colony built more than one lodge. Additional lodges were used in different ways according to local topography. For example, secondary lodges were sometimes occupied when the water level was low near the main lodge, or when human recreation disturbed the beavers. Most lodges were conical in profile and circular or oval in plan.

Food is accumulated for later consumption in caches. The caches can be a significant size where the winter is long. In Sweden branches and twigs collected during the late summer and autumn are stored inside and outside the lodge and, in the latter case, are anchored to the dam, river or lake bed (Curry-Lindahl, 1967).

#### **IV Environmental conditions associated with dam building**

The presence/absence and density of beaver dams are highly variable (Table 3) depending upon the number of beaver colonies and the degree to which environmental conditions encourage dam building. Only references to environmental conditions associated with dam building by *C. canadensis* were found in the literature consulted for this review. McComb *et al.* (1990, cited in Collen, 1995) found that reaches with dams were shallower, had a lower gradient, a greater tree canopy cover and gentler bank slopes than reaches without dams, and that dams were not built at sites with a rock substrate. Naiman *et al.* (1986) noted that most dams were built on 1st to 4th-order streams in their study area in Quebec, Canada.

**Table 3** Beaver (*C. canadensis*) dam density reported in the literature

Source	Location	Density
Butler and Malanson (1995) quoting McComb <i>et al.</i> (1990)	Eastern Oregon	0.14/km
Leidholtbruner <i>et al.</i> (1992)	Coastal Oregon	1.1/km 1.2/km
Naiman <i>et al.</i> (1986; 1988)	Quebec	10.6/km (average) 8.6–10.6/km (range)
	Minnesota	2.5/km (average) 2.0–2.9/km (range)
Woo and Waddington (1990)	North Ontario	14.3/km (average) 5–19/km (range)

Although beaver dams may be maintained in the same location for long periods of time (several centuries in some cases), dams may become abandoned and fall into decay, or they may pass through cycles where they fall into decline and then are later re-established (e.g., Warren, 1932; Sinitsyn, 1992). The circumstances governing dam abandonment, failure and reoccupation are all hydrologically important, but little information was found concerning these circumstances in the literature. Beier and Barrett (1987) identify river reaches abandoned by beaver and allocated them to two groups. The first group comprised reaches that were similar to those with active colonies but with relatively low food availability. These may be reoccupied when the vegetation recovers and then dam building and maintenance may recommence. The second group comprised reaches that were more similar to uncolonized than to colonized reaches and were probably only occupied for a short period of time prior to abandonment. The extent to which beaver dams might fail during major flooding (e.g., as a result of rapid snowmelt) is illustrated by Leidholtbruner *et al.* (1992), who found only one complete dam during a spring survey of 19 km of stream in coastal Oregon, but the density had risen to over one dam per km of stream by the following autumn.

## V Physical environmental impact of dam building

Beaver, through their dam-building and feeding activities, act as a keystone species which affects ecosystem structure and dynamics far beyond its immediate requirements for food and space (Naiman *et al.*, 1986). Johnston and Naiman (1987) illustrate the way in which beaver ponds and canals affect local hydrological processes to create a series of disturbance patches within the forest landscape. The patches include 1) the pond; 2) the surrounding riparian zone with its raised water table and browsed vegetation, exhibiting both waterlogged areas and areas of enhanced soil moisture content; 3) often a marginal floating mat of peat and vegetation extending along parts of the pond boundary; and 4) a zone of anaerobic sediments beneath the pond bed. All these patches are a direct effect of the changed hydrological conditions which are a consequence of beaver dam construction. Each colony of beaver may build several dams and thus create more than one pond. For example, Johnston and Naiman (1990) found that in the Kabetogama Peninsula, Minnesota, each beaver colony was associated with an average of

approximately two dams, the ponds inundating an average area of 4 ha. They also observed that the largest ponds, presumably representing the optimum sites for damming water, were constructed earliest in a 46-year period of beaver population expansion. '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 that can potentially be affected by beaver' (Johnston and Naiman, 1990).

