IMPACT OF DAMS ON POINT BAR HABITAT: A CASE FOR THE EXTINGUISHMENT OF THE SACRAMENTO VALLEY TIGER BEETLE, *C. HIRTICOLLIS ABRUPTA*

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ABSTRACT

Quantitative analyses of flow and stage data, remote sensing and geographic information systems analysis, and field studies were used to assess the impact of dams and diversions on the point bar habitat of the Sacramento Valley Tiger Beetle (*Cicindela hirticollis abrupta*). The reaches of interest include sites of known historic populations of *C. h. abrupta* along the Sacramento River from approximately 8 km north of Colusa southward to the confluence with the Feather River and along the Feather River between Yuba City and its confluence with the Sacramento River. The results from this study show that construction of two major dams has altered flows such that prolonged and increased flows during summer, fall, and early winter have most likely disrupted life cycles, flooded larvae, drowned overwintering adults and led to high mortality. Additionally, habitat availability has decreased over time because point bars have decreased in number and area causing increased distances between populations and isolation of populations. Moreover, point bar armouring, channel scouring, altered flows, redirected flows through weirs, and lithologic controls have produced a bimodal distribution of mean grain sizes in the Sacramento River in which the more northern bars contain gravel deposits and more southern bars possess fine sands. These conditions negatively affect moisture retention and sediment compaction and, consequently, burrowing conditions needed by this tiger beetle. Additionally, more stabilized flows (reduced variability) and increased fine-grained deposition have enabled development and encroachment of vegetation onto the sand bars. Finally, human stresses, such as foot traffic and vehicular traffic may have interfered with burrowing, ovipositing, and foraging. The combination of these stress factors has most likely led to a reduction in source populations and, ultimately, the apparent extinction of the entire metapopulation. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS: dam impact; point bar habitat; tiger beetle; extinction; GIS; stage duration; exceedance probability; Sacramento and Feather Rivers

INTRODUCTION

Natural periodic flooding that characterizes many river systems exerts an important control over the structure and function of aquatic and riparian ecosystems (Junk et al., 1989; Szaro, 1991; Bayley, 1995). The successful completion of the life cycles of many species occurring in these two ecosystems critically depends on the annual variations in these hydrologic conditions (Poff and Ward, 1989; Wenninger and Fagen, 2000; Lytle and Poff, 2004). Throughout much of the western United States (US), in particular, modifications in river flow have disrupted natural hydrologic regimes (Williams and Woman, 1984; Junk et al., 1989; Benke, 1990; Rodd and Mahoney, 1990; National Research Council, 1992; Lagasse, 1994; Glenn et al., 1995; Hauer and Lorang, 2004). The case of the Sacramento River and its tributaries serves as an instructive example where 65 dams, diversions, and other engineering projects have altered natural conditions to the detriment of stream and riparian wildlife populations and vegetation (State of California, 1994; Nelson and Lieberman, 2002; Sommer et al., 2004). Within the Sacramento River Valley, human activities have negatively affected populations of the chinook salmon, bank swallow, yellow-billed cuckoo and the Sacramento Valley longhorn elderberry beetle (State of California, 1994). This paper examines causes for the apparent extirpation of a tiger beetle species native to the Sacramento River system.

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Tiger beetles are a common component of river edge ecosystems throughout the world. Adults forage along the wet substrates where they capture small arthropods or scavenge on dead organisms. Larvae occur in permanent burrows of the beach or point bars where they capture small arthropods that pass near their burrow mouth. Because many tiger beetle species exist as metapopulations, their survival depends on frequent recolonization of new, often ephemeral habitats. The Sacramento Valley Tiger Beetle, *Cicindela hirticollis abrupta*, occurs on river point bars, and a reduction in the area or number of bars would result in an increase in the distances between and isolation of subpopulations. In turn, a decrease in bar numbers and/or size would limit beetle recolonization, lead to a reduction in source populations and, ultimately, extirpate the entire metapopulation. Indeed, various populations of this species throughout the US have declined or been extirpated over the past several decades as a result of water edge habitat disturbance from human activities (Nagano, 1980; Dunn, 1981; Knisley and Schultz, 1997; Larochelle and Lariviere, 2001). Along the Rio Grande, for example, Knisley and Hill (2001) found *C. hirticollis shelfordi* at fewer sites and in much smaller numbers than historic records indicated and hypothesized that the decline resulted from dams and water level changes. *Cicindela h. rhodensis* has also become extinct over much of its range in the northeast as a result of river and coastal shoreline changes (Larochelle and Lariviere, 2001).

