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ARTICLE

Managed Flood Effects on Beaver Pond Habitat in a Desert Riverine Ecosystem, Bill Williams River, Arizona USA

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Abstract The ecological effects of beaver in warm-desert streams are poorly documented, but potentially significant. For example, stream water and sediment budgets may be affected by increased evaporative losses and sediment retention in beaver ponds. We measured physical attributes of beaver pond and adjacent lotic habitats on a regulated Sonoran Desert stream, the Bill Williams River, after ≥11 flood-free months in Spring 2007 and Spring 2008. Neither a predicted warming of surface water as it passed through a pond nor a reduction in dissolved oxygen in ponds was consistently observed, but bed sediment sorted to finest in ponds as expected. We observed a river segment-scale downstream rise in daily minimum stream temperature that may have been influenced by the series of ~100 beaver ponds present. Channel cross-sections surveyed before and after an experimental flood (peak flow 65 m^3/s) showed net aggradation on nine of 13 cross-sections through ponds and three of seven through lotic reaches. Our results indicate that beaver affect riverine processes in warm deserts much as they do in other biomes. However, effects may be magnified in deserts through the potential for beaver to alter the stream thermal regime and water budget.

Keywords Beaver dam · Environmental flow · Regulated river · Sediment flux · Sonoran Desert · Thermal regime

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Introduction

North American beaver (*Castor canadensis* Kuhl) have an enormous range of effects on boreal, montane, and other temperate ecosystems (Gurnell 1998; Rosell et al. 2005). These effects are both short- and long-term, and involve hydrological, geological, biological, and chemical processes. For example, changes in surface water quality or quantity due to beaver dams have been described in boreal Canada (Hood and Bayley 2008), montane Colorado (Westbrook et al. 2006), and the Maryland coastal plain (Correll et al. 2000), and sediment retention in beaver ponds has been shown to have a strong local influence on montane stream networks (Persico and Meyer 2009). By contrast, few studies have examined beaver ecology in desert riverine ecosystems, and the importance of these ecological engineers in desert settings is poorly documented.

Streams, rivers, and associated riparian habitats in North American deserts provide essential resources for a diverse array of species (e.g., Brand et al. 2008). Most desert riverine ecosystems have been altered by water resources development, land use change, or invasion by exotic species (Patten 1998), with adverse effects on many

riparian-dependent species. Beaver are relatively uncommon in desert environments, due to the paucity of perennial watercourses, but they were historically present on many perennial desert stream reaches (Hoffmeister 1986). During the 1800s, these populations were reduced or eliminated by fur trappers or in efforts to control malaria (Tellman et al. 1997; Hastings 2002). Recognition of the key role of desert wetlands in sustaining regional biodiversity has led to efforts to preserve or restore wetland ecological values, including the reintroduction of beaver to some of the streams from which they were extirpated (Pollock et al. 2007; Soykan et al. 2009). Beaver are also benefiting from the use of environmental flows (prescribed reservoir releases, particularly low flows) aimed at conserving and enhancing desert riparian forests (Shafroth et al. 2010). Flow regulation has eliminated the large flood events that historically may have prevented continuous occupancy of some perennial reaches (Andersen and Shafroth 2010). In addition, some water projects have made ephemeral or intermittent stream flows perennial, coincidentally expanding hydrologic conditions suitable for beaver (Shafroth et al. 2002; Taylor et al. 2008).

The potential for beaver to profoundly affect riverine ecosystem structure and functioning (Baker and Hill 2003), together with their expanding presence on desert streams, make it important that water resource managers understand how flow management decisions affect beaver, the habitats beaver create, and the ecosystem processes beaver mediate (Shafroth et al. 2010). Here we document effects of beaver dams on freshwater habitats along a highly regulated desert river and assess how beaver pond and adjacent lotic habitats were changed by two experimental floods released to facilitate research on ecosystem response to different flood magnitudes and durations (Shafroth et al. 2010).

We expected to find that beaver dam effects on hydrology, water quality, and geomorphology in a desert environment would mirror effects found in mesic environments, i.e., that ponds would warm the surface water (McRae and Edwards 1994; Margolis et al. 2001), locally reduce dissolved oxygen concentration (Naiman et al. 1986; Snodgrass and Meffe 1998; Smith et al. 1991), and trap fluvial sediment (Meentemeyer and Butler 1999). We predicted that net bed aggradation would occur in beaver ponds behind dams that remained intact through a flood event and that pond bottom sediment would become coarser and less well sorted. We also predicted that scouring of the pond bottom and thus net bed degradation would occur in cases where the flood resulted in dam failure.

Study Areas

We worked along the ~58-km long Bill Williams River (BWR) in west-central Arizona (Fig. 1). The BWR flow regime is defined by releases from Alamo Dam, which disconnects the river from ~83% of its catchment. Dam operations have dramatically reduced flood magnitudes and increased base flows (House et al. 2006). No perennial streams enter the BWR, but sporadic flash floods in contributing washes can produce ecologically important flows in the river's middle and lower segments (Fig. 1). The maximum stream gradient is about 1%, whereas the mean is about 0.3% (House et al. 2006).

The riverine corridor lies in the transition zone between the Mojave and Sonoran deserts (Benson and Darrow 1981). The climate is hot in summer, cool in winter, and features a generally bimodal precipitation pattern. Although winter air temperatures can dip below freezing for short periods (generally <24 h), ice cover never develops on lentic or lotic reaches.