It is scarcely surprising that beaver dam construction can have far-reaching environmental impacts. Indeed, Hammerson (1994) reviews 21 environmental changes that occur when a section of stream is replaced by a beaver pond constructed by *C. canadensis*:

- Storage of precipitation, which is gradually released through dry periods, and reduced variability in discharge regime.
- Decreased current velocity.
- A several hundred-fold increase in the wetted surface area of the channel (in areas of gentle topography).
- Increased water depth.
- Elevation of the water table.
- In forested areas, an increase in the amount of open canopy.
- Loss of wildlife species that depend on living riparian deciduous trees.
- Enhancement or degradation of conditions for fishes.
- Creation of conditions favourable to wildlife that depend upon ponds, pond edges, dead trees or other habitats not present or in limited supply in stream systems not modified by beaver.
- Replacement of running-water invertebrate taxa by pond taxa, and an increase in the absolute importance of collectors and predators and a decrease in the relative importance of shredders and scrapers in impounded sites.
- A several-fold increase in the mass of insects emerging from the water surface per metre of stream length.
- Increased plankton productivity.
- Increased trapping of sediment and a decrease in turbidity downstream.
- More favourable conditions for the growth of plants such as willow and alder.
- A great increase in the amount of organic carbon, nitrogen (and its availability) and other nutrients in the channel; an increase in carbon turnover time; and an increase in nitrogen fixation by sediment microbes.
- Amelioration of stream acidity.
- An increase in aerobic respiration, the amount in a pond being 16 times that in a riffle.
- In low-order streams a substantial shift to anaerobic biogeochemical cycles in sediments beneath the aerobic pond sediments.
- An increase in the amount of organic matter suitable for methane-producing microorganisms and increased carbon output by methanogenesis.
- Reduced oxygen levels in the water in spring and early summer due to decomposition of the augmented organic matter.
- Increased resistance of the ecosystem to perturbation.

This article focuses on the physical environmental effects of dam construction on fluvial systems. These effects are considered below in relation to surface water storage and river flow regime, bank hydrology and riparian water-table dynamics, sedimentation and fluvial geomorphology.

## 1 Surface water storage and flow regime

The amount of water stored within a beaver pond is a function of the dam dimensions and the local valley geomorphology, particularly down-valley slope and cross-valley profile (Johnston and Naiman, 1987). As a result, beaver dams located on streams in constricted, steep, upland valleys pond back less water, are more restricted in area and vary little in their spatial extent with changing water levels. Furthermore, the topography of upland river corridors does not favour the construction of beaver canals. In contrast, the wider, lower-gradient valleys favoured by beaver for dam construction support spatially extensive, complex pond and canal systems. The volume of water stored is also a function of the degree to which the beaver dam is watertight. Devito and Dillon (1993) monitored water levels and outflows from a 3.8 ha beaver pond in central Ontario. Their data illustrate how the pond controlled downstream discharge as a result of overtopping of the dam when the pond was full, and as a result of some limited seepage through or under the dam when water levels fell below the dam crest. However, once the water dropped more than 5 cm below the dam crest, the downstream river flows became very small, indicating how watertight the dam was. Thus, hydrologically, a well constructed beaver dam acts like a low weir, causing water storage which impacts on both high and low flows in the river system. Although the effect of a single beaver pond on river flows will be small, a sequence of ponds may have a significant effect. Ehrman and Lamberti (1992) found that reaches of 3rd-order streams with woody debris dams retained water 1.5–1.7 time longer than those with minimal woody debris. The impact of a sequence of well constructed beaver dams on water retention within a river reach will be much greater. Effects on the transmission of river flows will include an increase in the time of rise of the flood hydrograph and a decrease in the magnitude of the flood peak discharge, whereas gradual seepage from the ponds during dry periods may sustain low river flows, seepage to the riparian zone, and areas of water storage within the channel network far longer during dry periods than would occur in river channels without beaver dams. The extent of such impacts upon both high and low flows depends upon the storage capacity of the ponds and the degree to which the dams are watertight. Storage capacity is greatly affected by local topography and whether the dam is entirely in-channel or extends across the floodplain. As dams are constructed, maintained or fall into decay, their effect on the river flow regime will vary greatly.

## 2 Bank hydrology and riparian water-table dynamics

Water levels in beaver ponds reflect the balance between the volume of water entering (river flow, precipitation, groundwater seepage), flowing out of the pond (river flow, groundwater seepage) and evaporating from the pond surface. Thus, the water level varies seasonally and during flood events (Naiman *et al.*, 1994). Variability in the relative levels of water upstream and downstream of beaver dams and within the adjacent riparian zone can give rise to complex surface water–groundwater interactions. For example, White (1990) described longitudinal (i.e., downstream) convective flow patterns beneath beaver dams, whereas Lowry (1993) noted a correlation between seasonal and flow-event controlled water levels in a beaver pond in central Oregon and the lateral riparian groundwater levels. Larger fluctuations occurred in groundwater levels in the riparian zone surrounding the pond than in those adjacent to an unponded section of

river. In addition, local hydraulic gradients suggested enhanced recharge of the riparian aquifer adjacent to the pond in comparison with the unponded reach.