Knisley (2003) postulated that altered water levels, due to controlled water releases from two large dams, caused the apparent extirpation of *C. h. abrupta* populations within the Sacramento River system. In particular, Knisley (2003) suggested that decreased flood frequency and less variable flows impacted *C. h. abrupta* habitat negatively by stabilizing the bars, decreasing sandy habitat area, and increasing vegetation growth. Knisley (2003) also postulated that prolonged high water levels could have flooded the point bar habitats and, consequently, drowned larvae which spend 4–5 months on the bars during development and adults which overwinter there. Thus, changes to the flow regime could have both reduced habitat availability and disrupted the life cycle of *C. h. abrupta*. Moreover, altered water levels changed the river's sediment transport regime, stream gradient, stream bank characteristics (including vegetative cover), and water quality (State of California, 1994; Singer and Dunne, 2004).

The primary anthropogenic factors that may have affected *C. h. abrupta* habitat include, but are not limited to, hydraulic mining (1852–1895), irrigation (beginning c. 1910), the Sacramento River Flood Control Project (beginning c. 1917), Shasta Dam (1945), the Trinity River Diversion (1963), and the Orovillo Dam (1968). In addition, urbanization, gravel mining and bank protection may have contributed to the reduction in suitable *C. h. abrupta* habitat conditions (Jones, 1967; State of California, 1994). In particular, damming has caused downstream sediment starvation, scouring, and consequent habitat loss along the river's fringing bar and floodplain system (State of California, 1994; US Department of Interior. Bureau of Reclamation, 2003). This research determined the post-dam construction impact on *C. h. abrupta* habitat within the Sacramento River Valley, California using the following variables: (1) Pre- and post-dam flow/stage characteristics of the Sacramento River and Feather River; (2) Pre- and post-dam sand ('edge' or point) bar numbers and area; and (3) Sand bar geologic and biotic characteristics. Specifically, this research sought to identify the limiting hydrologic and geologic factors responsible for the apparent demise of this species.

**SACRAMENTO VALLEY TIGER BEETLE: Cicindela hirticollis abrupta**

*Cicindela hirticollis* is a widely distributed species in the US with 11 recognized subspecies. It occurs in a variety of sandy water edge habitats including both Atlantic and Pacific coasts, major estuaries, large lakes and major rivers of the US and Canada. Casey (1913) first described the Sacramento Valley Tiger Beetle, *C. h. abrupta*, from Sacramento and Graves *et al.* (1988) confirmed its validity as a subspecies (Figure 1). The known historic distribution of *C. h. abrupta* was limited to a few sites along the Sacramento and Feather Rivers (Graves *et al*., 1988). Further studies of the historic and current distribution confirmed this limited historic distribution (but it was probably more widespread within this range) and found it no longer existed at these or other potential habitats within central California (Knisley and Fenster, 2005). Adults of *C. h. abrupta* and other subspecies in California are most common in April, May and September but active from late March to October. Adults forage actively along the water edge of sand bars and typically oviposit in moist sediment within several meters from the water edge where they establish the larval habitat. The life cycle includes three larval stages and is probably completed in 1 year in California.
STUDY AREA

The Sacramento River is the largest river in California, providing 35% of the water supply while draining 17% of California’s land area (State of California, 1994). The Sacramento River watershed includes 70,000 km$^2$ and has its headwaters near Mt. Shasta (Figure 2). The Feather River watershed covers 8352 km$^2$ and has its headwaters in the northern Sierra Nevada Mountains. The confluence of these two rivers occurs approximately 20 km north of Sacramento at Verona. From the confluence, the Sacramento River drains south and west into San Francisco Bay.

The primary study area for habitat assessment included the portion of the Sacramento River Valley with known historic populations and the most recent records of C. h. abrupta (Knisley, 2003; Knisley and Fenster, 2005; Figure 2). The beetle occupied an area of the Sacramento River from the city of West Sacramento north to Colusa and along the Feather River near Nicolaus (Knisley, 2003; Figure 2). Information we obtained from earlier collectors, aerial photographs, and field surveys indicated that all of these known collection sites contained extensive, wide and low sand bars that were periodically flooded by high waters and where moist sediment occurred near the surface. The majority of the collection records, including the most recent ones (until 1985), came from an extensive sand bar located on the Feather River near Nicolaus (the abundance in the record keeping may relate to site accessibility; Knisley, 2003). The beetle’s disappearance from this site probably followed soon after these records were obtained because various workers searched for, but could not find, the beetle during the 1990s (Knisley and Fenster, 2005). Along the Sacramento River, the last known collection records for this beetle came from Colusa in 1955. However, the timing of potential extirpation after this date is unknown (Knisley and Fenster, 2005). The inability to locate the beetle along the Sacramento River Valley resulted in a petition to list C. h. abrupta as federally endangered under Section 4 of the United States Endangered Species Act of 1973.

