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Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona

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ABSTRACT

Beaver convert lotic stream habitat to lentic through dam construction, and the process is reversed when a flood or other event causes dam failure. We investigated both processes on a regulated Sonoran Desert stream, using the criterion that average current velocity is $<0{\cdot}2$ m s^{-1} in a lentic reach. We estimated temporal change in the lotic : lentic stream length ratio by relating beaver pond length (determined by the upstream lentic–lotic boundary position) to dam size, and coupling that to the dam-size frequency distribution and repeated censuses of dams along the 58-km river. The ratio fell from 19 : 1 when no beaver dams were present to <3 : 1 after 7 years of flows favourable for beaver. We investigated the dam failure–flood intensity relationship in three independent trials (experimental floods) featuring peak discharge ranging from 37 to 65 m^3 s^{-1}. Major damage (breach $\geq$3-m wide) occurred at $\geq$20% of monitored dams ($n = 7$–86) and a similar or higher proportion was moderately damaged. We detected neither a relationship between dam size and damage level nor a flood discharge threshold for initiating major damage. Dam constituent materials appeared to control the probability of major damage at low (attenuated) flood magnitude. We conclude that environmental flows prescribed to sustain desert riparian forest will also reduce beaver-created lentic habitat in a non-linear manner determined by both beaver dam and flood attributes. Consideration of both desirable and undesirable consequences of ecological engineering by beaver is important when optimizing environmental flows to meet ecological and socioeconomic goals. Published in 2010 by John Wiley & Sons, Ltd.

KEY WORDS beaver dam; *Castor canadensis*; ecohydrology; habitat conversion; lotic-lentic ratio; managed flood; riverine ecosystem; Sonoran Desert

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INTRODUCTION

Beaver (*Castor canadensis* Kuhl) are semi-aquatic, herbivorous rodents whose dam-building activities can profoundly affect the hydrology, geomorphology, chemistry, and ecology of small streams and rivers (Warren, 1927; Naiman *et al*., 1988; Gurnell 1998; Rosell *et al*., 2005). For example, beaver dams raise local surface water and ground water levels, affecting riparian vegetation (Cunningham *et al*., 2006), and the dams change lotic stream habitat to lentic habitat within the impoundment, affecting aquatic invertebrate assemblages (McDowell and Naiman, 1986). The impoundment, or beaver pond, alters the rate at which water, solutes, and sediment move downstream, thereby affecting stream water quality, including temperature and suspended sediment and particulate organic matter concentrations (White, 1990; Gurnell, 1998; Rosell *et al*., 2005). In addition to hydrologic and fluvial geomorphic effects from dams (Hood and Bayley, 2008; Persico and Meyer, 2009), beaver physically alter habitats by cutting down trees, building lodges, dredging pond material, creating woody debris, and excavating canals and bank dens (Meentemeyer *et al*., 1998). These activities can dramatically alter the structure of a riverine landscape (Martell *et al*., 2006).

Dam construction is an innate behaviour whose adaptive significance is hypothesized to derive from the pond, which improves beaver access to food and provides food storage and shelter opportunities while simultaneously reducing predation risk. The processes associated with dam construction, maintenance, and demise—particularly with their decay and natural destruction—are not well understood. Beaver dams, which are accumulations of intermixed woody and herbaceous materials, cobbles, and fine sediment (Baker and Hill, 2003), are susceptible to damage or destruction during floods. Beaver may repair or abandon a damaged dam, and a functional dam may be abandoned, e.g. if resident beaver die or emigrate.

Beaver were historically resident in the North American warm deserts at least along the Colorado River (Grinnell, 1914; Hall, 1946; Hoffmeister, 1986) and the Rio Grande (Bailey, 1905; Findley *et al*., 1975). The size of these rivers precluded dam-building, and beaver relied on bank dens. Historic beaver abundance along the smaller desert streams where dams could have been constructed is unclear. Anecdotal accounts suggest beaver were common in the American Southwest in the

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early 1800s (Weber, 1971), but permanent populations may have been concentrated in high-elevation, relatively mesic headwater areas. Beaver may have been absent from most reaches of small to moderate-sized desert streams because these streams were susceptible to loss of surface flow during dry seasons or years, and they were subject to large floods, which occurred in many cases often enough to prevent the formation of extensive stands of woody riparian vegetation (Davies *et al.*, 1994). Even if surface flow was present, a lack of food and dam-building materials on these reaches may have made them unattractive to beaver, at least in the years immediately following a destructive flood.

Water resources development has had mixed effects on North American desert beaver. For example, some beaver populations that persisted through the fur-trapping era were eradicated during the 1800s as part of efforts to drain marshes and control malaria (Hastings, 2002). Elsewhere, streamflow diversions and ground water pumping have dried up reaches (Stromberg *et al.*, 2007) that beaver may have occupied. On the other hand, the dams and storage reservoirs now common on desert streams (Graf *et al.*, 2002) have commonly eliminated large floods, and increased low flows (Poff *et al.*, 2007), improving stream suitability for both beaver and the woody riparian vegetation they and other species depend on (Shafroth *et al.*, 2002). Similarly, addition of municipal wastewater effluent can change ephemeral or intermittent base flows to perennial, and thereby create conditions favourable for beaver (Taylor *et al.*, 2008).

The desert riverine ecosystems suitable for beaver, especially riparian woodlands and forests, are key contributors to regional biodiversity (Fleischner, 1994; Brand *et al.*, 2008). These ecosystems provide lotic and lentic habitats for aquatic organisms (Jackson and Fisher, 1986; Lytle and White, 2007) and the water, food, shelter and other resources required by a large array of riparian-dependent species, including neotropical migratory birds (e.g. Johnson *et al.*, 2008). Many riverine woodland habitats in the desert southwest have been lost or degraded as a result of land use changes, water resources development, and expansion of non-native species (Graf *et al.*, 2002; but see also Webb and Leake 2006; Webb *et al.*, 2007). Efforts are now underway to restore or rehabilitate degraded riparian forests to sustain or enhance populations of riparian dependent desert wildlife. These efforts include using controlled reservoir releases to create both the floods necessary for riparian forest recruitment and the base flows necessary to sustain tree vigour (Rood *et al.*, 2005; Shafroth *et al.*, 2010).

In this article, we report the results of a study designed to improve our understanding of how beaver and their dams affect desert riverine ecosystems and how controlled floods can be used to enhance, sustain, or disrupt those effects. First, we document the rate at which beaver converted lotic habitat to lentic on a regulated desert stream during a 7-year period of stable base flows. We then describe the effects of three controlled floods on beaver dam integrity and the hydrologic conditions that the beaver had created. The latter data allow us to test the hypothesis that controlled floods intended to drive the fluvial geomorphic and hydrologic processes necessary for native tree recruitment will simultaneously destroy beaver dams.

STUDY AREA

We worked along the ~58-km-long Bill Williams River (BWR) downstream of Alamo Dam in west-central Arizona (Figure 1). The river descends from an elevation of ~300 m above sea level (ASL) at the dam base to ~136 m at its mouth at Lake Havasu, a reservoir on the Colorado River. The BWR passes through a series of five relatively wide alluvial reaches separated by more confined canyon reaches. The longitudinal profile of the BWR is relatively flat, even in canyon reaches. The maximum stream gradient, based on analysis of USGS 7·5-min topographic maps, is about 1%, whereas the mean is about 0·3% (House *et al.*, 2006).