Based on 19th-Century descriptions of the BWR ecosystem (Favour 1962; Gordon 1988) and paleohydrologic evidence (House et al. 1999), the pre-dam BWR was largely unsuitable as beaver habitat because of the stream's spatial intermittency at base flow and, most likely, patchy

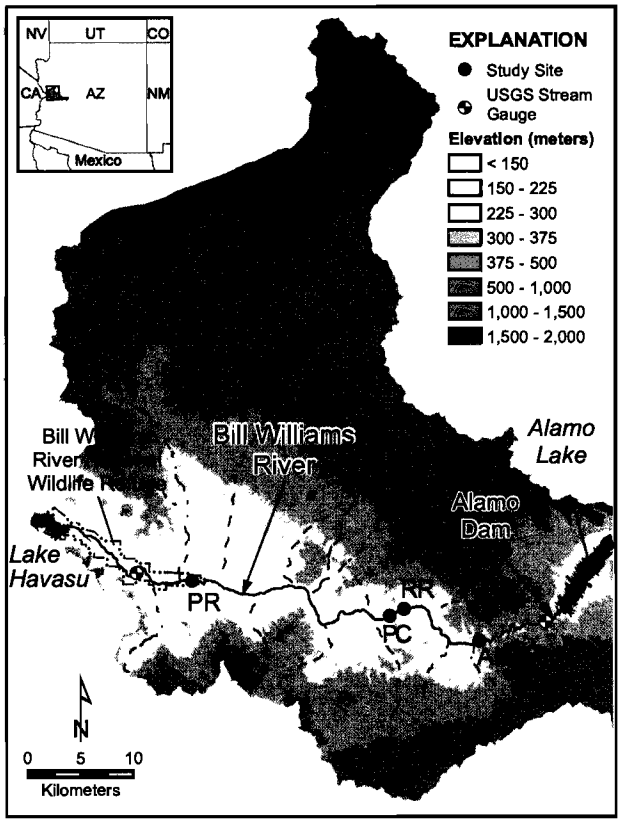

Fig. 1 Map of the Bill Williams River and its catchment below Alamo Dam, showing locations of the Above Lincoln Ranch (ALR), Rankin Ranch (RR), Pipeline Crossing (PC), and Planet Ranch (PR) study segments and the Alamo (upstream) and Parker (downstream) USGS stream gages. Drainage patterns of ephemeral tributaries (*dashed lines*) have been simplified for clarity

woody riparian vegetation. However, beaver were present along the mainstem Colorado River (Lockwood 1929) and in the BWR catchment headwaters (Möllhausen 1858), and therefore likely occupied perennial reaches of the BWR. Since completion of Alamo Dam in 1968, perennial flow reaches and woody vegetation have increased (Shafroth et al. 2002) and beaver have colonized perennial reaches all along the river. Controlled floods with peak discharges ~200 m^3/s destroyed most or all beaver dams present in 1993, 1995, and 2005, but surviving or recolonizing beaver constructed new dams after each flood event (Andersen and Shafroth 2010). Approximately 100 dams and associated ponds were present at the time of this study. Based on examination of aerial photography, most ponds tend to be linear and only moderately wider than the wetted channel of adjacent lotic reaches (Andersen and Shafroth 2010).

We investigated hydrology, water quality, and geomorphology in beaver ponds and adjacent lotic habitat in four study reaches distributed among the BWR's wide alluvial reaches. The upstream-most reach, Above Lincoln Ranch (hereafter, ALR; Fig. 1), is ~10 km below Alamo Dam and has a largely cobble channel, whereas the Rankin Ranch (RR) reach, ~6 km below ALR, featured a sand bed. Below RR and contiguous with it, the Pipeline Crossing (PC) reach featured a sandy channel in its upper portion and sections of mixed coarse sand, gravel, and cobble in its lower portion. The Planet Ranch (PR) reach, ~22 km below PC in the lower Planet Valley, featured a sandy channel with some gravel bars. A ~6-km long section of the channel in the Planet Valley above PR is dry during periods of base flow.

We assigned a unique identifier to each beaver dam in each study reach (e.g., Dam PC-A is in Reach PC, Location A) and used the same identifier for the associated pond (e.g., Pond PC-A). The last letter in the identifier was assigned in order from downstream to upstream, i.e., Dam PC-E is upstream of Dam PC-D. All study sites were on public lands.

Methods

Hydrology

Stream Discharge and Riparian Water Table Height We assessed stream flow in the study reaches from records of real-time instantaneous discharge and mean daily discharge for USGS gages BWR below Alamo Dam, AZ (# 09426000), located 0.6 km below the outlet works, and BWR near Parker, AZ (# 09426620), 8.2 km upstream of the river's mouth (Fig. 1). Comparison of gage records provides a means to both assess flow diminution during its downstream passage and identify uncontrolled (flash) floods originating in tributary washes. These two gages are hereafter referred to as the "upstream gage" and "downstream gage," respectively. Neither gage was affected directly by the presence of a beaver pond. We recorded the stage change associated with the 2008 flood pulse at RR and PR, using one and two manually-read staff gages, respectively.

Surface Water Velocity and Depth In 2008, we established cross-channel velocity transects at PC (n=32) and PR (n=11), systematically arranging them from downstream to upstream of beaver dams. We measured stream or pond depth (D) and current velocity (V) at three positions on each transect using a Pygmy Flow meter (range 0.03 to 1.5 m/s). Measurements were typically made ~1 m from each bank and at or near mid-channel, with one of the measurements at the thalweg. If dense emergent vegetation was present at a bank, the measurement was taken ~1 m from the vegetation 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-sec period at a depth from the surface equal to 60% of the stream depth. We calculated a mean water depth (D_{AVE}) and mean current velocity (V_{AVE}) for each transect.

We measured D and V on each transect during a four-day period immediately prior to the 2008 flood pulse and repeated all measurements within one week following flood recession, when discharge in each study reach was equal or similar to the pre-flood (base flow) rate. Where appropriate, we evaluated change to D_{AVE} and V_{AVE} resulting from the flood pulse using paired t-tests.

Water Quality

We measured stream water quality parameters [temperature, dissolved oxygen (DO), pH, and conductivity] at ALR (2007 only), RR (2008 only), PC, and PR prior to the 2007 and 2008 floods and at RR (2008 only) and PC during flood recession. In each reach, four positions were simultaneously monitored along a longitudinal transect spanning at least one beaver pond. Data were collected for ~5 h in mid-day (2007) or ~24 h (2008) using Hydrolab Corporation (Austin, Texas) MiniSonde® multiprobes programmed to take measurements at 30-min (2007) or 60-min (2008) intervals. We assumed the surface water was well-mixed (Caissie 2006) and made no attempt to standardize sensor location in the water column. The multiprobes were also used to assess pre- and post-flood ground water quality at PR in shallow (≤2.3 m deep), hand-bored, PVC-lined observation wells installed on a cross-channel transect. Wells A and B were installed in 2007 on the left floodplain at positions 8 and 40 m, respectively,

from the margin of the beaver pond traversed in the PR longitudinal transect. Well C was installed in 2008 on the right floodplain, 4 m from the pond margin. All wells had the bottom 1-m slotted. We measured surface water temperature at 30-min intervals during the 2008 flood at RR using HOBO® U22 Water Temp Pro v2 dataloggers.