METHODS

A combination of field, laboratory, and computer-aided techniques were used to characterize present-day point bar habitat conditions and quantify historical temporal and spatial changes to the known habitat. Quantitative analyses of flow and stage data assessed the impact of altered flows on the hydrology of the Sacramento River and Feather River. A remote sensing and geographic information systems (GIS) analysis enabled a detailed regional habitat assessment of an approximately 45 km reach along the Feather River between Yuba City and the confluence of the Sacramento River and Feather River near Verona, and a shorter reach (~10 km) on the Sacramento River near Colusa. The on-site field sampling and assessment focused on Sacramento River miles 144–152 (12.9 km reach north and south of Colusa); Sacramento River miles 88–94 (9.7 km reach near Knight’s Landing); and an 8 km reach along the Feather River from Algodon to Nicolaus (Figure 2).
Stageflow analyses

We used stageflow data from two United States Geological Survey (USGS) and California Department of Water Resources (DWR) stream gages in the Sacramento River Valley to assess the impact of temporal and spatial hydrologic changes in the reaches of *C. h. abrupta* habitat and to standardize river conditions on aerial photographic data sets (see below). Consequently, the selected gages are located in proximity to historic population sites of *C. h. abrupta* and in areas containing extensive aerial orthophotography data sets.

USGS gage 11389500 on the Sacramento River at Colusa contains discharge data from 11 April 1921 to present and has an upstream drainage area of 31 313 km². In order to assess the impact of Shasta Dam and the Trinity River diversion on the flow regime, we followed the convention of State of California (1994) who divided the hydrologic history of the Sacramento River into three periods based on human alterations: (1) April 1921 to December 1943: pre-Shasta dam; (2) December 1943 to December 1963: post-Shasta dam and pre-Trinity River diversion; and (3) December 1963 to present: post Trinity River diversion of water into the Sacramento River. The Trinity River Diversion project (a.k.a. post Shasta and pre-Whiskeytown Dam), effectively diverts 68% of its water through a power plant into Keswick Lake which then (in coordination with downstream tributary inflows) discharges it into the Sacramento River. The Trinity River Diversion resulted in a 15% increase in the mean annual discharge of the Sacramento River (State of California, 1994).
C. h. abrupta habitats along the Feather River are primarily impacted by alterations to flow as a result of Oroville Dam although the State of California (2002) states that the confluence of the Feather River and Yuba River is the downstream extent of observable affects. Construction of Oroville Dam began in 1961 and ended in 1968. Consequently, we separated these data into two hydrologic periods (1941–1968 and 1969–1983) in order to analyse the impact of Oroville Dam on Feather River flows. However, along the Feather River, gage data at Yuba City (gage 11407700) at the northern limit of the study area only span the period 1 October 1964 to 30 September 1984 and, therefore, do not contain both pre- and post-dam data. Downstream on the Feather River at Nicolaus (gage 11423000/NIC; drainage area = 21.355 km²), the hydrologic data were available in two formats. For the period 1 April 1942 to 30 September 1983, the USGS provides discharge data (cfs). In January 1984, the California DWR took over operations of this gage, but reports only stage data (ft). This discrepancy constrains quantitative time series stream flow/stage analyses. Moreover, the lack/unavailability of USGS rating curves precluded conversion of the data to a consistent format. In order to analyse point bar changes along the Feather River, we standardized flow and stage data by exceedence probabilities (EPs). This method also enabled us to develop a consistent format for the bar area analysis by linking pre-1984 discharge values with post-1984 stage values (see below).

Aerial photographic analysis of point bar habitat

A remote sensing analysis of selected reaches within the Sacramento River system was used to quantify the temporal and spatial changes to point bar size and numbers. Orthophotographs were obtained from a variety of sources that included the US Bureau of Reclamation, US Department of Agriculture, USGS, California DWR, and private aerial photographic service companies. Most photographs contained scales of 1:12,000, but ranged up to 1:40,000 for one gage (16 June 1993 on the Sacramento River). All orthophotographs were rectified and georeferenced for use in ArcGIS (ArcView 8, ESRI, Inc). In addition, hand-held global positioning system (GPS) data, obtained from the perimeter of selected bars during the field assessment and data collection phase (2–4 October 2003), were input into ArcMap. River points bars that were considered to be suitable habitat contained a 'fresh,' unvegetated, sandy appearing surface on the photographs. Relief, stabilized, and/or vegetated point bars were not considered habitat unless they had been exposed and reworked by recent erosion or experienced recent deposition.