All of the BWR lies within the Mojave and Sonoran deserts (Benson and Darrow, 1981). Annual precipitation at Parker, AZ, near the river's mouth, is 12·2 cm, with monthly maxima in January and August (National Weather Service Station 026 250; 1893–2005 data). Annual potential evapotranspiration is ~1·8 m (Baker and Ffolliott, 2000). Although winter air temperatures can dip below freezing for short periods (generally $<$24 h), ice cover never develops on lentic or lotic reaches.

Prior to the construction of Alamo Dam, a flood-control structure completed in 1968, the BWR was a small stream with spatial and temporal variation in the distribution of perennial and dry channel conditions at base flow [discharge (Q) mean = ~2·6 m^3 s^{-1}; House *et al.*, 2006]. Large floods ($Q_{\mathrm{MAX}} \geq 1700$ m^3 s^{-1}) were somewhat common (10-year recurrence interval; House *et al.*, 2006). Since completion of the dam, managed releases constitute essentially all base flows and most flood flows along the entire length of the BWR. Disconnection from the subbasins drained by the Big Sandy and Santa Maria rivers (11 200 km^2, ~83% of the total BWR catchment) has greatly reduced both the frequency and magnitude of natural (uncontrolled) floods (House *et al.*, 2006). No perennial streams enter the BWR, but sporadic flash floods in contributing washes can produce relatively large, ecologically important flows in the river's middle and lower segments. Releases from Alamo Dam are controlled via outlet works with a maximum capacity of 247 m^3 s^{-1} (US Army Corps of Engineers, 2003). Base flows in the BWR, which vary in magnitude spatially and seasonally, are determined by the normally continuous release of 0·3–1·4 m^3 s^{-1} from Alamo Dam, depending on lake elevation and season. Periods of zero release are very rare and typically of short duration (US Army Corps of Engineers, 2003).

Riparian vegetation along the BWR is dominated by several woody species common to low-elevation south-western riparian ecosystems, including *Populus fremontii*

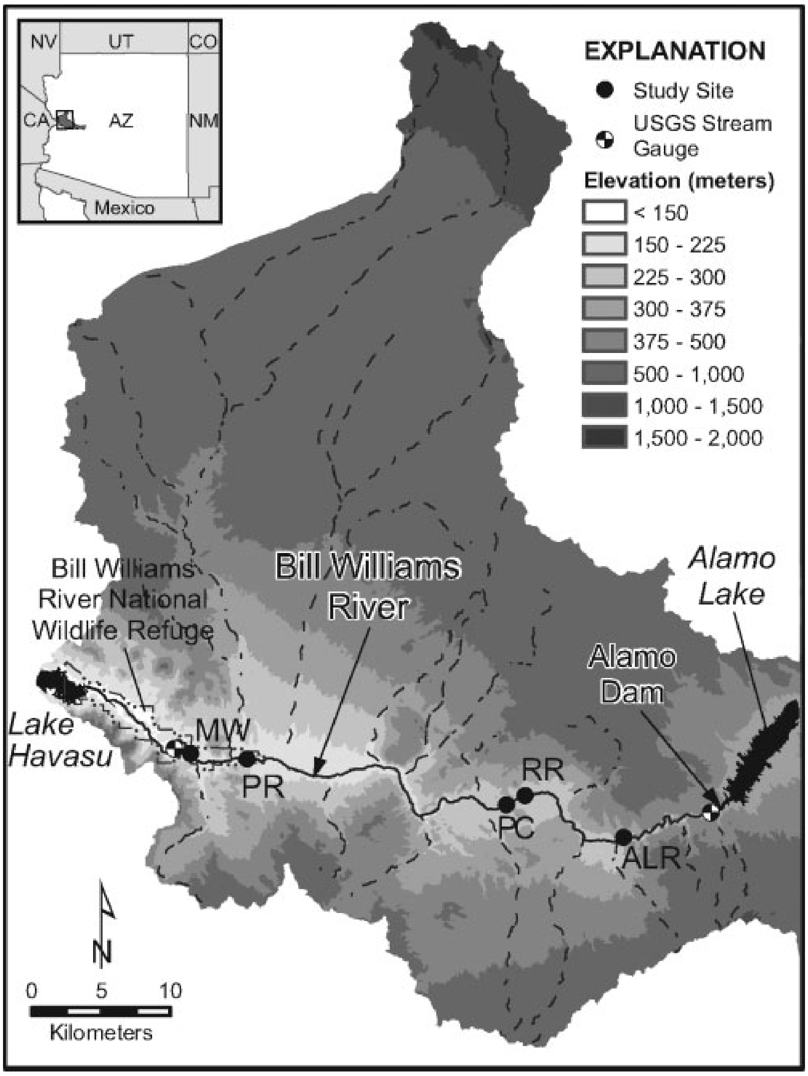

Figure 1. Map of the Bill Williams River (BWR) and its contributing basin below Alamo Dam showing the five reaches where flood effects on beaver dams were monitored from the ground [filled circles: Above Lincoln Ranch (ALR), Rankin Ranch (RR), Pipeline Crossing (PC), Planet Ranch (PR), and Mineral Wash (MW)] and the up- and downstream USGS stream gauges (quartered circles). Tributary wash drainage patterns (dashed lines) have been simplified for clarity. Digital elevation data are from the ASTER GDEM, Courtesy of NASA.

S. Watson (Fremont cottonwood), *Salix gooddingii* Ball (Goodding willow), *Tamarix* spp. [*T. ramosissima, T. chinensis*, and their hybrids (saltcedar; taxonomy follows Gaskin and Kazmer, 2009)], *Baccharis salicifolia* (R. & P.) Pers. (seep willow), and *Prosopis* spp. (mesquite). Woody vegetation abundance, which has increased since Alamo Dam began operating, varies as a result of water availability, with perennial reaches supporting the most abundant vegetation (Shafroth *et al*., 2002). Herbaceous vegetation tends to be sparse, except adjacent to perennial channels where water and light availability are high (Shafroth, personal communication). In addition to providing flood control and reservoir recreational opportunities, Alamo Dam is managed to sustain biodiversity of native riparian species in the BWR corridor (US Army Corps of Engineers, 2003; Shafroth and Beauchamp, 2006).

We worked at five study sites, which we identify based on location in or proximity to one or another of the wide alluvial reaches. From up to downstream, the study sites were designated Above Lincoln Ranch (ALR), Rankin Ranch (RR), Pipeline Crossing (PC), Planet Ranch (PR), and Mineral Wash (MW) (Figure 1). All study sites were on public lands.

METHODS

Hydrology

We used records of real-time instantaneous discharge and mean daily discharge for USGS gauges BWR below Alamo Dam, AZ (# 9426000) and BWR near Parker, AZ (# 09426620) to assess flows during the 1995–2008-study period. The gauge near Parker is located close to the river's mouth and provides information on inflows originating from locations other than Alamo Dam and on the downstream attenuation of flow releases from Alamo Dam. These two gauges are hereafter referred to as the 'upstream' and 'downstream' gauge, respectively. The upstream gauge well-represents discharge levels for the

ALR, RR, and PC sites, whereas flows at PR and MW are better represented by the downstream gauge. In 2008, we installed hand-read staff gauges at PC and PR to monitor local river stage dynamics.