We calculated the daily mean water temperature (T_{AVE}) in 2008 as the arithmetic mean of the hourly temperatures. In the few cases where temperature data were collected for ≥22 but <24 h, we estimated the one or two missing hourly values by assuming a constant daily cycle and extrapolating from measured values.

Geomorphology

Prior to the 2008 flood pulse, we marked and surveyed a total of 20 permanent cross-sections perpendicular to the channel. Cross-sections spanned both lentic (beaver pond) and lotic habitat at PR (n=4) and PC (n=13), but only lotic habitat at RR (n=3). A cross-section above a beaver dam was classified as being in the associated beaver pond if mean pre-flood (base flow) current velocity at that position was ≤0.2 m/s, the criterion adopted by Andersen and Shafroth (2010) to differentiate lentic from lotic reaches. We further differentiated in-pond cross-sections into those ≤20 m above the dam (Lower Pond) and those farther upstream (Upper Pond). All cross-sections outside of a beaver pond were in locations that qualified as lotic based on current velocity. We resurveyed all cross-sections within one week of the flood, beginning ca. 36 h after the return of flow release to the pre-pulse base flow rate.

We collected sediment samples from the wetted channel before and after the 2008 flood pulse on sediment transects established on a subset of the channel cross-section locations at PC (n=11) and PR (n=4). We used a "can-on-a-stick"-type sampler (Edwards and Glysson 1999) to collect three subsamples along each transect and at approximately the same locations pre- and post-flood. Larger organic matter (OM) on the sediment surface was lightly brushed away before collecting the sample, and we did not attempt to retain easily suspended fine silt, clay, or OM. Each subsample was collected to a depth of 10 cm and included ~450 cm^3 of sediment. We dried, sieved (mesh sizes φ_{-5} to φ_3 in whole increments), and weighed each subsample and calculated proportions (by weight) in each grain size class. We used program GSSTAT (Poppe et al. 2004) to calculate particle size statistics for each subsample using method of moments and calculated mean values for mean and median particle sizes (φ scale) for each transect. We assumed a normal distribution of sample means and performed ANOVA on the 11 transect means at RR and PC to test for a difference in mean particle size among the three positions (Lower Pond, Upper Pond, and Lotic). We used post-hoc Bonferroni pairwise comparisons to determine which locations differed. We used paired t-tests to compare pre- and post-flood means.

We recorded the midpoint of each beaver dam, velocity transect and channel cross-section using a Trimble GeoExplorer® 3 GPS unit. Horizontal precision was typically ≤5 m. Distance between reach endpoints was determined using ArcGIS (Version 9).

Results

Hydrology

Alamo Dam releases (base flow) during the 11-month periods prior to the 2007 and 2008 floods averaged 1.05 and 0.93 m^3/s, respectively, with daily mean flow ranging from 0.23 to 5.58 and from 0.05 to 1.78 m^3/s, respectively. The 5.58 m^3/s daily mean occurred during a three-day period of higher than usual flow releases (daily means of 3.74 to 5.58 m^3/s) in October 2006. There was no evidence that a natural flood occurred during either period. Thus, we consider our pre-flood measurements in the two years to be independent characterizations of BWR beaver pond attributes following many months at base flow hydrologic conditions.

The 2007 and 2008 flood pulses differed in duration and magnitude. In 2007, flows rose rapidly to Q_{MAX} (~37 m^3/s at the upstream gage), remained there for 16 h, and then rapidly returned to base flow (Fig. 2). The rise and fall were similarly rapid in 2008, but Q_{MAX} (~65 m^3/s) was nearly twice that of the 2007 flood, whereas duration at peak was only ~8 h. In both years, the flood pulse was greatly attenuated when it reached the downstream gage (Fig. 2). The instantaneous peak discharge measured at the downstream gage was greater in 2007 (5.1 m^3/s) than in 2008 (1.6 m^3/s), despite the higher release Q_{MAX} in 2008.

Evidence suggests each flood pulse overtopped all dams present at PC. Crests of BWR beaver dams are typically ≤15 cm above pond surface elevation, and although no stage measurements were made in 2007, high water marks noted near Pond PC-D following the 2007 flood pulse suggested the river rose ~50 cm there. River stage at the RR staff gage rose 1.05 m in response to the 2008 flood pulse (Fig. 3; see also Andersen and Shafroth 2010). Based on similarities in channel geometry, the rise was probably also ~1 m immediately downstream at dams PC-I, -H, -G and -F, and perhaps -E. Below Dam PC-E, secondary channels became available, and stage rise would have been lower. The stage rise at PR, although only 22 cm, was sufficient to overtop all PR dams.

An increase in current velocity (Fig. 4a) and reductions in both water depth (Fig. 4b) and surface elevation (Fig. 4c) were clearly evident in ponds above dams that sustained

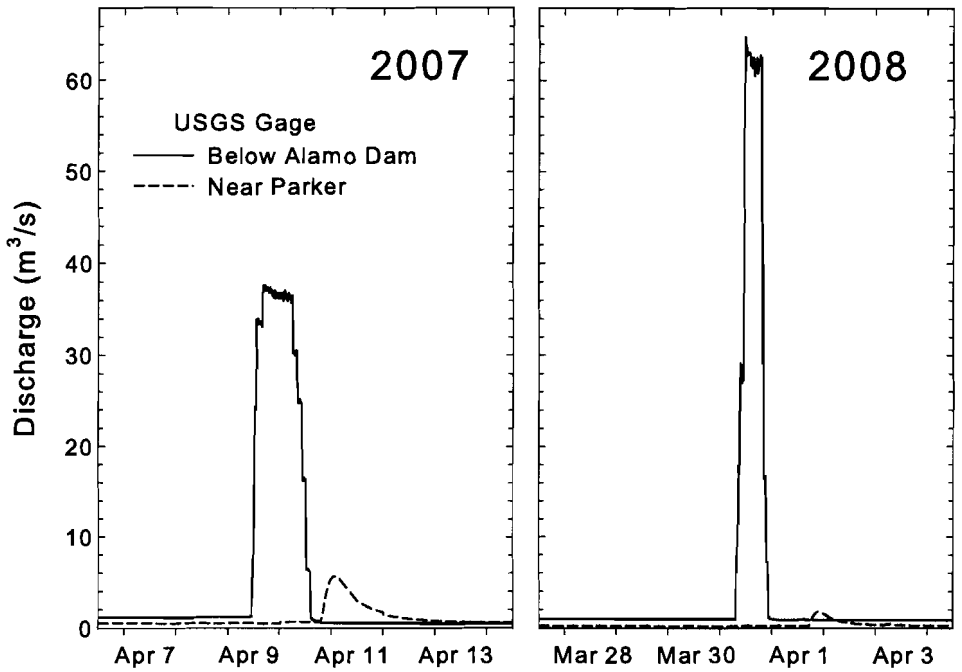

Fig. 2 Bill Williams River discharge during the 2007 and 2008 controlled flood pulses as measured at the USGS gages located just below the Alamo Dam outlet works (No. 09426000) and near the river's mouth (No. 09426620)