### 3 Sedimentation

In-channel sediment storage provides a buffer between episodic inputs of sediment to the river system and their regulated transmission downstream. The ability of a river channel to store sediment depends on its overall dimensions and slope, and on the presence of features such as bends and obstructions, including beaver dams. Although the role of beaver ponds in trapping sediment has been recognized in North America, there is little information on the volumes of sediment and their rates of accumulation (Butler and Malanson, 1995).

Sediment deposited in beaver ponds can be both mineral and organic in nature. At the point where the river system enters the pond, deposits of mainly mineral sediment may settle out of the flow, but within the major body of the pond, sediments are a mixture of mineral and organic material derived from the inflowing stream, bank failure, excavations of canals and burrows, input of organic matter from riparian vegetation, import of organic matter by beaver and primary production within the pond. The material accumulates on the bed and rates of sedimentation can be very high. For example, Butler and Malanson (1995) estimated rates of sedimentation ranging from 2.1 to 27.9 cm.yr<sup>-1</sup> for eight locations on four beaver ponds in Glacier National Park, Montana. A major study of sedimentation in beaver ponds by Naiman *et al.* (1986) estimated retention of  $3.2 \times 10^6$  m<sup>3</sup> sediment within beaver ponds on 2nd to 4th-order streams in their Quebec study area. If sediment were evenly distributed over the total area of stream bed it would reach a depth of 42 cm. This gradual infilling of beaver ponds ultimately results in the development of beaver meadows, which are organically rich, gently sloping, alluvial plains (Ruedemann and Schoonmaker, 1938).

The trapping of sediment in beaver ponds has resulted in the deliberate introduction of beaver to inhibit sediment transfer, stabilize stream banks and restore riparian habitat in some areas of North America (e.g., Ruedemann and Schoonmaker, 1938; Farrar, 1971; Apple, 1982; Brayton, 1984; Johnson, 1984; Bergstrom, 1985). Furthermore, recent erosional downcutting in low-order streams in North America has been attributed to the removal of beaver (Parker *et al.*, 1985). However, Butler and Malanson (1995) note that the provenance of the sediment is unclear. In particular, it is important to separate accumulation of fluvially transported sediment from that introduced into the ponds by beaver activity such as the excavation of canals and burrows. Such a separation would allow the accumulation rates of fluvially transported sediment to be estimated, so that the role of beaver dam-building activity in attenuating the transfer of sediment within drainage basins could be quantified.

The fate of the organic component of the accumulated sediment also has important and long-term environmental consequences. Naiman *et al.* (1994) combine observations from several study sites in Minnesota to evaluate the long-term biogeochemical characteristics of boreal forest drainage networks affected by beaver, so providing a useful summary of this aspect of the impact of beaver ponds. They show that

beaver influence the distribution, standing stocks, and availability of chemical elements by hydrologically-induced alteration of biogeochemical pathways and by shifting element storage from forest vegetation to sediments and soils . . . As the upland vegetation dies and decays after dam construction, only a portion of the chemical elements are exported downstream (except for calcium and magnesium) or returned to the atmosphere

(C and N only). Consequently the organic horizons of pond sediments accumulate substantial standing stocks of chemical elements that are available for vegetative growth when dams fail, the ponds drain, and meadows are formed ... These influences are spatially extensive and long-lasting, affecting fundamental environmental characteristics of boreal forest drainage networks for decades to centuries (Naiman *et al.*, 1994: 912).

#### 4 Fluvial geomorphology

The geomorphological consequences of beaver dams have not been widely considered in the literature, but inferences can be made by combining the above summary of impacts on individual fluvial processes with observations of the geomorphological effects of accumulations of large woody debris. Thus, both sources of information are combined here to assess the geomorphological impact of beaver dam construction in relation to channel morphology, channel stability and drainage network development.