To characterize stream hydrology at base flow, in 2008 we measured stream or pond depth (D) and current velocity (V) using a Pygmy Flow meter (range $0{\cdot}03-1{\cdot}5$ m s^{-1}) at three points along each of 32 channel cross-sections at PC and 11 at PR. Most cross-sections were systematically placed at positions ranging from downstream to upstream in a manner to pass through one or another of six beaver ponds. We recorded both cross-section and dam midpoint locations using a GPS unit, allowing us to determine the distance (K) between the cross-section and the nearest downstream dam. We measured D and V typically ~1 m from each bank and at or near mid-channel, with one of the three measurements at the thalweg. If thick emergent vegetation was present at a bank, the measurement was taken ~1 m from the stand edge. If there was no measurable velocity near the bank, the measurement was taken at the first location where velocity could be recorded. Velocity was measured over a 40-s period at a depth equal to 60% of the stream depth. We calculated mean current velocity (V_{AVE}) for each cross-section from the three measurements and then used least-squares regression to generate the best fit linear or exponential model relating K to V_{AVE} for each of the six ponds. We reasoned that the true relationship between V_{AVE} and K should be asymptotic and perhaps sigmoidal in form, but seatterplots indicated that, with possibly one exception, our data were limited to the linear or accelerating portion of the curve, thus justifying use of the exponential function. We used SigmaPlot® 2000 (version 6·00) to fit a function of the form $y = a + be^{(cx)}$, where a, b, and c are the fitted parameters.

Each pond-specific model was then used to calculate the distance (K_T) from the dam to the upstream point at which the rising mean current velocity reached $V_{AVE} = V_T = 0{\cdot}2$ m s^{-1}, our threshold velocity differentiating lentic from lotic stream reaches. Thus, by definition, the length of each beaver pond (i.e. the distance it extended upstream) was K_T. At distances above a dam greater than K_T, we assumed $V_{AVE} \geq 0{\cdot}2$ m s^{-1} and lotic habitat prevailed until another beaver pond was encountered. Our choice of $V_T = 0{\cdot}2$ m s^{-1} is based on the fact that sand particles have a critical erosion velocity (the lowest velocity at which a particle resting on the streambed will move) of ~$0{\cdot}2$ m s^{-1} (Allan, 1995). Other workers have used a lower velocity criterion to distinguish lentic and lotic habitat, e.g. $0{\cdot}1$ m s^{-1} (Pellet *et al.*, 1983). Our $0{\cdot}2$ ms^{-1} threshold velocity leads to non-conservative, but nevertheless ecologically reasonable values of beaver pond longitudinal extent.

Beaver dam abundance

We counted beaver dams along the BWR on four occasions between 2002 and 2008 using sets of aerial photographs or low-level aerial videography combined with direct observation (Table I). The entire river was censused in 2002, 2005, and 2008, whereas only selected reaches were examined in 2006. Discharge was low on dates when aerial imagery was collected (Table I). Relatively large (>5-m bank-to-bank length) beaver dams in areas without canopy cover are readily apparent on the aerial photographs as straight or regularly curved edges perpendicular to flow direction. In some cases, we identified a dam with certainty because it was confirmed present in a ground observation. In all other cases, we assigned each identified dam to a category reflecting our level of confidence in its actually being a dam: very high, high, moderate, or poor. We used natural history information, our extensive personal observations of the river system, and our best judgment in cases where the presence of dam was ambiguous. We adopt a conservative approach here and include in our counts only dams identified with high or better confidence.

Table I. Mean daily discharge at the USGS gauge 'Bill Williams River below Alamo Dam, AZ' on the dates when aerial imagery was obtained or study sites were visited. The mean daily discharge for the 2 days prior to that date are also tabulated.

Date	Event	Discharge (m^3 s^{-1})		
		Two days earlier	One day earlier	On date
7 May 2002	Aerial photography (1 : 15 840 stereo colour-IR film)	1·13	1·13	1·13
5 September 2005	Aerial photography (1 : 15 218 stereo colour-IR film)	0·91	0·91	0·91
13 December 2005	Site visit	5·75	0·76	0·74
22 February 2006	Site visit	0·99	0·99	0·99
26 April 2006	Site visit	1·10	1·08	1·08
21 June 2006	Aerial photography (1 : 12 000 non-stereo natural colour film)	1·33	1·33	1·30
30 November 2006	Site visit	0·85	0·85	0·85
4–12 April 2007	Site visit	1·19	1·19	Variable[a]
7 March–3 April 2008	Site visit; low-level videography	1·02	1·02	Variable[b]

[a] Pulsed release initiated 10 April, 16 h at max = 28·32 m^3 s^{-1}, then reduced to 0·57 m^3 s^{-1} on 12 April (Figure 2).
[b] Videography on 7 March. Pulsed release initiated 31 March, 8 h at max = 64·85 m^3 s^{-1}. Repeat videography on 3 April.

Lentic habitat extent

Beaver ponds as seen on the BWR aerial photography tended to be linear and often only moderately wider than the wetted channel, which made delineation of their upstream extent problematic. To circumvent this problem, we estimated the total linear extent of lentic habitat present at a point in time indirectly by coupling an empirical pond length–dam size relationship we developed from field data (see below) with our dam census data and an estimate of the number of dams present in each of several size-attribute classes. We investigated the change in the lotic : lentic stream length ratio due to beaver by estimating the longitudinal extent of beaver ponds in May 2002, about 7 years after large flood flows presumably destroyed all dams and thereby eliminated beaver-created lentic habitat. We reassessed the extent of lentic habitat in March 2008, ~3 years after the end of a sequence of high flows that had again presumably destroyed all dams and 1 year after a sequence of 2 years that each featured a smaller flood.

Based on extensive personal observations in both canyon and alluvial reaches during periods of base flow, we assumed that without beaver only ~5% of the river's length consisted of pools qualifying as lentic habitat. We also assumed that each undamaged beaver dam was similarly 'leaky', and that all dams featured the same freeboard (height of dam crest above pond surface). Given these conditions and a uniform channel gradient, the upstream extent of any pond will be positively related to maximum dam height (i.e. height above the channel thalweg) and other attributes that increase as dam size increases. In March 2008, during base flow conditions, we measured four variables indexing dam size at each of 27 dams in the MW ($n = 4$), PR ($n = 8$), PC ($n = 8$), RR ($n = 5$), and ALR ($n = 2$) reaches, including the six dams for which K_T values were determined. These variables were bank-to-bank length along the dam crest (L), maximum water depth in the pond near the dam (D_{MAX}), dam breadth (B), and maximum water drop (W, elevation difference between pond surface at the dam and tailwater surface at the dam base). We used the data collected at the six dam/pond complexes where K_T was determined in a stepwise forward multiple linear regression analysis ($P = 0{\cdot}15$ for variable entry and removal) to develop an empirical model that allowed us to estimate K_T at other dams where only size data were collected.

We classified the 27 measured dams by size, using the metric(s) identified in the multiple regression analysis, and applied the resulting size–frequency relationship to the full count of dams on the BWR. A K_T value was determined for the midpoint of each size class, multiplied by the number of dams in that size class, and the resulting length value summed over size classes to determine the total length of lentic habitat present. We assumed that the 2002 dam size distribution matched that found in 2008 (see below), an approach we consider conservative because dams present in 2008 were likely to be younger and thus perhaps smaller than those present in 2002.