Areas examined included: (1) one point bar of known historic beetle populations on the Sacramento River at river mile 144 near Colusa; and (2) an approximately 45 km reach along the Feather River from Yuba City to the confluence of the Feather River and Sacramento River near Verona (Figure 2). The Sacramento River data base consisted of eight sets of aerial photographs that spanned the period 1937–1999 (Table I). The set contained at least one photograph from each decade and concentrated on a single point bar with known historical populations of C. h. abrupta. In addition, the site was located near the Colusa stream gaging station. This data base provided excellent hydrologic control and relatively extensive temporal coverage in a region of previously reported beetles. Stages on the days of aerial photography ranged from 9.4 m (95.8% EP) to 15.3 m (26.3% EP) (Table II). Additionally, we conducted a qualitative assessment of habitat using aerial photographs and field observations of the Sacramento River from Colusa to the confluence of the Sacramento River and Feather River (river miles 80–142), with emphasis on the regions north and south of Knights Landing. For the Feather River, the spatial

<table>
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<th>Stage (m)</th>
<th>Rank of 1286</th>
<th>Exceedence probability %</th>
</tr>
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<tr>
<td>6 September 1937</td>
<td>9.4</td>
<td>1249</td>
<td>95.8</td>
</tr>
<tr>
<td>5 June 1942</td>
<td>15.3</td>
<td>338</td>
<td>26.3</td>
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<td>30 July 1958</td>
<td>13.7</td>
<td>532</td>
<td>41.2</td>
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<td>31 May 1964</td>
<td>12.8</td>
<td>745</td>
<td>57.9</td>
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<tr>
<td>25 September 1974</td>
<td>13.6</td>
<td>531</td>
<td>41.3</td>
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<tr>
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<td>14.5</td>
<td>369</td>
<td>28.7</td>
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<td>14 June 1999</td>
<td>13.7</td>
<td>503</td>
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coverage included the identical river reaches as described under (2) above including the Nicolaus area where the vast majority of collection records exist. The temporal coverage spanned the period 1956–1999 with one data set per decade. Most aerial photography covered the entire reach of interest in 1 day. In two cases within this Feather River reach, however, the photography that produced the mosaic coverage spanned several days or years. In these cases, stage, rank and EPs were averaged as needed.

The number of bars exposed and their areas depend on the river stage at the time of photography. Consequently, these variables were adjusted by standardizing by the river conditions. However, because of the shift in data availability for the Feather River gage, bar areas were standardized by EPs calculated for the two individual hydrologic periods rather than by discharge or stage (Table II). Standardizing the average bar areas by the EP gives the average bar area per unit EP. In theory, we would expect photographs obtained during low EP events to show the smallest bar areas and photographs obtained during high EPs to show the greatest areal exposure of point bars.

Sediment size distribution of point bar habitat

In order to investigate the geologic character of point bars in the reaches of known historical C. k. abrupta habitat, we examined individual point bar grain size distributions and longitudinal grain size trends within each river system. During the period 2–4 October 2003, we sampled six sand bars along a 13 km reach of the Sacramento River near Colusa (river miles 144–152) and five sand bars along a 10 km reach north and south of Knight's Landing (river miles 88–94). In addition, we sampled six sand bars along the Feather River from Algodon to Nicolaus covering an approximately 11 km reach. Point bar sample site locations were selected based on beetle behaviour. Adults forage actively along the water edge of sand bars and typically oviposit in moist sediment within several meters from the water edge where they establish the larval habitat. Consequently, samples were obtained from three locations along the perimeter of each point bar including the upstream, mid-bar and downstream portions. This sampling scheme provided 18 samples from Feather River bars and 36 samples from Sacramento River bars. We used standard sample splitting and dry sieving by Ro-tap mechanical shaking techniques to sort samples into 1 φ size ranges (Krumbein and Pettijohn, 1938). Grain size distribution statistics were calculated using the logarithmic method of moments (Folk and Ward, 1957).
**Impact of Dams on Tiger Beetle Extermination**

![Graph showing daily stage duration and percentage of time stage is equalled or exceeded for USGS gage 11389500 on the Sacramento River at Colusa by hydrologic periods.](image)

Figure 3. (A) Daily stage duration curve for USGS gage 11389500 on the Sacramento River at Colusa by hydrologic periods.

**Results**

*Flow/Stage characteristics of the Sacramento River*

Analyses of the Colusa stream gage data show that the daily and mean stage values increased following dam construction. Daily stage values ranged from 8.3 m prior to Shasta Dam completion (25 July 1931) to 20.0 m after Shasta Dam (4 March 1983) over the period of record. The data show that the pre-Shasta mean stage (11.0 ± 1.3 m) was the lowest of the three hydrologic periods and the post-Trinity average stage (14.2 ± 1.9 m) was the highest of the three periods (post Shasta Dam, pre-Trinity Diversion = 13.8 ± 1.9 m). Moreover, 10-year increments of stage data reveal a post-Shasta increase in average daily stages (more than 2.7 m) and standard deviations (±0.3 to ±0.7 m). However, stages recorded at the Colusa gage are lower than the stages at upstream gages (i.e. Vina, Hamilton City, and Butte City gages) because of weirs that redirect flood overflow (State of California, 1994).