major flood damage. For example, dams PC-E and -F were almost completely removed by the flood, and V_{AVE} increased from ~0.1 m/s to ~0.4 m/s (Fig. 4a), D_{AVE} dropped to about 50% of pre-flood values (Fig. 4b), and water surface elevations in the associated ponds fell ~40 cm (Fig. 4c). On velocity transects classified as lotic on the basis of pre-flood current velocities (e.g., the three at RR and the two farthest downstream at PR; see Fig. 4a) and on pond transects upstream of dams that sustained little or no flood damage (e.g., dams PC-H and PR-A), the changes in V_{AVE} and D_{AVE} were variable in direction but generally small in magnitude. Cross-sectional area comprised of water (Fig. 4d) and wetted perimeter (Fig. 4e) decreased largely in concert with changes to water surface elevation and water depth.

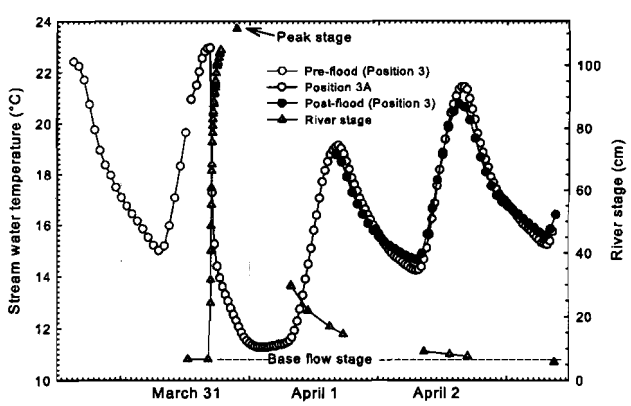

Fig. 3 River stage (*triangles*, scale on right axis) and surface water temperature dynamics (*circles*, scale on left axis) produced by the 2008 flood pulse at the Rankin Reach (RR). Pre- and post-flood temperature data are from Position 3 in the RR longitudinal water quality transect, whereas temperatures immediately before, during, and after the flood were recorded at Position 3A, ~50-m downstream from Position 3. The time of occurrence of peak stage is estimated

Water Quality

Surface Water Temperature Pre-flood monitoring in 2007 captured the maximum daily stream temperature (T_{MAX}) solely at PR. We estimated T_{MAX} at ALR to be 19.5°C, based on the observed temperature increase from 10:30 h (14.9 to 15.2°C) to 14:30 h (17.9 to 18.1°C). In 2008, we documented nearly complete diel cycles at each of the four measurement positions in each reach examined (RR, PC, and PR). Our prediction that T_{MAX} would consistently increase from upstream to downstream of beaver ponds was supported in some but not all reaches. At PR, the 2007 data show T_{MAX} increasing as expected only at the upper three positions (from 24.1 to 25.2°C). Water temperature at the downstream-most position (Position 1) was relatively cool and nearly constant (~21.4°C), but warmer than the upgradient ground water (stable at ~20.0 and ~19.4°C in wells A and B, respectively), indicating ground water influx. The 2008 data revealed the predicted T_{MAX} increase at PR and RR, but the gradient was reversed (i.e., T_{MAX} decreased) at PC (Table 1).

Analysis of the water temperature gradient based on T_{AVE} indicated that downstream cooling was occurring at both RR and PC, whereas water first cooled and then warmed as it passed through PR (Table 1). The 2008 T_{MIN} values at PR (range 17.3–18.9°C; Table 1) were similar to