Effects of flood pulses on dams

We assessed the effect of flood pulses on beaver dams qualitatively by monitoring changes in the physical structure and functionality of dams produced by controlled releases from Alamo Dam. Three floods were evaluated, each preceded by a base flow-only period ≥11 months long. The releases took place in March 2006, April 2007, and March 2008 and featured a peak discharge (Q_{MAX}) of 57, 37, and 65 $m^3 s^{-1}$, respectively, measured at the upstream gauge. Prior to the first flood, dams were visited and characterized at PC and at ALR. Dam condition plus evidence of the presence of beaver suggested each dam was being maintained (hereafter, a functioning dam being maintained by beaver will be termed an 'active' dam). The sites were revisited ~30 days following reestablishment of baseflow at Alamo Dam, and again 5 months later (Figure 3). These two sites plus PR were visited a few days prior to initiation of the second flood event and again a day or two after flow at the upstream gauge had returned to base level. These three sites plus MW and RR were monitored immediately before and after the third flood. Beaver dams in each area were assigned consecutive letter identifiers, with the lower most dam assigned the letter A. Specific dams are denoted in the text by site and location within a site (e.g. Dam PC-A is at Site PC, Location A) and the associated beaver pond is denoted using the same code (e.g. Pond PC-A). The effect of the third (2008) flood pulse on dams outside the five primary study sites was assessed through visual observations made during low-elevation helicopter flights along the entire river conducted a few weeks prior to and immediately after the pulse and analysis of videography collected during the same flights.

We considered a dam to be functioning if it was intact (i.e. no breach was present), creating a pond, and if water depth was increased relative to the depth below the dam. Complete loss of functionality was defined as the absence of any break in the stream surface gradient at the dam site. We classified dam damage into three categories. A dam with a breach >3 m wide was considered to have suffered major damage. A breach smaller than 3 m was considered 'moderate damage', and any observable damage not producing a breach was considered 'minor damage'. We used stepwise forward multinomial logistic regression to search for a relationship between a dam's size and its damage category after the 2008 flood, using the set of 27 dams for which we had collected size data. All statistical analyses were conducted using SYSTAT® 11 unless noted otherwise.

RESULTS

Hydrology

A month-long flood release from Alamo Dam in early 1995 ($Q_{MAX} = 189$ $m^3 s^{-1}$, mean daily $Q = 84$ $m^3 s^{-1}$)

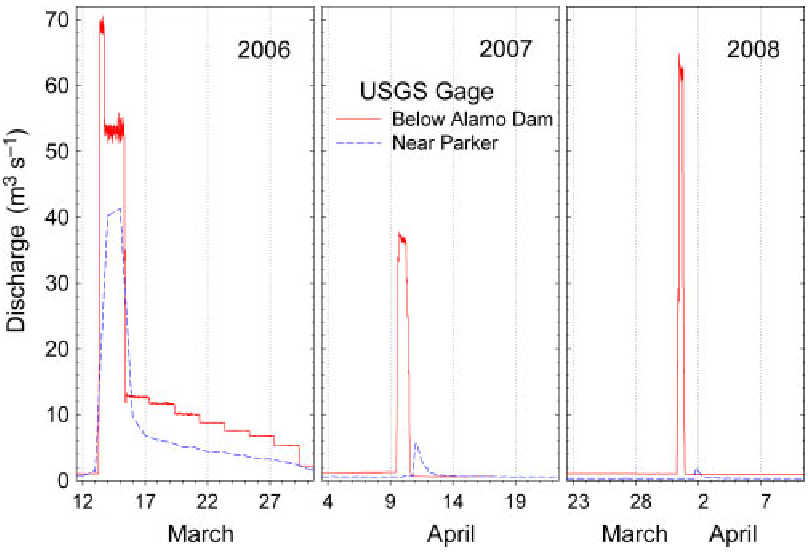

Figure 2. Temporal patterns of the 2006, 2007, and 2008 controlled flood pulses on the Bill Williams River as measured at the upstream (solid line) and downstream (dashed line) gauges, showing the downstream attenuation of the flood peak. With one exception, data are uncorrected real-time instantaneous (15-min interval) measurements at the upstream (Bill Williams River below Alamo Dam) or downstream (near Parker) USGS gauges. The exception is the 2006 data set for the downstream gauge, which consists of mean daily values. Scales are the same in all graphs.

was followed by a 9·5-year period in which releases rarely exceeded 1·4 $m^3\ s^{-1}$ (Figure 3). That period of relatively uniform base flow included May 2002, when we censused beaver dams and estimated pond extent. A 3-day flood release in 1998 featured $Q_{MAX} = 18{\cdot}4\ m^3\ s^{-1}$, and a 5-day release in 2001 featured $Q_{MAX} = 8{\cdot}9\ m^3\ s^{-1}$. The downstream gauge recorded three small natural flash floods between early 1995 and 2004: in September 1995 ($Q_{MAX} = 8{\cdot}5\ m^3\ s^{-1}$), in August 2001 (1·9 $m^3\ s^{-1}$), and in September 2002 (1·3 $m^3\ s^{-1}$).

Long-duration flood releases again occurred in 2004–2005 (2005 $Q_{MAX} = 205\ m^3\ s^{-1}$; Figure 3). Subsequent releases were low (~1 $m^3\ s^{-1}$ measured at the upstream gauge), with the exception of the experimental spring flood pulses in each of 2006, 2007, and 2008. All three experimental floods rose to peak flow quickly, but duration at Q_{MAX} and the subsequent recession rates varied (Figure 2). Peak discharges recorded during the 2004–2005 flood events as well as the first experimental release were similar at the up- and downstream gauges, whereas in 2007 and 2008 the discharge peaks were strongly attenuated by the time the pulse reached the downstream gauge (Figure 2).

Base flow mean current velocities below or far upstream of dams were consistently $>0{\cdot}2\ m\ s^{-1}$. We measured $V_{AVE} = 0{\cdot}42\ m\ s^{-1}$ in a dam-free reach with a relatively steep gradient (~0·5%; $n = 7$ cross-sections, PC) and 0·37 $m\ s^{-1}$ in a dam-free reach with a flatter gradient ($n = 3$ cross-sections, PR). All five cross-sections with average velocities $>0{\cdot}4\ m\ s^{-1}$ on the portion of the PC reach containing dams ($n = 26$ cross-sections) were at least 180 m above a dam.

Beaver dam abundance

We counted 104 dams along the BWR in our first full census (May 2002), distributed among all river segments. Our level of confidence in identifying dams was 'very high' for about half of the dams. We identified 42 beaver dams in our second full census (September 2005), which followed the large (~200 $m^3\ s^{-1}$) flood of early 2005 (Figure 3). Our confidence in the identification was rarely 'very high', however, and most (68%) of the mainstem dams were concentrated in one valley (Lincoln Ranch). The ground observations made in December 2005 confirmed the presence of two of those dams at each of ALR and PC, and confirmed the absence of dams at MW and in the 3-km-long reach immediately above the cluster of PC dams. Thus, functioning, presumably active dams were again present on at least two river reaches only 5 months after cessation of large floods (Figure 3).