The discharge regime, sediment load and structural elements within the channel determine the shape of the river channel. Beaver dams represent very important structural elements within the channel. The construction of beaver dams impedes flow in river channels producing steps in the river's long profile. This impact on the river's long profile has hydrological consequences, through the ponding and diversion of water, which affect riverbank hydrology, flood peak attenuation for flood events up to and slightly above bankfull, and hydraulic consequences through complex changes in the downstream pattern of energy dissipation. Large obstructions such as beaver dams partly or completely block the flow, creating areas of high or low flow velocity and thus shear stress on the channel bed and banks, and so regulating the scour and deposition of sediment. The exact configuration of the resulting channel morphology and the interaction with moving bedload depend on the shape and size of the roughness element and its position and configuration within the stream channel (Lisle, 1981). The presence of beaver dams is likely to produce the increased diversity in channel width and depth (Keller and Tally, 1979; Hogan, 1986), in-channel morphological features (Keller and Swanson, 1979) and patchiness of bed sediment of differing calibre (Sullivan *et al.*, 1987) that have been identified as characteristics of streams containing accumulations of woody debris. Contrasts in the downstream morphological effects of both beaver dams and woody debris accumulations are related to the leakiness of the structures and the degree to which over-, through- or underflows occur in high-velocity localized threads. The patchier the flow and the greater the fall of the water, the greater the sediment sorting and morphological diversity that may result. Where the beaver dams extend out across the floodplain, their downstream consequences are likely to be more varied. For example, diffuse seepage through the floodplain part of the dam may lead to the development of areas of floodplain wetland, whereas concentrated flow may result in the excavation of additional stream channels.

Woody debris accumulations have been shown to play a major role in controlling the stability of low-order streams. This role is particularly well illustrated by observations of the consequences of woody debris removal. Bilby (1984) observed large changes in channel structure in the first storm after debris clearance from a small western Washington stream. Channel cross-sections were substantially altered by the removal of stored sediment and the number, volume and area of pools decreased. Similar results are presented by Smith *et al.* (1993), who observed a four-fold increase in bedload transport at bankfull discharge in a second-order gravel-bed stream during the first six months after experimental debris removal. Given their similar sediment-storing role, beaver dams can be expected to have a similar effect in enhancing the stability of streams.

Dam building by beaver can also impact on the drainage network in a complex manner, particularly in locations where floodplains are wide and channel gradients are low. For example, Woo and Waddington (1990: 226) describe drainage patterns on subdued topography in subarctic northern Ontario:

In most cases water spilled from the beaver pond returns to the channel at a short distance below the dam. In other situations, new flow diversion channels may be created that act as spillways when the ponds are full ... Then water may not get back to the original channel until it has travelled tens or hundreds of metres downstream. When these diversion channels are reoccupied over a period of time, they may be sufficiently downcut to become permanent routes along which water will flow.

Townsend (1953) mapped beaver dams and channel networks associated with rivers 3–15 m wide with floodplains 1–2 km wide in Montana. Here dam building had caused extensive changes to the drainage network, with river channels subdividing into several distributaries at dam and pond locations where the water level had been raised sufficiently for flow diversions to occur across the relatively flat landscape.

In summary, the impact of dam construction on sediment storage and flow diversion in areas of low relief will have implications for channel planform and dynamics. The sedimentation effects of beaver dams reduce any tendency towards the development of a braided channel consisting of mobile bars of sediment separating active threads of the river flow, although it must be stressed that the establishment of dams in an active braided environment is extremely unlikely. Nevertheless, the flow diversion effects of beaver dams can encourage the establishment of more stable multithread channel systems. At a local level, a series of interconnected, ephemerally, intermittently and perennially occupied channels may be created to accommodate flood flows, seasonally higher flows and baseflows. Over larger areas of very low relief, the presence of beaver dams may encourage the development of an anastomosing channel pattern with stable vegetated land occupying the areas between the multiple river channels.

Beaver dam failure may also have significant geomorphological consequences. There is little information in the literature on this topic, and that which exists relates entirely to the failure of large dams constructed by *C. canadensis* in North America. When high flows and water levels seriously threaten to damage beaver dams, the beaver often open a small channel on the dam crest to lower the water level (Butler, 1995). Even so, beaver dams can fail catastrophically with severe consequences when large volumes of water are impounded. Butler (1995) suggests that excessive, high-intensity precipitation, rapid snowmelt, animal burrowing through the dam (and presumably anthropogenic interference), and collapse of upstream dams may cause catastrophic dam failure. 'Catastrophic' failure can only occur if the dammed water volumes are large enough and, given the typical dimensions of dams, such large volumes will be relatively rare and will occur on low-gradient streams. Butler (1995) describes a number of catastrophic failures of beaver dams resulting in, for example, transport of clasts > 1 m in diameter, incision of 0.5–0.6 m of a channel bed, and severe sediment deposition downstream. However, the very limited literature on this subject suggests that such failures are rare.