*Stage duration and exceedence probability.* Daily stage duration curves for the various hydrologic periods on the Sacramento River reveal that any given post-Shasta stage has a higher EP than for any given pre-Shasta stage (Figure 3). For example, the 10% pre-Shasta Dam EP of 15.0 m rose to 16.6 m after Shasta Dam and 17.3 m after Trinity Diversion. The 50% EP rose from 11.1 m prior to Shasta Dam to 13.2 m after the dam and 13.8 m after Trinity Diversion. The 90% EP also rose from 9.6 to 12.3 and 12.4 m during the same time period. In short, after construction of Shasta Dam, any given stage became more likely to be exceeded than prior to Shasta Dam and stages that flooded the bars increased after dam construction. Moreover, the stage duration curves show that the EPs of 1963–2003 exceeded those of 1941–1963 indicating that flooding of bars became even more likely after completion of the Trinity Diversion (Figure 3).

*Seasonality analysis (mean monthly probabilities).* Comparison of mean monthly probabilities from the Colusa gage for the hydrologic periods indicates that Shasta Dam increased minimum flows and decreased maximum flows (Figure 4) and corroborates the results of State of California (1994). Although missing data for the months February, March and April prevented an analysis of pre- and post-Shasta changes for those months, extrapolations and available data reveal general trends. The most noticeable effects of the dam on stage occurred between June and November (Figure 4). For example, the stage at the 10% EP during June increased from 9.7 to 12.4 m after Shasta Dam and to 13.0 m after Trinity Diversion. The June monthly stage at 50% EP increased from 11.8 to 13.0 and 13.6 m during these same time periods. Likewise the 90% EP rose from 13.7 to 14.0 and 15.1 m during June. The July stages increased by nearly 3 m at the 10% EP, 2.5 m at the 50% EP, and 1.6 m at the 90% EP. Comparatively, the
January stages increased by only 0.5 m at the 10% EP, but lowered by 1.9 m at the 50% EP and 0.2 m at the 90% EP. In short, after construction of Shasta Dam, stages became greater during the months June–November, but the range of stages decreased during this same time period.

Flood frequency analysis. Limited data exist for the pre-dam period and preclude a pre- versus post-dam analysis. However, long-term post dam data show that peak floods range from 16.7 to 21.1 m (Figure 5). A noticeable inflection point on the flood frequency plot occurs at approximately 20.6 m whereby, above this stage,
smaller changes in peak flood stages result in longer recurrence intervals (Figure 5). It should be noted that, of the top 11 floods that were greater than the inflection point stage of 20.6 m, three occurred in the 1990s (3 January 1997, 21.0 m; 5 February 1998, 20.7 m; and 11 January 1995, 20.6 m). Additionally, all peak floods occurred between the months of November and March.

Flow/stage characteristics of the Feather River

Similar to the Sacramento River and Shasta Dam, discharge increased along the Feather River after installation of Oroville Dam. Overall, discharge data from the Nicolaus stream gage for the period 1 April 1941 to
Figure 6. (A) Daily discharge for (old USGS) gage 11425000 (now DWR/PLG NIC) on the Feather River at Nicolaus from 1 April 1941 to 31 September 1983. Dashed lines indicate period of Oroville Dam installation (1961–1968). (B) Pre- (1 April 1941 to 31 December 1967) and post- (1 January 1968 to 30 September 1983) Oroville Dam daily discharge duration curves using USGS gage 11425000 data.

30 September 1983 show that the daily flow values ranged from 2.9 m$^3$ s$^{-1}$ (1 July 1966) to 8863.2 m$^3$ s$^{-1}$ (23 December 1955) with a mean flow of 240.5 m$^3$ s$^{-1}$ from 1941 to 1983 (Figure 6A). The 10, 50 and 90% pre-Oroville EPs were 538.0, 10.3 and 16.9 m$^3$ s$^{-1}$, respectively whereas the post-Oroville EPs increased to 580.5, 156.3 and 51.2 m$^3$ s$^{-1}$, respectively at the same EPs (Figure 6B). These data indicate that flow increased by approximately 7% (at the 10% EP) to 67% (at the 90% EP) after Oroville Dam.

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Daily stage plots from 1984 through 2003 reveal that the period 1993–2003 contained longer duration and a greater number of high flows than the period 1984–1993 (Figure 7). For example, 10 floods greater than +1 σ occurred in the period from 1993 to 2003 while only 2 floods greater than +1 σ occurred prior to 1993. In addition, 39.4% of stages exceeded the mean of 7.2 m after 1993 while only 15.6% of the stages exceeded the mean between 1984 and 1993. Krusheley (2003) noted that a stage of 6.7 m completely floods the bar at Nicolasas where beetles once occurred. The stage data indicate that, prior to 1993, 29.7% of the stages exceeded 6.7 m whereas, after 1993, 52.2% of the recorded stages surpassed the bar flooding stage of 6.7 m. The low stages occurring during the 1984–1993 time period correspond to the longest drought period on record (6 years; State of California, 1994). However, the likelihood of bars flooding in the Nicolasas reach nearly doubled after 1993.