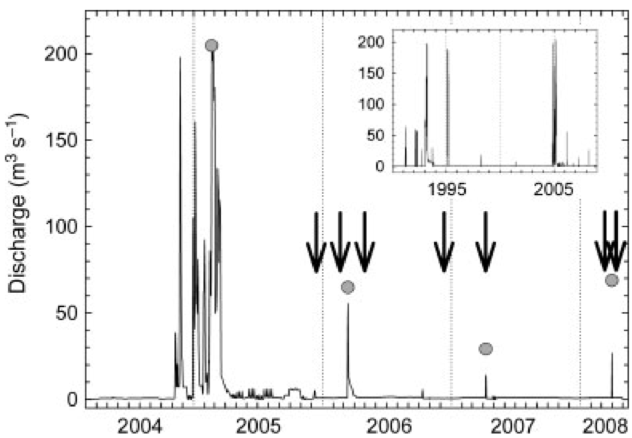

Figure 3. Daily mean discharge in the upper Bill Williams River for the period March 2004 through April 2008, based on data collected at USGS gauge Bill Williams River below Alamo Dam, AZ. The inset shows the same values for 1990–2008. Arrows indicate when site visits and beaver dam examinations took place before and/or after the experimental flood releases in 2006–2008. Filled circles indicate peak instantaneous discharge (PID) during the flood event. The difference between PIDs and the peak daily mean discharge during the release results from the short duration of each PID (Figure 2).

High turbidity in the upper stream reaches resulted in low contrast between dams and surface water in the natural colour 2006 aerial photography, making dams difficult to discern despite the smaller scale (Table I). The images were most useful in documenting the continued absence of dams in the lower reaches (PR and MW), and the absence of major changes in flow paths at PC and ALR since our earlier (April 2006) ground observations, a pattern consistent with no new dam construction since the March 2006 flood.

Our fourth and last full dam census (March 2008), based on combined ground observation (43 dams) and analysis of helicopter videography over river reaches not visited (48 additional dams) resulted in a total count of 91 dams, again distributed throughout the river's length.

Extent of lentic habitat

Our analyses produced both linear and exponential models relating V_{AVE} to distance above the dam (Figure 4). Adjusted r^2 values were generally high in both model sets; the lowest r^2 among the five models judged significant ($P \leq 0{\cdot}082$) was 0·94. The data for Pond PC-H (Figure 4) failed to produce a significant model, so we fit the exponential model developed for the similar and nearby Pond PC-G (Figure 4) to the non-zero V_{AVE} data for Pond PC-H to estimate K_T there. The values of K_T derived from the models ranged from 121 to 229 m. In those cases where estimation of K_T required extrapolation beyond the data (i.e. all measured values of V_{AVE} were $<0{\cdot}2$), we judged the K_T values to be realistic (Figure 4).

The multiple regression analysis indicated that a model containing maximum pond depth (D_{MAX}) and dam length (L) best predicted K_T [$P = 0{\cdot}026$, adjusted $R^2 = 0{\cdot}85$; $K_T = (166{\cdot}21 \times D_{MAX}) + (2{\cdot}1197 \times L) - 36{\cdot}83$; all units in metres]. D_{MAX} and L were uncorrelated in both the subset of six dams used in the multiple regression analysis ($r = 0{\cdot}23$) and the full set of 27 dams examined prior to the March 2008 flood ($r = 0{\cdot}33$, $P = 0{\cdot}10$). The D_{MAX} values for the 27 ponds ranged from 0·37 to 1·14 m, and were normally distributed

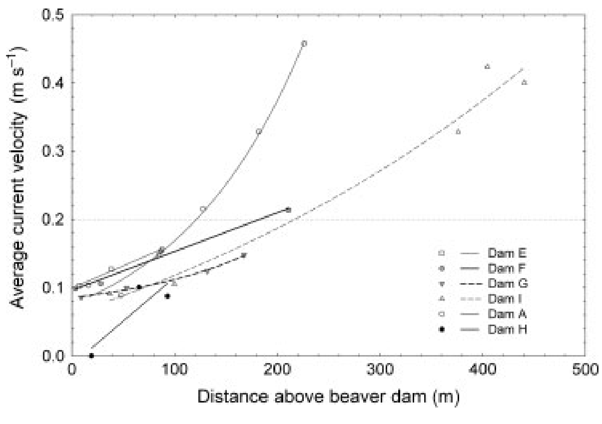

Figure 4. The relationship between average current velocity (V_{AVE}) in a beaver pond and the distance above the dam for reach PC. The lines represent linear and exponential models used to estimate the distance (K_T) at which $V_{AVE} = 0{\cdot}2$ m s^{-1}, the threshold velocity separating lentic and lotic habitat (horizontal dashed line).

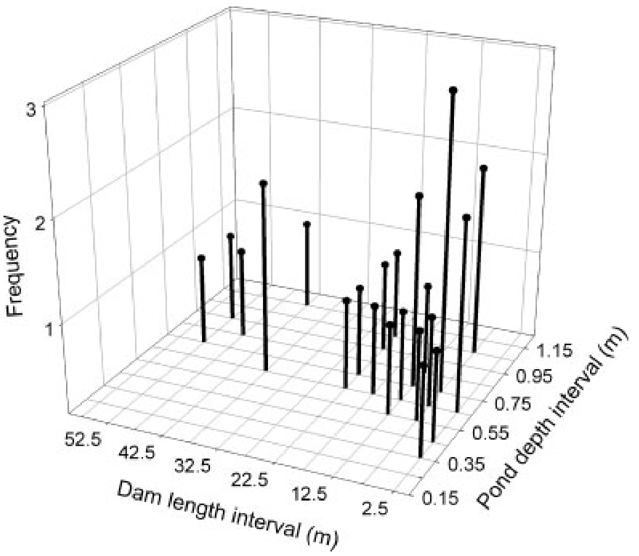

Figure 5. Bivariate frequency distribution for dam size variables D_{MAX} (maximum impoundment depth near the dam, grouped in 0·1-m intervals) and L (dam length along crest, grouped in 5-m intervals) for 27 dam/pond complexes examined along the Bill Williams River prior to the 2008 experimental flood. Frequencies are plotted at midpoint value for each interval.

(Shapiro–Wilk test for normality, $P = 0{\cdot}58$). More than half had maximum depths $>0{\cdot}6$ m and $\leq 0{\cdot}8$ m (mean $D_{MAX} = 0{\cdot}75$ m $\pm 0{\cdot}035$ (SE). Dam lengths were not normally distributed ($P < 0{\cdot}001$), but could be represented by a lognormal distribution (Shapiro–Wilk test on log L values, $P = 0{\cdot}25$). Based on these results, we generated a bivariate frequency distribution matrix for the 27 measured dams using a 0·1-m increment for D_{MAX} and a 5-m increment for L (Figure 5).

Application of the observed bivariate distribution matrix (Figure 5) to the 2008 population of 91 dams and calculating the K_T value for each associated pond (using the multiple regression equation applied to each size-class cell and scaling up by frequency) produced an estimate of 11·6 km of lentic habitat in the associated beaver ponds. Analogously, the 104 ponds present in 2002 produced 13·2 km of lentic habitat, representing ~23% of the river's total length. Assuming that 5% (2·9 km) of the BWR was lentic habitat due to natural (abiotic) geomorphic features present after the 1995 floods, when no beaver ponds existed, our analysis indicates beaver were shifting aquatic habitat from lotic to lentic at the average rate of 3·4% per year during 1995–2002.

The relative paucity of beaver dams in the September 2005 aerial photography suggests lentic habitat extent was much below that present in 2002. This decline in dams was almost certainly a result of the multiple large magnitude flood peaks in 2004–2005 (Figure 3).