## **VI Beaver impact along the river continuum**

The far-reaching impact of beaver on river systems caused Naiman *et al.* (1986) to consider their influence on the River Continuum Concept (RCC: Vannote *et al.*, 1980). The

RCC views river systems as longitudinally interconnected channels where hydrological, geomorphological and biological processes operate along a continuum. The concept does not fully allow for interruptions to the continuum such as ponds and lakes (major water bodies were subsequently addressed by the Serial Discontinuity Concept: Ward and Stanford, 1983) or for major lateral interactions, although this was considered by Sedell *et al.* (1989) for large rivers. Interruptions and lateral interactions characterize the impact of beaver, particularly on small streams, where they are most likely to construct dams. Naiman *et al.* (1986: 1267) specifically suggest that, where beaver are present, 'the implied characterisation of small streams (approximate orders 1–3) by the RCC needs to be redefined to include numerous zones of open canopy, large accumulations of fine detritus, increased wetland area, increased biogeochemical interactions with riparian plants and soils, reduced allochthonous inputs per unit area, and concomitant adjustments in the functional attributes of the invertebrate community'. The view of Sedell *et al.* (1989: 53) that 'the large river system is a sequence of patches of varying lengths and widths, and not a simple continuum' seems also to apply to small streams subject to extensive beaver activity.

The fairly restrictive environmental requirements for dam construction suggest that significant lengths of channel will remain free of dams, even in headwater streams where the channel is sufficiently narrow for damming. Furthermore, in zones of dam construction, there will be patches which are unaffected by the backwaters from the dams. Dams regulate the range of river flows so reducing the range in discharge and flow velocities between dams in comparison with the predam situation. They also cause much of the river's energy to be dissipated at the dam locations rather than gradually along the stream's long profile. Both these effects are likely to increase the stability of river channels between dams and beaver ponds. More significantly, sediment movement is heavily regulated by the presence of beaver ponds, resulting in a reduced sediment supply to intervening sections of river channel, with all size ranges of sediment (including fine suspended sediment) being trapped by large ponds. The result of sediment retention is the potential for local erosion of the channel between sections affected by dams and for the enhanced transport and sorting of sediments in river stretches that are free of dams and are downstream of dam locations.

Further downstream, where the main river systems are too wide for damming, beaver occupy sloughs, backswamps, backwaters, lakes and minor channels on the floodplain (Naiman *et al.*, 1988; Butler, 1995; Townsend and Butler, 1996). In these locations, they construct dams and canals from which they cut wood and open up the floodplain forest. Wood cut by beaver or delivered by other means to the channel in upstream reaches can accumulate in the main channel even where it is too wide for dam construction. In large single-thread channels, wood may accumulate as marginal ribbons of debris at the edge of the active channel or in the riparian vegetation. In braided systems, it may be deposited within the active channel forming a focus for enhanced sedimentation and possibly bar development (Piégay and Gurnell, 1997).

## VII Conclusions

In assessing the potential hydrogeomorphological influence of beaver dam construction, four groups of issues are important: 1) limitations in the information that can be derived from the literature; 2) the suitability of the habitat for colonization by beaver; 3) the

potential of the habitat to encourage dam construction; and 4) the likely hydrogeomorphological impact of dam construction under the range of environmental conditions within which construction may occur.

## 1 Limitations in the available information

This review has revealed a number of limitations in the information available within the literature for estimating the likely hydrogeomorphological impact of colonization and dam building by *C. fiber*:

- Most of the literature describes aspects of the environmental impact of *C. canadensis* rather than *C. fiber*. While there are likely to be major similarities in the impact of the two species, their impact cannot be assumed to be identical.
- Most of the literature has been written from a biological perspective, so that many of the important hydrogeomorphological characteristics of beaver activity are not described in detail. Important factors that govern the hydrological and geomorphological influences of beaver dams that are not well covered in the literature include the following:
  - Beaver do not always build dams, but when they do are the dams grouped in particular areas and what is their size distribution? How does their character and distribution change with changing population density? What are the specific associations between physical environmental characteristics such as channel dimensions, gradient, flow regime and velocity, bank and bed materials and the presence/absence, dimensions and permanence of dams? In particular, what are the dimensions and gradients of the river channels that are dammed, rather than simply the dimensions of the dams?
  - What is the typical spacing of dams, including the degree to which dams are evenly spaced or clustered and the degree to which that relates to dam and river dimensions?
  - What are the characteristics of the way that water drains from dams? Is it predominantly by diffuse seepage, dispersed overtopping or is it funnelled into high-velocity threads?
  - What is the length of channel unaffected by ponding between dams or dam clusters? To what extent is the minimum 60–80% channel length free of backwater cited by Naiman *et al.* (1986) for unexploited *C. canadensis* transferable to *C. fiber*?