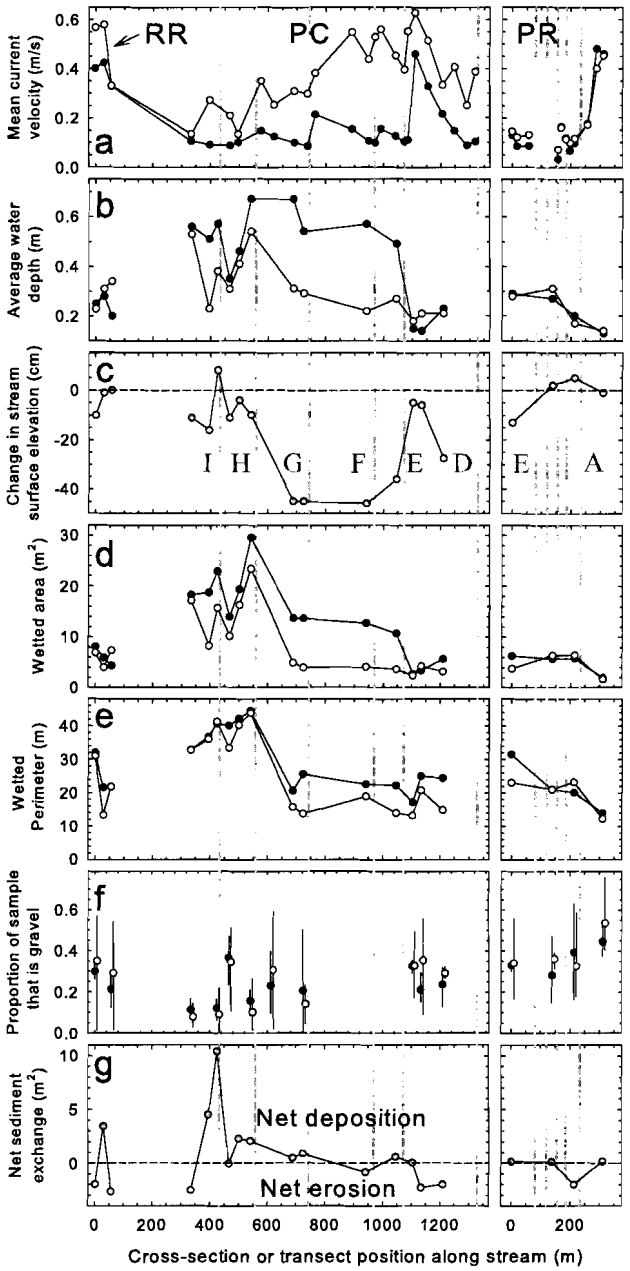

Fig. 4 Longitudinal patterns in pre- (*black-filled circles*) and post-flood (*open circles*) stream hydrologic parameters (panels **a**,**b**,**d**, and **e**), the change in absolute elevation of the stream surface (*gray-filled circles*, panel **c**), pre- and post-flood mean (*circles*) and range (*vertical bars*) of the proportion (by weight) of gravel in streambed sediment samples (panel **f**), and net sediment gain or loss (panel **g**) resulting from the 2008 flood pulse on the Bill Williams River, Arizona. Data are from channel cross-section surveys and velocity and sediment transects in the adjacent RR and PC reaches (*left panels*) and the PR reach (*right panels*), arranged from upstream to downstream (i.e., flow is from left to right). The post-flood (*open circles*) sediment transect position (panel **f**) has been shifted to the right for clarity. Vertical dashed gray lines show positions of beaver dams; adjacent gray letter in panel **c** is the dam ID

the ground water temperature recorded there at that time (a stable 18.7°C in Well C).

A river-scale gradient in each of T_{MAX}, T_{MIN}, and T_{AVE} was evident in the 2008 pre-flood data (Fig. 5). Counter to expectations, the highest T_{MAX} value was recorded at the upstream reach (RR) and the lowest was recorded at the lowest reach (PR), but differences were small (<1°C; Table 1). In contrast, T_{MIN} increased substantially as one moved downstream (Table 1), with the result that the amplitude of the diel temperature cycle shrank from ~7°C at the upstream RR reach to ~4°C at the PR reach, ~24 km down river (Fig. 5). A downstream warming of ~2°C was apparent in T_{AVE} from RR to PR (Table 1), assuming within-reach patterns remained constant over the three-day long monitoring period.

The 2008 floodwaters first reached RR when surface water temperature was near T_{MAX}. The flood produced a rapid 12°C drop in water temperature, from ~23°C to ~11°C (Fig. 3). A diel cycle was re-established by the following day, by which time flood recession was nearly complete. However, daily mean temperature was still rising toward the pre-flood level ~two days post-recession (Fig. 3). Assuming the 11°C floodwater temperature at RR represented the pre-flood stream temperature at Alamo Dam, the pre-flood T_{MIN} values (Fig. 5) showed a consistent rise with distance below the dam (linear regression P=0.03).

Surface Water Chemistry The 2008 water quality data indicated that under base flow conditions the BWR is slightly to moderately alkaline and moderately high in dissolved ions (Table 1). The same pattern was evident in the 2007 pre-flood data (not shown). Conductivity in 2008 ranged from 704 to 797 μS/cm at RR and PC, and from 619 to 690 at PR. DO values were consistently ≥5.7 mg/L at RR and PC, but as low as 1.8 mg/L in a beaver pond at PR (Table 1). At the upstream reaches, DO showed the expected diel cycle of high mid-day (8 to 9 mg/L) and low night-time (~6 mg/L) values associated with daytime photosynthesis and nocturnal O_2 uptake by aquatic organisms. Ground water inflow at PR Position 1, inferred from the 2007 temperature data, was also reflected in the 2007 mid-day surface water DO concentrations, which dropped from >10 mg/L in beaver pond PR-C to <2 mg/L at Position 1. Concurrent DO values in the PR ground water were <1 mg/L.

We detected no effect of the 2008 flood on conductivity or pH (Table 1). In contrast, DO at the three upstream positions at RR showed weak cyclical values that hovered around the pre-flood minimum, while the lowest position, in beaver pond PC-H, showed a dramatic decline to <4 mg/L that lasted ~24 h. At PR, the first post-flood DO measurement in the beaver pond, made about 36 h after the flood peak (~1 pm on 3 April; see Fig. 2), indicated a

Table 1 Pre- and post-flood surface water temperature (T, °C), conductivity (μS/cm), pH, and dissolved oxygen (DO, mg/L) measurements recorded over ~24-hr periods in 2008 along longitudinal transects passing through beaver ponds in three alluvial reaches of the Bill William River, Arizona. Position 1 is downstream-most and Position 4 is upstream-most, with position in bold font in a beaver pond. Values are based on hourly measurements, with measurements at PR, PC, and RR collected on sequential days. Weather conditions were stable and dry over the entire measurement period; see text for further details

Position	Rankin Ranch (RR)				Pipeline Crossing (PC)				Planet Ranch (PR)			
	1	**2**	3	4	1	2	**3**	4	1	2	**3**	4
Pre-flood												
24-h mean, T_{AVE}	18.1	18.2	18.2	18.2	19.2	19.3	19.3	19.4	20.4	20.4	19.5	20.2
Daily max, T_{MAX}	22.6	22.5	22.4	22.4	22.0	22.3	22.4	22.5	22.3	22.3	22.0	21.9
Daily min, T_{MIN}	14.8	14.9	15.0	15.1	16.4	16.5	16.5	16.4	18.9	18.9	17.3	18.8
Conductivity	781–787	704–714	784–791	727–762	795–799	721–742	793–797	737–764	684–690	619–629	660–677	635–663
pH	6.5–8.1	7.7–8.4	7.8–8.5	7.7–8.5	7.0–10.1	7.7–8.1	7.7–8.2	7.7–8.2	6.9–7.8	7.3–7.5	7.0–7.5	7.6–7.8
DO	6.3–9.0	5.7–8.0	6.0–8.5	6.2–8.8	6.7–8.6	5.9–7.4	5.7–7.8	6.1–8.2	3.7–5.0	2.8–4.0	1.8–3.8	3.3–4.9
Post-flood												
24-h mean, T_{AVE}	17.6	17.6	17.6	17.6					20.2	20.2	18.9	20.1
Daily max, T_{MAX}	21.0	21.0	20.8	20.8					22.3	22.2	19.7	21.6
Daily min, T_{MIN}	14.5	14.6	14.7	14.7					18.8	18.8	17.9	18.9
Conductivity	769–801	600–723	778–813	723–798					689–693	593–603	611–694	639–678
pH	6.6–7.9	7.7–8.0	7.7–8.0	7.5–7.9					6.4–6.6	7.6–7.6	7.3–7.6	7.5–7.6
DO	2.7–7.0	5.9–6.4	6.1–6.7	6.0–9.2					3.9–4.6	3.3–3.8	0.5–4.1	3.6–4.0