Flood effects on beaver dam abundance and functional integrity

Influence of the 57 m^3 s^{-1} 2006 flood release. ALR contained four dams when visited 4 months prior to the first experimental flood, and the PC site contained seven functioning dams arranged in three groups. The flood

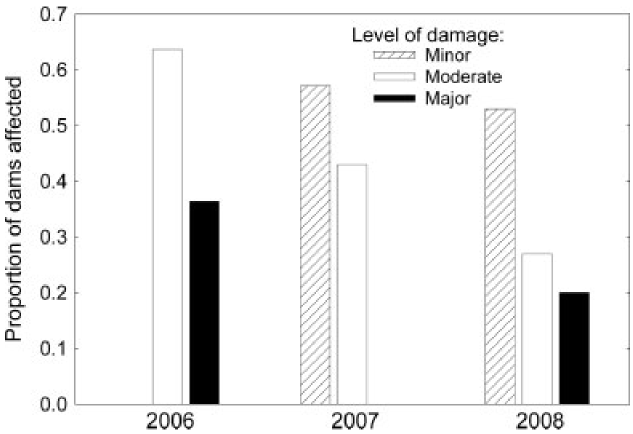

Figure 6. Proportions of monitored dams in each of three damage classes following the spring flood pulses on the BWR. Major damage includes breaches >3-m wide. Moderate damage includes all breaches <3-m wide. Minor damage includes loss of some dam component materials and increased leakiness, but little loss of dam functionality. Sample sizes were 11, 7, and 86 for 2006, 2007, and 2008, respectively.

resulted in complete destruction of three of the four dams at ALR and one of the seven at PC. All other dams suffered moderate damage, including breaches that resulted in pond drainage (Figure 6). At ALR, the three upstream dams were completely washed away (Figure 7), whereas the lower most dam retained some functionality and appeared to be under repair or redevelopment when the site was revisited ~1 month post-flood. The presence of beaver, solely at the lowest dam, was confirmed at the subsequent visit 7 months later (November 2006). Channel geometry at ALR assured that some pool habitat remained at the upstream dam location (Figure 7), but no evidence of beaver activity was noted there.

Comparison of pre- and post-flood maps (based on rectified aerial photography) of the water surface along the 825-m-long reach containing dams at PC indicated the flood reduced total aquatic habitat extent (initially 2·09 ha) by 33%. This estimate is probably conservative, given the slightly higher discharge in the pre-flood imagery (Table I). Repair of the most upstream set of three dams was underway when the site was revisited in November 2006.

Influence of the 37 m^3 s^{-1} 2007 flood release. No monitored dam suffered major damage from the second experimental flood, which had a peak 35% smaller than the first flood. At PC, the pre-flood visit documented that a wing had been added to one of the three dams under repair 7 months earlier, extending it completely across the stream (Dam PC-D). The other two dams, immediately downstream of Dam PC-D, were functional but appeared to have been abandoned. There was no evidence of beaver activity elsewhere at PC, but an active dam (Dam PC-E) spanned the stream at a previously unmonitored location ~1 km upstream. At PR, we found an active dam on each of two parallel channels.

The floodwaters overtopped all dams at PC, but none had clearly suffered major damage when last observed during the middle stage of flood recession. Dam PC-D (Figure 8), which was noted to have been partially breached at its right abutment by the previous flood, was again partially breached at that point. Dam PC-E was breached in its centre (<3-m breach = moderate damage).

The larger of the two dams at PR was also breached in its centre and its pond drained, even though Q_{MAX} was possibly reduced to <10 m^3 s^{-1} by the time the pulse reached it (Figure 2). The smaller dam was overtopped but suffered only minor damage, retaining its functionality.

Influence of the 65 m^3 s^{-1} 2008 flood release. The last and largest (in terms of Q_{MAX}) experimental flood overtopped all 38 dams monitored from the ground (Figure 9), including those at PR, where the rise in river stage caused by the flood had attenuated to only 20% of the value recorded above PC (~0·22 and ~1·10 m, respectively). Nine dams suffered major damage, including the complete destruction of a new, 'replacement' dam built at the ALR site shown in Figure 7 and one dam at each of the lowest sites, PR and MW. The latter two dams were constructed primarily of cattail (*Typha* sp.) stems and the dispersion pattern of post-flood debris suggested each dam may have moved downstream as a unit. Other destroyed dams had been constructed of less buoyant materials, including branches and rocks, and in most cases remnants were present at the dam abutments. We detected no relationship between damage extent and any of the four dam size variables (stepwise logistic regression analysis $P_{enter} \geq 0·65$).

Figure 7. (Left panel) A 33-m-long dam (ALR-D) on the upper Bill Williams River on 22 February 2006, just prior to the 13 March flood release. (Right panel) Same location on 26 April, 5 weeks following the flood release. The site remained unoccupied for at least a year. A replacement dam, constructed sometime between April 2007 and March 2008, was removed by the 2008 flood pulse.

Figure 8. (Left panel) View of Dam PC-D from its tailwater on 30 November 2006. (Right panel) Dam PC-D being overtopped by floodwaters associated with the 37 $m^3\ s^{-1}$ April 2007 release. The image, captured ~24 h after flood recession was initiated at Alamo Dam, shows the water surface elevation in the pond behind the dam ~30 cm below the peak stage reached during the flood but still ~20 cm higher than the pre-flood stage, which was similar to the level depicted in the left panel. This dam was also overtopped during the 2008 flood pulse, but again functionality was only slightly diminished.

Figure 9. Repeat photographs showing Dam PC-G a few hours prior to arrival of the 2008 flood pulse (top panel) and being overtopped by that pulse (middle panel). The dam suffered a central 3·9-m breach (= major damage) that lowered the pond's surface elevation (bottom panel), but retained some functionality based on the 40-cm drop through the breach present ~2 days post-flood. Photographs by Brad Cannon and Tom Liptrott, US Bureau of Land Management.

Of the 48 dams monitored via videography, 8 suffered major damage, 16 moderate damage, and 24 were judged to have suffered at most only minor damage (Figure 6). The proportions in the three damage categories were equivalent in the ground and aerial assessments (Pearson chi-squared test, $P = 0{\cdot}28$). Based on the pooled data sets, the 2008 release caused major damage to 20% of the BWR beaver dams (Figure 6).

DISCUSSION

Counting dams using aerial imagery

Our airphoto-based estimate of 104 dams along the BWR in 2002, after 7 years of low, stable flows, is probably below, but close to, the number actually present. A ground census undertaken in the Bill Williams National Wildlife Refuge (Figure 1) in early 1997 (K. Blair, USFWS unpublished data) produced counts of 30 active and 9 inactive dams in the lowest 13 km of the river, a tally consistent with our total count. However, a second census of the same reach in early 2000 found 54 dams, indicating that new dams had been constructed. The continuation of the 1997–2000 flow conditions, clearly conducive to dam building, could have promoted additional new dam construction during 2000–2002 and another increase in the dam count. The similarity between our 2002 estimate and our 2008 estimate (91 dams), based on the presumably more accurate combination of ground and helicopter counts, and the consistency of both these estimates with earlier counts on the refuge—all made when dams were very common—suggest that our 2002 estimate is reasonable.