## 2 Habitat suitability for colonization

This review has illustrated the extensive literature on the topic of habitat suitability and, in the absence of significant anthropogenic interference, the very wide range of physical conditions under which beaver colonies exist. The only relatively restrictive physical requirements seem to be a preference for finer riverbank materials on relatively low-gradient streams (indicated either explicitly, or through the requirement for medium to low flow velocities). This reflects the ability of beaver to modify the habitat to suit their requirements through dam, burrow and lodge construction. For example, wide fluctuations in water level can be regulated, although extremely low flows (e.g., intermittent streams) and widely and rapidly fluctuating flow levels (e.g., >1.5 m) can cause difficulties for beaver. In contrast to the wide range of physical conditions under which

beaver colonies may exist, the riparian vegetation cover is extremely important and requirements are quite restrictive. Hardwoods and a good herb layer are minimum requirements, and the presence of willow and aspen is ideal.

### 3 The potential of the habitat to encourage dam construction

A number of inferences can be drawn from the restricted literature, which are outlined below in relation to different characteristics of the fluvial system.

*a Stream order:* Dam building occurs mainly on streams of 1st to 4th order. Such streams typically have widths up to 10–15 m. Since these are also the orders of streams in which woody debris accumulations frequently dam streams, the range in stream order presumably reflects the capability of well constructed woody structures to dam river systems. Furthermore, the flow regime in lower-order streams is often less reliable than in larger rivers. Dams can maintain water levels during summer low flows and can reduce the seasonal and storm event range in water levels by attenuating discharges through a sequence of ponded water stores, and by spreading the flows across a dam crest that is wider than the original river channel.

*b Stream gradient:* Although low-order, narrower stream channels permit dam building, steep headwater streams present a number of difficulties. An increase in slope increases the power of the stream and so increases the likelihood that high flows will precipitate dam failure. Steep-gradient channels provide a reduction in the potential ponded area resulting from dam building. Since beaver dams are typically <1.5 m high, increasing gradient can rapidly reduce the pond area to a level where it provides insufficient protection for the animals and insufficient extension of the potential foraging area for the beaver colony. As a result construction on gradients that are greater than 4% is very unlikely.

*c Substrate, sediment transport and channel dynamics:* Although beaver have been observed to construct dams on a wide range of calibres of substrate, bedrock streams are not favoured, presumably because of the poor anchorage for the dam structure. Furthermore, dams and their associated ponds are unlikely to survive for long where there is high sediment transport and where the channel banks are highly mobile. Lower bedload transport and channel mobility are most likely to be features of low-gradient (i.e., low-power) streams, with a relatively stable flow regime. Such conditions will also lend themselves to the deposition of fine alluvial bank materials that are suitable for burrow construction. From these requirements, beaver are unlikely to attempt to dam braided rivers and steep rock-bed channels, and are most likely to dam single-thread, low-bedload, wandering channels.

Within a suitable stream system, beaver select the optimum sites for dam construction first. Thus zones of locally low-gradient channel with a wide river corridor of subdued topography and suitable bank materials will be selected, resulting in the largest area of water inundation and access to foraging sites in response to the minimum building effort by the beaver colony.

#### 4 The likely hydrogeomorphological impact of dam construction

The effects of dam construction within a catchment are as follows:

- Introduction of a stepped long profile to the stream channel, where stream energy is mainly dissipated at the locations of the beaver dams which form the major steps in the system. The ponds above the dams will act to sustain low flows and to attenuate flood peaks.
- An increased complexity in the hydrology of the riparian zone with alternating patches of high and low water table, spatially varying soil-water regimes, and complex stream-riparian aquifer flow paths.
- Increased sediment storage within the channel system, decreased and attenuated sediment yield from the catchment.
- Sorting of bed sediments, where a variety of particle sizes is present. Sorting will occur within the beaver ponds, where coarser sediments will be deposited in the pond heads and finer sediments within the main pond body. Sorting may also occur downstream of the dams within dam-free channel sections where sediment supply is limited by upstream storage within beaver ponds.
- Storage, decomposition and processing of organic matter closer to its source area within the beaver ponds.
- Development of a more complex local channel network to accommodate high flows and the potential in extensive areas of low relief for an anastomosing type of river planform to develop.
- As a result of all the above, an overall increase in both lotic and riparian habitat diversity and an increase in channel stability.

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