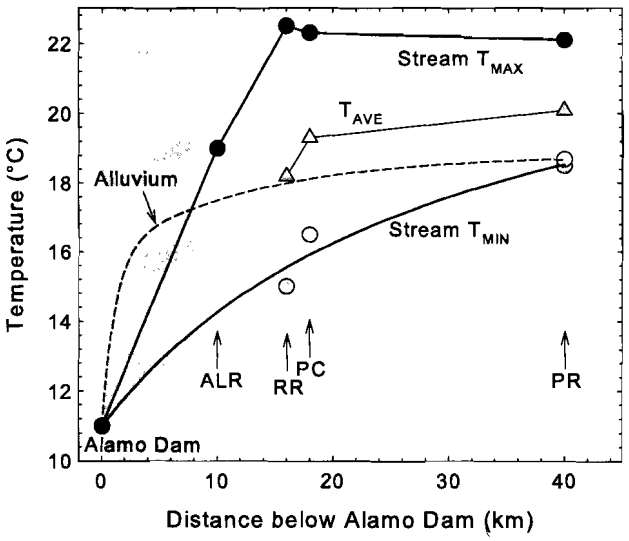

Fig. 5 Models of the relationships between surface water daily maximum (T_{MAX}) and minimum (T_{MIN}) temperature and distance along the Bill Williams River below Alamo Dam, based on Spring 2008 data (except for ALR T_{MAX} datum, which is estimated from 2007 data). A hypothetical temperature curve for alluvium through which hyporheic water passes is also shown (*dashed line*), based on inferred temperatures at Alamo Dam (equal to outlet water temperature) and PR (equal to ground water temperature; *open circle*). The shaded area depicts the segment of the BWR along which stream water is heated as it passes through the hyporheic zone; below that segment the water, depending on its temperature when it enters the alluvium, may be heated or cooled during hyporheic flow. Beaver ponds would affect hyporheic flows and thereby the position of each of the four curves

DO value <0.9 mg/L. DO in the pond dropped to 0.5 mg/L before rising to ~3 mg/L late that evening.

Geomorphology

The sediment particle size distributions under base flow conditions showed the expected gradient from finest in the downstream portion of the beaver pond (Lower Pond), to intermediate in the upper pond, and coarsest in lotic habitat (Table 2). ANOVA indicated a location effect at PC ($F_{2,8}$= 5.31; P=0.034), but only the two extremes (Lower Pond and Lotic) were significantly different (P=0.036). Sample sizes precluded statistical analysis at PR, but the trend in mean particle size followed the expected pattern. The mean and median particle sizes in all three locations were consistently coarser at PR than at PC (Table 2).

The 2008 flood resulted in a mixture of erosion and deposition on most channel cross-sections, including those through beaver ponds (Fig. 6). A net sediment gain was recorded on nine of the 13 channel cross-sections through beaver ponds, whereas net erosion occurred on four of the seven cross-sections in lotic reaches. Eight cross-sections (six in ponds) showed little change (<1 m^2; Fig. 4g). The most extensive deposition occurred in Pond PC-I, where >10 m^2 of bed material was added on one cross-section and 4.5 m^2 on a second (Figs. 4g and 6). The greatest net erosion, only −2.6 m^2, was along a RR lotic cross-section (Fig. 4g).

The flood led to a significant increase in mean particle size on the PC reach (Table 2; paired t-test, n=11, P= 0.012), but the gradation in mean particle size from finest in the pond near the dam to coarsest in lotic habitat remained evident ($F_{2,8}$=4.37; P=0.052). No consistent shift in mean particle size was evident on the four transects at PR (Table 2). The proportion of sediment in size classes classified as gravel tended to increase in lotic reaches and decrease in beaver ponds (Fig. 4f).

Discussion

Our pre-flood data characterizing stream and beaver pond hydrology, water quality, and geomorphology support the hypothesis that beaver affect stream habitats and riverine processes in warm deserts in essentially the same manner as they do in cooler, more mesic environments. We found beaver ponds had sediment particle size gradients and, at least in some cases, water temperature and DO gradients similar to those associated with beaver dams in non-desert environments (Meentemeyer and Butler 1999; Margolis et al. 2001; Snyder et al. 2006).

Although we found no novel effect, the unique attributes of desert streams could change the ecological significance of particular beaver effects. Warm-desert streams differ from mesic-region streams in their hydrologic (Poff 1996), thermal (Caissie 2006), and sediment regimes (Poff et al. 2006). Because the processes leading to water loss and high stream temperatures are major determinants of ecosystem structure in the water-limited desert riverine environment (Grimm et al. 1997), changes in their form or rate due to the presence of beaver dams could have particularly dramatic local or cumulative effects. For example, aquatic invertebrate (Stanley et al. 1994; Miller and Golladay 1996) and riparian plant (Stromberg et al. 2005) community structures differ between perennial and intermittent reaches, and an increase in evaporative losses caused by beaver dams could push already low downstream flows across the perennial-intermittent threshold.