Changes in the extent of lentic habitat

Our estimated 3·4% average annual lotic-to-lentic conversion rate due to beavers constructing new dams is premised on the assumption that all dams are destroyed during floods as large as those that occurred in 1995 and 2004–2005 ($Q_{MAX} \geq 189\ m^3\ s^{-1}$ and duration >2 weeks). This assumption is supported by the fact that no intact dams were found during a field reconnaissance by one of us (PBS) to several parts of the BWR in July and August 1995, about 4 months following the 1995 flood, nor was any dam noted during vegetation sampling conducted at eight locations scattered along the

BWR in April 2005, only a month after termination of the 2004–2005 floods. This average conversion rate would be somewhat lower if we had used a conservative value for K_T, the lentic–lotic threshold current velocity. However, a value of $0{\cdot}1$ m s^{-1} would have reduced lentic extent in some beaver ponds to zero (Figure 4). The variation among the velocity gradients in the sampled ponds (Figure 4) reflects variation in dam leakiness and perhaps infiltration rates into the channel bed.

The actual lotic-to-lentic conversion rate in a given year would depend on several factors, including stream hydrology, the nature of both existing dams and riparian vegetation, and beaver demographics. We hypothesize that the increase from no dams in 1995 to 104 in 2002 was facilitated by the relatively small and constant release from Alamo Dam after 1995, together with the post-dam increase in woody vegetation (Shafroth *et al.*, 2002). Stream water depths are typically <1 m and often much less outside beaver ponds when the release is at 'base flow' level ($\sim$1 m^3 s^{-1}), making most reaches hydrologically appropriate for dam building (Hartman and Törnlöv, 2006). The increase in dams also suggests that either beaver were already present on the BWR and at least some survived the 1995 floods, or that colonization from the Colorado River was rapid. We know of no information on the direct effect of floods on beaver displacement or survivorship, but the rapid appearance of dams following the 2005 flood supports the hypothesis that large floods like those of 1995 and 2004–2005 do not completely remove beaver from the BWR corridor.

It is unclear if conditions unique to desert riverine environments constrain dam-building activity. The mean density of dams along the entire BWR was $\sim 1{\cdot}8$ dams km^{-1} in May 2002, but as high as 6 dams km^{-1} in particular reaches. These densities are similar to the maximum of 4 dams km^{-1} found by Demmer and Beschta (2008) in their 17-year study of a 25-km segment of a low-gradient, unregulated Oregon stream whose lower reaches were in semiarid terrain. In contrast, Naiman *et al.* (1986) reported an average density of $10{\cdot}6$ dams km^{-1} in southeastern Quebec, Woo and Waddington (1990) reported a mean of $14{\cdot}3$ dams km^{-1} in subarctic northern Ontario, and Cooke and Zack (2008) reported up to 52 dams km^{-1} in short sections of small streams in semiarid Wyoming.

Flood effects on beaver dam abundance and functional integrity

We presume the 11-month (minimum) period prior to each experimental flood was sufficient time for beaver to have repaired any weakness in an active dam caused by prior floods. Thus, we consider each flood an independent test of a given dam's response to a flood. The 57 and 65 m^3 s^{-1} flood pulses each damaged $\geq$50% of dams. The 37 m^3 s^{-1} flood also caused at least moderate damage to $\sim$40% of dams, but that value should be interpreted cautiously because of the small sample size. Perhaps most importantly, we observed significant damage to dams even after Q_{MAX} had been attenuated to values approaching 5 m^3 s^{-1} (Figure 2), and we were unable to detect any relationship between level of damage and dam size. Given that prescriptions for using a controlled flood to generate new fluvial surfaces (e.g. for riparian tree establishment) on the BWR or elsewhere could easily include Q_{MAX} values $\geq$5 m^3 s^{-1}, and perhaps much larger, our results support the hypothesis that such floods will simultaneously damage beaver dams and lead to a reduction in beaver-created lentic habitat.

Dam quality and vulnerability to damage by floods

The dams we monitored varied not only in size, but also in leakiness and probably in age, qualities that could affect a dam's resistance to damage from a flood. Many authors (e.g. Townsend, 1953; Woo and Waddington, 1990) report differences in the apparent soundness of beaver dams. By definition, a functioning beaver dam is sufficiently strong to withstand the erosive stream power prevalent during its construction. That dam can also withstand, by definition, the hydrostatic pressures generated by gravity acting on the impounded water. These pressures, exerted on all dam materials in contact with the impounded water (and perpendicular to the material's surface), increase with the depth of the material below the pond surface. One net effect is pressure in a downstream direction on the upstream face of the dam. Another is net upward hydrostatic pressure on submerged objects, equal to the weight of water displaced (buoyancy), which in the case of fresh wood, is greater than the weight of the submerged portion—hence fresh wood floats and a beaver must manipulate it in some manner (e.g. push it into the channel bottom sediment) if it is to remain fully submerged. The net downstream and upward pressures are transmitted throughout the dam by the surface-to-surface contacts among the more-or-less rigid dam components. Downstream movement of dam materials is prevented by static friction between the dam and the streambed, which is dependent on the weight of dam materials—a function of their mass and buoyancy—and the dam-bottom 'surface' roughness, which is increased if the beaver has pushed branches or other dam components into the channel sediment. Age will affect a dam's resistance to failure in a complicated manner, because wood components will add weight as they loose buoyancy (become waterlogged), but bottom roughness and internal integrity will weaken as the wood looses mass and rigidity through decomposition.

Variability in dam resistance to failure could thus arise from differences in type and condition (including age) of dam components, the nature of the channel bed underlying the dam, the physical condition or motivational state of the animal(s) during construction and maintenance, or a combination of these factors. This complexity may account for our failure to detect a relationship between dam size and flood damage level. Although we do not know the precise ages of the dams we monitored, we presume none was initiated prior to April 2005 and thus that all were relatively young. Construction materials included cobbles, small logs and branches from Fremont cottonwood, Goodding willow, and saltcedar, as well as cattail stems. Cattails are common along the BWR and beaver cut stems to access the rhizomes, which are eaten (Baker and Hill, 2003). Among the plant parts used in dam construction, cattail stems likely have the highest initial buoyancy, lowest initial strength, and fastest decay rate. Wood will weaken during decomposition, but that process has not been investigated in a dam-like environment on a warm-desert river. Freshly cut, small ($<1{\cdot}5$ cm diameter) cottonwood and willow branches immersed in the BWR lost 30% of their biomass in 7 months and 60% in 1 year (DC Andersen, unpublished data), suggesting breakdown of wood in a dam may be rapid.

Arrival of a flood pulse causes an increase in the downstream- and upward-directed hydrologic forces on the dam. Dam failure results when these forces overcome the resistance to movement at the dam's base or, by removing dam components, progressively lighten the dam and compromise its structural integrity. The central section breaches in dams at PR and PC may have been a result of those sections, at or near the thalweg, being exposed to both the highest stream power (Marston, 1994) and greatest downstream-directed hydrostatic pressure, because current was fastest and the pond deepest there. Hillman (1998) described the breaching of the 'entire middle section … from top to bottom' of an active 32-m-long beaver dam following a 'not unusual' rainstorm. Hillman (1998) hypothesized that the dam had been weakened or undermined by muskrats (*Ondatra zibethicus*) tunnelling under or into the dam. Muskrats are present along the Colorado River and on portions of the BWR, but we saw no evidence of their activity at any of the monitored dams. Reid *et al.* (1988) documented river otters (*Lontra canadensis*) constructing tunnels through beaver dams, but their activity—directed at accessing fish—is likely restricted to regions where ponds become ice-covered.