*Seasonality Analysis (Mean Monthly Probabilities).* Seasonal analyses for the Feather River using 1944–1983 discharge data show that discharge increased during summer, fall, and early winter following dam construction (Figure 8). For example, during July, the discharge increased from 72.2 to 229.4 m$^3$/s at the 90% EP, from 22.1 to 153.1 m$^3$/s at the 50% EP, and from 10.4 to 70.6 m$^3$/s at the 10% EP. In fact, July and September experienced a fourfold increase in flow after construction of the dam while August witnessed an eightfold post-dam increase in discharge. In contrast, winter and spring flows generally decreased or remained constant at BPs = 75% (Figure 8). For example, during February, flows increased by 17% from 762.6 to 894.0 m$^3$/s at the 90% EP, but decreased from 625.5 to 606.4 m$^3$/s at the 75% EP, 389.1 to 258.5 m$^3$/s at the 50% EP, and from 131.4 to 92.2 m$^3$/s at the 10% EP. Additionally, like the Sacramento River and Shasta Dam, minimum flows increased and maximum flows decreased along the Feather River after installation of Oroville Dam.

*Sand ('edge' or point) bar habitat assessment: Sacramento River*

The results from the remote sensing analysis of the Colusa point bar that previously contained populations of *C. h. abrupta* show a relatively weak correlation between stage and bar area although the expected trend of decreasing bar area with increasing stage emerged (Figure 9A). However, the standardized data (in m$^2$/m based on known stage at the time of photography) indicate that during the construction of Shasta Dam (1937–1942), the
Figure 8. (A) Pre-Oroville Dam and (B) Post-Oroville Dam monthly probability plots for gage 11425000 on the Feather River at Nicolaus by hydrologic periods

point bar experienced a dramatic decrease in area by more than 50% (Figure 9B). After construction (1942–1999), the bar continued to diminish in size, but at a rate that was an order of magnitude lower than prior to 1942 (Figure 9B). Moreover, the photographs and field data reveal an increase in vegetation on the bar and increased human recreational activities that include foot and vehicle traffic (Figure 10). This combination of point bar habitat data indicates that intensive habitat alterations have occurred in this area.
The qualitative assessment using aerial photographs and field observations of the sand bars located between the confluence of the Sacramento River and Feather River (river mile 80) and Colusa (river mile 142) and direct field observations between river miles 88 and 94 showed similar unsuitable habitat conditions. In particular, the bars in this reach were widely separated, situated high above the water surface, and steeply sloped (Figure 11).

*Sand (‘edge’ or point) bar habitat assessment: Feather River*

The results from the remote sensing analysis of Feather River point bars along the 40 km reach from Yuba City to Verona show that, without correcting for discharge or stage, the total bar area and the average bar area (at the time of
Figure 10. (A) Aerial orthophotographs of the Sacramento River point bar at Colusa on 6 September 1937 and (B) 14 June 1999 (at same scale) showing a major increase in vegetative covering. Arrows point to point bar on left bank. (C) Ground photograph showing variation in anthropogenic stresses on point bar habitat. This figure is available in colour online at www.interscience.wiley.com/journal/tra

aerial photography) along the Feather River reach generally decreased over the 42-year period (1956–1998) (Figure 12). The total number of bars, again not corrected for discharge or stage, fluctuated during this time period (Figure 12B).

The standardized data (by EP because of the data reporting discrepancy) of Feather River point bars reveal more dramatic changes. Specifically, these data show that the pre-dam period contained both abundant and large river bars that diminished in numbers and size after dam construction (Figure 12). The first aerial photographic data set from 1956 revealed that this reach contained 21 bars with the largest average area (66.875 m$^2$), but the lowest EP (8.7%) of the five dates (Figure 12). This data set indicates that this sediment-rich reach consisted of very large bars—even during high flows. In 1967, the number of bars increased to 35 displaying an average area of 50,343.6 m$^2$ as expected for a relatively high EP of 80.6%. In 1975 following dam installation, the bars exhibited the
second largest average area of the five dates (54 251.7 m$^2$) during high flow conditions (EP = 21.0%). However, the number of bars decreased by more than half from 35 in 1967 to its lowest number of 15 in 1975. In 1986, the number of bars increased by fragmentation to 35, while at the same time, decreasing their size (29 145.1 m$^2$). Given the high EP (91.8%) we would expect, and found, a large number of bars exposed on the 1986 photographs. However, their
areas reduced in size by 46%. Finally, the 1990s data show that bars exhibited the second smallest average area (31,967.9 m²) of the 1956–1998 data set (behind 1986) and the second lowest number of bars prior to this date despite the average EP (57.3%). In short, the GIS aerial photographic analyses show that the point bars decreased in both number and area during the 42-year study period (Figure 12).
The photographic data also show that an increase in vegetation occurred on some of the point bars over time—especially near the critical habitat area near the water's edge (Figure 13). In addition, our early October field investigation revealed that several of the bars in this river system contained dense vegetation extending from the landward extent of the bar (e.g., levee or terrace) to the water's edge (Figure 13; see 'Sedimentologic Characteristics' below).