Estimates of evaporative loss changes due to the presence of a beaver pond are rare. Vowinckel and Orvig (1973) modelled annual evaporative losses in cool, mesic southern Quebec, Canada and reported values suggesting a 0.5-m deep beaver pond lost ~12% more water than an unflooded decidous forest. Neither the accuracy nor precision of their estimates are known. The evaporation rate from a freshwater surface (E) is typically modelled as

Table 2 Sediment mean and median particle size (in φ units; see Note) in beaver ponds and adjacent lotic habitat on the Bill Williams River, Arizona, before and after the 2008 flood pulse. Mean values for the PC and PR reaches are tabulated, with standard error and sample size in parentheses (SE, *n*). Each mean is calculated from *n* transect means, with the latter derived from values at three locations on each transect (see Methods); *n*=1 for Upper Pond and Lotic reaches at PR. The distance between a Lower Pond transect and the closest downstream dam was 8–20 m at PC (*n*=3) and 16–20 m at PR (*n*=2). The analogous distance for an Upper pond transect was 92–132 m at PC (*n*=3) and 81 m at PR (*n*=1). Comparison of mean and median values indicates the direction of skew in the particle size distribution

Reach	Mean particle size (φ)			Median particle size (φ)		
	Lower Pond	Upper Pond	Lotic	Lower Pond	Upper Pond	Lotic
PC Before	0.22 (0.07, 3)	–0.12 (0.32, 3)	–0.47 (0.05, 5)	0.22 (0.10, 3)	–0.05 (0.30, 3)	–0.44 (0.05, 5)
After	0.08 (0.12, 3)	–0.26 (0.31, 3)	–0.56 (0.04, 5)	0.09 (0.13, 3)	–0.25 (0.32, 3)	–0.55 (0.03, 5)
PR Before	–0.57 (0.25, 2)	–0.69 (—, 1)	–1.01 (—, 1)	–0.47 (0.27, 2)	–0.25 (—, 1)	–0.79 (—, 1)
After	–0.55 (0.05, 2)	–0.53 (—, 1)	–1.29 (—, 1)	–0.37 (0.04, 2)	–0.35 (—, 1)	–1.27 (—, 1)

Note: φ diameter is computed by taking the negative log (base 2) of the particle diameter in millimeters. Thus, the smaller or more negative the value of φ, the larger the particle. By convention, the smallest gravel has a φ value between −1 and −2, and is just larger than the largest sand grain. Very fine sand has a φ value between 3 and 4. Transformation of particle sizes into φ units results in an approximately normal particle size frequency distribution (see, e.g., Bunte and Abt 2001)

$E=f(u) \cdot (e_s - e_d)$, where $f(u)$ is a function of horizontal wind speed (u), e_s is the vapor pressure at the evaporating surface, and e_d is vapor pressure in the above atmosphere (Penman 1948; Earls and Dixon 2008). Both e_s and e_d are strongly dependent on temperature, and thus e_s will be increased where a beaver pond warms surface water. For example, a rise in water temperature from 20°C to 25°C will increase the evaporation rate by 78% given an unchanging wind speed, 30°C air temperature and 30% relative humidity.

Surface water was warmed in some of the BWR beaver ponds but not others. This variability has also been noted in mesic regions. McRae and Edwards (1994) experimentally removed dams and found little effect on the difference between upstream and downstream temperatures, attributing the inconsistent insolation effect to local ground water inflow

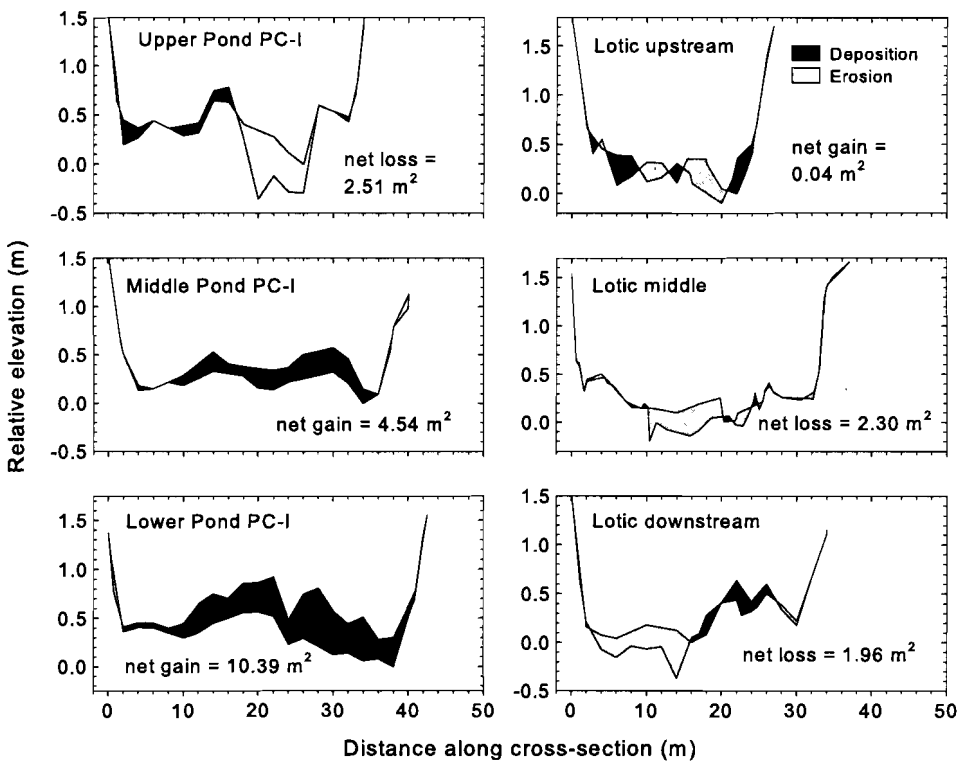

Fig. 6 Change in channel bed topography produced by the 2008 Bill Williams River experimental flood on channel cross-sections through beaver pond PC-I, which reminded functional, and in the lotic reach immediately below Dam PC-E, which was removed by the flood. The longitudinal position of each cross-section is shown in Fig. 4, bottom panel

and shading. We found T_{MAX} values consistent with warming in ponds at RR and PR, but not at PC, and no reach had T_{AVE} warmer in the pond than immediately upstream (Table 1). In our single comparison, ground water was cooler than T_{MAX} at PR. We assume phreatic ground water inputs were absent, and interpret these patterns as indicating hyporheic flow through alluvium with a temperature$<T_{MAX}$ was moderating warming in all three reaches, and most strongly at PC. Evidence of this process was the relatively cool, constant water temperature noted at PR Position 1 in 2007. Beaver dams increase hyporheic flows (Kasahara and Wondzell 2003; Westbrook et al. 2006), and Hester et al. (2009) demonstrated that the associated increase in advective heat flux can modify the temperature of both the substrate and surface water.