The dams suffering major damage at PR and MW, where peak discharge was perhaps as low as 5 m^3 s^{-1} (Figure 2), contained relatively large amounts of cattail stems. The weakness of cattail stems would ensure both low-static friction at the dam base and low-internal cohesion, each of which would reduce dam resistance to floods. To our knowledge, no study has evaluated damage or failure of dams at similarly low discharges. Butler and Malanson (2005) compiled the few references concerning dam failures, but they provide no information on associated discharge levels. Hillman (1998) also reviewed the literature and reported beaver dams being washed out by flows of 283 m^3 s^{-1} (Rutherford, 1953), of 28–72 m^3 s^{-1} (Butler, 1989), and 325 m^3 s^{-1} (Butler, 1989). Westbrook *et al.* (2006) reported dams destroyed by two separate flood events with peak flows of 12 and 18 m^3 s^{-1}, and Dalbeck and Weinberg (2009) reported destruction of a series of dams by a flood with a peak flow of 14 m^3 s^{-1}.

Dam repair and replacement

We documented repair of breached dams and one case of reconstruction at a site (ALR-D; Figure 7) where the 2006 flood pulse had completely removed a dam. The cause of the 1-year long delay in dam replacement is unknown, but could be due to local physical constraints (e.g. an increase in stream power), death or emigration of the resident beaver, or a behavioural choice made by resident individuals. Cook (1943) reported that a colony of beaver maintaining two dams immediately undertook repairs when a July flood 'burst both dams and drained the ponds'. When both dams were again washed out the following March, however, only one received immediate attention, with repair of the other delayed until autumn. Repair of breaches that funnel most or all of the flow through a relatively narrow gap (e.g. Figure 9) may be possible only at very low discharge because of the high stream power otherwise present. The lowest discharge along all reaches of the BWR, given a constant release from Alamo Dam, occurs during summer, when evapotranspiration is the highest. Beaver may be able to initiate dam construction during this 'window' at sites where higher stream power makes it impossible at other times of the year. Townsend (1953) documented the spring washout and subsequent summer reconstruction of numerous beaver dams in a study conducted on the West Fork and upper Clearwater rivers in Montana. In at least one case, a change in colony structure (due to death of an adult) was associated with the absence of repair. Although no discharge data for his study location is available, 1975–1997 data for the lower Clearwater River suggest spring discharges were <85 m^3 s^{-1}, and perhaps much less. Rutherford (1953) noted that, in Colorado, beaver initiated work in March or April to replace dams destroyed in a 283 m^3 s^{-1} flash flood that had occurred late in the previous summer.

Beaver bioengineering, thresholds, and ecosystem processes

A limit to the extent of beaver ponds is set by geomorphological constraints (Johnston and Naiman, 1990) and the territorial behaviour displayed by the individuals and family groups responsible for building and maintaining dams. Boyce (1981) and Baker and Hill (2003) suggested that territorial behaviours resulted in ≥ 1 km between colonies. This limit is consistent with the $0{\cdot}35$–$0{\cdot}60$ colonies per river kilometer reported for two large cold-desert rivers (Breck *et al.*, 2001). We suspect that a density limit had been reached on the BWR at the time of our assessment in 2002, when the lotic : lentic ratio based on linear extent had fallen to $<3:1$. If undesirable shifts in lotic habitat extent, vegetation pattern, the river-scale hydrologic budget (e.g. due to evaporative losses from ponds), or other factors make it desirable to hold the lotic : lentic ratio at a higher value, our results demonstrate that controlled releases can be used to remove dams and manage the ratio.

It is reasonable to expect a threshold in flood intensity above which the probability of dam failure

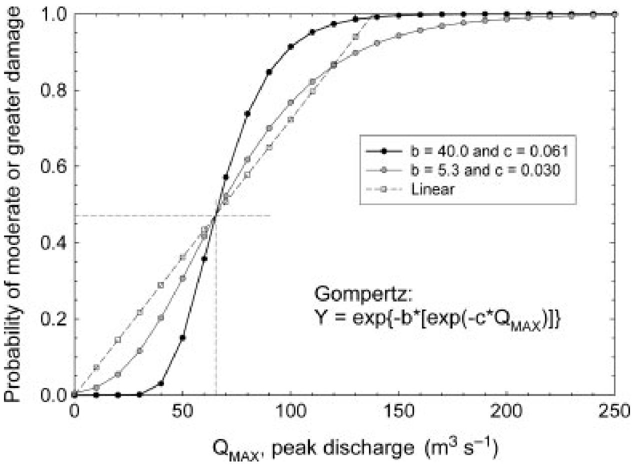

Figure 10. Three possible general models, applicable to the entire BWR, for the relationship between Q_{MAX} during a controlled flood and the probability of a beaver dam suffering at least moderate damage (a breach). All models were parameterized using the 2008 results (47% of the dams at least moderately damaged by a 65 m^3 s^{-1} peak release; dashed grey lines) and ~100% of dams being damaged by a 200 m^3 s^{-1} release. The sigmoid models are Gompertz equations parameterized as noted in the figure.

rapidly increases. Flood intensity, however, has multiple independent components, including the rate of rise to Q_{MAX}, Q_{MAX} itself, the duration of flow at or near Q_{MAX}, and the form of fluctuations around Q_{MAX} (i.e. multiple flow peaks). How these components affect the probability of dam failure is unclear. Shafroth *et al.* (2010) suggested a sigmoidal model for linking Q_{MAX} to dam failure. Figure 10 presents two such models as well as a linear model fit to the data point produced by our most extensive data set, the 2008 results, and low failure probabilty at low discharge and a maximum at $Q_{\mathrm{MAX}} \leq 200$ m^3 s^{-1}. Although speculative, the models point to the heuristic value of assessing effects of a flood with $Q_{\mathrm{MAX}} \sim 40$ m^3 s^{-1}, where model probabilities differ greatly and experimental cost (in terms of water released) is relatively small. The hydraulic and fluvial geomorphic processes that lead to beaver dam failure are also involved in reshaping channel beds and banks. River scientists have long recognized that the ability of a stream to do work (e.g. move bed sediment) increases with discharge, but this ability, termed stream power, is also affected by water depth and other variables linked to channel geometry. Costa and O'Connor (1995) argued that flood duration as well as Q_{MAX} determined the amount of geomorphic work that actually takes place, and suggested that total (= cumulative) stream power over the duration of a flood (= total energy expended during the flood) is the best indicator of a flood's geomorphic effectiveness. If so, models relating dam failure probability to cumulative stream power may prove most insightful.

Because of the numerous factors affecting dam failure probability, parameterizing any model will be difficult unless both flood and beaver dam attributes are known in some detail. Flood attributes will be especially important when, as on the BWR, the flood pulse can become highly attenuated as it moves downstream. The manner in which discharge and stream power are distributed across the channel at individual dam sites will also influence. Coupled hydrological and ecological research tied to release events on the BWR and other regulated streams where beaver build dams can generate unique insight into how dam- and flood-specific attributes each affect the dam-failure probability curve. Through the adaptive management process, the same flood events can be used to refine estimates of the (site-specific) flow thresholds needed to create substrate for native riparian tree recruitment or removal of undesirable non-native seedlings (Shafroth *et al.*, 2010). Once the flow thresholds associated with these related fluvial geomorphic processes are known, water resource managers can optimize environmental flows to achieve both ecological and flow-dependent socioeconomic goals (Arthington *et al.*, 2006).

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