Sedimentologic characteristics: Sacramento and Feather Rivers

Four primary results indicate that coarse-grained sediments dominate the point bars in the upper reaches (but downstream of the dams) of the Sacramento River and Feather River and that the bars fine substantially downstream. First, coarse to very coarse sands dominated the water's edge samples along the Sacramento River in the region of Colusa (mean of all bars = 1.4 mm; Figure 14A). Second, the Sacramento River near Colusa is seven times more coarsely-grained (mean of all bars = 1.4 mm) than the Sacramento River near Knight's Landing to the south (mean of all bars = 0.2 mm). Third, the lower Sacramento River near Knight's Landing contains the finest sand bars of all three sample locations (each point bar averaged 0.2–0.3 mm, fine sand). Finally, the point bars in the
Figure 14. Mean grain sizes for water's edge point bar samples along the (A) Sacramento River and (B) Feather River. The Sacramento River samples come from a 13 km reach near Colusa (river miles 144-152) and a 10 km reach near Knight's Landing (river miles 88-94). The Feather River samples cover an 11 km reach from Algodon to Nicolaus. Percentages indicate gravel percent.

Feather River are dominated by very coarse sand to the north (the mean of the northern-most bar in the study area near Algodon = 1.0 mm) and coarse, but (mostly) by medium, sands to the south (0.4-0.5 mm) (Figure 14B). Both the Sacramento River and Feather River systems had similar sorting values which ranged from 0.5 to 0.6 mm.

Despite the mean grain size results noted above, the northern-most point bars along both rivers possessed gravelly surfaces and gravel berms (Figure 15). Surface samples ranged from sandy gravel to gravelly sand.
diameter = 4 cm). The Feather River point bars ranged from 21.2% gravel at the northern most point bar to 0% at the southern most point bar (Figure 14B). The northern point bar contained more than 10 times more gravel than the bar located immediately to the south. The point bars in the Colusa reach on the Sacramento River averaged 46.4% gravel (range = 15.3–60.5%) whereas the point bars in the Knight’s Landing reach to the south averaged 0.1% (range = 0.0–0.7%) (Figure 14A). At some locations, these gravelly surfaces extended to depths of approximately 10–20 cm. Additionally, portions of individual sand bars contained megaripples providing evidence for relatively high-energy flows, while other portions of the same bars contained silt and mud pointing toward a less energetic depositional environment. In many locations, a veneer of silt and clay covered the megaripple troughs and crests (approximately 1–2 cm thick). This wet layer of fine particles provides ideal conditions for the growth of incipient grasses and vegetation.

DISCUSSION

The results of this study support Knisley’s (2003) hypotheses that changes in flow regime caused by engineering works, in general, and upstream dams and diversions, in particular, have led to a decline in water edge habitat
quantity and quality and, consequently, to the apparent extirpation of the Sacramento Valley Tiger Beetle, *C. h. abrupta*. The changes to the Sacramento River and Feather River included altered water levels, prolonged flooding of habitat, reduced number and size of sand bar habitats, and reduced habitat quality due to particle size changes, increased vegetation growth and human activity.

Similar to other streams with flood control dams (e.g. Williams and Woman, 1984), flow releases from Shasta Dam and Trinity Diversion on the Sacramento River, and Oroville Dam on the Feather River increased the likelihood for flooding the point bars. On the Sacramento River, a nearly 3 m increase in post-dam water levels (in average daily stage) in concert with increased low stages and decreased high stages have resulted in wetter and more stable conditions—despite the largest drought on record (1986–1992). The Feather River showed similar trends in high flow/stage conditions, but both low flows and high flows increased at Nicolaus after construction of Oroville Dam. These factors have contributed to even greater periods of bar inundation than those found along the Sacramento River.