A theoretical consideration also suggests that the reduced current velocities and increased surface water areas in the BWR beaver ponds will not necessarily accelerate warming. The input of radiant solar energy per unit volume of water during its passage through a reach, whether pond or lotic, is inversely proportional to the product of V_{AVE} and D_{AVE} (see Online Resource 1). In this study, the values of this product in beaver ponds and in lotic reaches overlapped considerably (Online Resource 1), suggesting that creation of a pond might actually reduce heat gain. Nevertheless, the mean V*D value for BWR beaver ponds was only half that for lotic reaches, suggesting construction of a dam will likely increase surface water heat gain. Beaver dam effects on water temperature may be most apparent during summer, when insolation is highest.

The observed river-scale downstream rise in T_{AVE} (Table 1) is typical of rivers in all climate regions (Caissie 2006). The absence of a similar longitudinal gradient in T_{MAX} downstream of RR (Fig. 5) suggests that daytime solar radiation and other energy inputs were already sufficiently intense by early April to maximally warm the dam outflow during its passage to RR, with evaporative and other cooling mechanisms subsequently constraining T_{MAX} to a relatively constant level (Mohseni and Stefan 1999; Bogan et al. 2006).

The river-scale downstream rise in T_{MIN} (Table 1, Fig. 5) may reflect extensive hyporheic heat exchange. The PR ground water temperatures (19–20°C) suggest seasonal temperature dynamics in the unsaturated BWR alluvium are similar to those documented in unsaturated sandy alluvium (30 cm depth) under mesquite along the nearby Colorado River: an annual minimum (13 to 16°C) in December to February, a rise to 20°C in March or April, and a peak above 30°C in August (D.C. Andersen, unpublished data). If so, the cool water released from the dam was gaining heat during episodes of hyporheic flow through the relatively warm alluvium, as well as from insolation during daytime surface flow. This caused T_{MIN} to rise until it reached the temperature of the alluvium (Fig. 5), after which further increase would be dampened by hyporheic cooling.

A reduction in beaver pond DO is expected where high amounts of detritus fuel the activity of aerobic decomposer microbes (Cirmo and Driscoll 1993; Songster-Alpin and Klotz 1995). Numerous studies from non-desert regions report retention of fine particulates, including OM, in ponds (e.g., Naiman et al. 1986). In the only desert-region assessment we are aware of, Harper (2001) reported OM concentrations nearly three times higher in beaver pond sediments than in upstream or downstream lotic reaches along a perennial Mojave Desert stream. An inconsistent DO reduction in beaver ponds (Table 1) has been attributed to various factors, including variation in OM availability (Snodgrass and Meffe 1998; Stevens et al. 2006).

Flood Impacts on Hydrology, Water Quality, and Geomorphology

Based on the 2008 flood's rapid rise and recession and the short duration at Q_{MAX}, the damage to beaver dams and associated hydrologic changes (Table 2, Fig. 4) were probably similar to those that would result from a natural flash flood of similar Q_{MAX}. Clearly, geomorphic and hydrologic changes to physical habitats were moderate relative to those produced by floods of higher Q_{MAX} and longer duration, such as the 2005 release (~200 m^3/s) that destroyed all dams along the BWR (Andersen and Shafroth 2010) and transported ~2.7×10^5 metric tons of silt and sand into Lake Havasu (Wiele et al. 2009).

The abrupt DO decline noted in Pond PC-H following the 2008 flood pulse suggests the possibility that pre-flood heterotrophic respiration was carbon-limited, as has been documented in a geomorphically similar Sonoran Desert lotic stream reach (Uehlinger et al. 2002). If OM was washed into the pond from Dam PC-I, which seems likely, a high oxygen demand by microbial decomposers could have been triggered. An influx of dam debris into Pond PR-C is also the likely explanation for the pre- to post-flood DO decline observed there (Table 1).

The expected flood-induced aggradation in ponds where dams retained functionality was noted in several cases following the 2008 flood (Figs. 4g and 6). A major question is the extent to which the short duration of the 2007 and 2008 floods limited dam damage (Andersen and Shafroth 2010) and thereby restricted downstream sediment transport. For example, significant sediment deposition occurred upstream of and near dam PC-I, which remained largely intact (Fig. 6). Only two of 13 cross-sections through beaver ponds showed notable net sediment loss after the 2008 flood (Fig. 4g), and in one of those cases (Dam PR-A) the downstream dam also remained more-or-less intact.

Presumably, overtopping and through-flow permitted current velocities sufficiently high to mobilize pond bed material. Net erosion was prominent on two of the three cross-sections in the lotic reach immediately below Dam PC-E, which was completely removed by the flood (Fig. 6).

Beaver Ponds, Floods, and Desert Stream Aquatic Habitat

Our data indicate that beaver ponds on warm-desert streams, like their counterparts in other climate regions, provide physical habitat for lentic-adapted organisms and retain fine materials that can affect benthic invertebrate diversity and productivity (e.g., Anderson and Rosemond 2007). This study also suggests that beaver ponds have potential to influence temperature regimes of surface water, shallow sediment, and perhaps (via hyporheic flows) floodplain soils. Because these temperatures affect a wide array of plants, animals, and microbial processes, the heat flux patterns in the BWR and other desert riverine ecosystems, both with and without beaver, deserve study. The possibility that beaver increase evaporative losses in an already water-limited ecosystem further underscores the need to elucidate seasonal thermal patterns and their link to hydrologic processes.

Despite their relative rarity in desert environments, beaver populations on desert streams are of considerable resource management and conservation interest (Pollock et al. 2007; Soykan et al. 2009). Environmental flows can be used as a tool either to promote the persistence and expansion of beaver (via managed base flows) where their effects are considered desirable (Pollock et al. 2007) or to remove beaver dams (via controlled floods) where the dams or ponds are clearly linked to an undesirable shift in riparian or aquatic ecosystem attributes. The 2008 experimental flood (65 m^3/s) destroyed some beaver dams, but the majority survived (Andersen and Shafroth 2010), and our results suggest that a portion of the sediment mobilized by the flood was captured behind them. The BWR is serving as a research laboratory where monitoring responses to a variety of flood magnitudes and durations should provide insight into the hydrologic and geomorphic effects of beavers on riverine ecosystems in and beyond the desert Southwest. A clearer understanding of both beaver effects and how to manage them in desert as well as non-desert environments will help water resource managers design environmental flows to achieve both ecological and water supply/conservation goals in systems where beaver are present.

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