The timing of these increased and prolonged water levels during early summer through fall, especially the four- to eightfold post-dam increases in discharge, could have significantly disrupted several of the life stages of *C. h. abrupta*. In the spring adults typically emerge from overwintering sites in the sandy back beach of the sand bars to begin mating and ovipositing on the sand bar habitats. Prolonged high water levels would reduce or eliminate both sites and time needed for oviposition. High water levels in the late spring to mid summer would have the greatest impact on larvae that hatched from successfully oviposited eggs. Tiger beetle larvae are known to survive in water edge habitats that have been fully submerged for periods of 1–2 weeks or more (Hamilton, 1885; Willis, 1967; Wilson, 1974), but recent laboratory drowning studies with *C. hirticollis* found that most larvae survived less than 4 days and none longer than 8 days (Brust *et al.*, 2005). Laboratory tests of *Phaeoxantha klugi*, a tiger beetle of the Amazonian floodplain, found that larvae could survive much longer (an average of 26 days) when placed in sediments for several weeks before becoming gradually flooded (Zerm and Adis, 2003). In particular, Zerm and Adis (2003) speculated that the increased survival resulted from metabolic depression caused by the gradual flooding which these beetles experience in their native habitat. A recent study with *C. hirticollis*, however, found that larvae within their closed burrows in laboratory chambers responded to flooding by readily digging out of their burrows and floating to the water surface (Brust *et al.*, 2006). Such a behaviour likely would be detrimental to larvae of *C. h. abrupta* if river flow carried them downstream where habitat was unavailable or unsuitable for colonization.

Adults of all species of tiger beetles tested for immersion tolerance, including *C. hirticollis* (Brust *et al.*, 2005), survived only a few days (Zerm and Adis, 2003). Unless the overwintering adults of *C. hirticollis* have an unknown adaptation, the post-dam prolonged periods of flooded bars from November through January would drown them. The results from this study show that higher flows have most likely disrupted mating and ovipositing of *C. h. abrupta* adults, and development and emergence of larvae. Similarly, Cortes *et al.* (2002) and Nelson and Lieberman (2002) found that increased summer flows negatively impact benthic invertebrate assemblages.

Another water edge tiger beetle, *Cicindela arogona*, was found, sometimes in abundance, at approximately one-third of the bars surveyed on both the Feather and Sacramento Rivers (Krisley, 2003). This species is much more widely distributed in the west than *C. hirticollis*, and is not restricted to sandy habitats but found in sites with different substrate types and moisture regimes (Larochelle and Lariviere, 2001). As a habitat generalist and perhaps with greater dispersal and colonization abilities, it would probably be less impacted from the river changes than was *C. hirticollis* (Krisley, 2003). Other point bar invertebrates were not surveyed during this study, but we observed toad bugs (Hemiptera: Gelastocoridae) and several species of ground beetles (Coleoptera: Carabidae) at numerous point bars along both rivers.

The remote sensing, GIS, and field results also corroborate Krisley’s (2003) hypothesis that a decrease in habitat availability had a major impact on the beetle population on both the Feather River and Sacramento River. During the pre-Oroville dam period, the Feather River contained both abundant and large point bars. Initially following dam construction, the number of bars decreased (by more than half from 1967 to 1975), but enlarged indicating that the surviving bars grew at the expense of the vanished bars. The low number of 1975 post-dam bars with large areas points to a river system adjusting to alterations in flow first by decreasing the number of bars, but not substantially decreasing the areal extent of the remaining bars. During the 1980s, the bars increased in numbers while fragmentation reduced their sizes. During the 1990s, both the number and areal extent of bars decreased. Moreover, a twofold increase in stage during the 1990s at the Nicolaus stream gage coincided with the reduction in bar
numbers and areas. The detailed analysis of the large point bar of known historical habitat at Colusa along the Sacramento River showed similar temporal and spatial trends. At present, the bar is more than an order of magnitude smaller than it was in 1937 and smaller in size than any time over the past 65 years. To the south of Colusa, channel stabilization and natural sediment supply reduction along the Sacramento River has resulted in higher, steeper, and more densely vegetated sand bars. These conditions have both reduced and isolated \textit{C. h. abrupta} habitat making it difficult for growth and survival of larvae, recolonization, and perhaps led to the gradual decline and extirpation of the metapopulation along the Feather River and Sacramento River systems.

Human alterations to the Sacramento River system have greatly influenced the surficial characteristics of the point bars. Flood reduction, bank stabilization and bar stabilizing flows diminish sediment availability for point bars by reducing the potential for cutbank erosion and increasing upstream sediment trapping (Singer and Dunne, 2001). The downstream longitudinal decrease in mean grain size found on the Sacramento River and, to some degree, the Feather River point bars points toward a natural, progressive downstream loss in stream competence. However, natural processes cannot explain the predominance of very coarse-grained sand and gravel deposits found in the upper reaches of the study areas (Figure 15).

Although Bryan (1923) reported 'one inch gravel' at Colusa prior to Shasta Dam construction, at least four possible explanations can account for the cobble-sized gravel that armoured the upper surface (\( \approx 10-20\) cm) of the point bars in the Colusa region. First, the State of California (1981, 1985) reported that upstream sand and gravel mining, the loss of upstream gravel supply after Shasta Dam installation, and subsequent channel scouring from altered high flows caused cobbles to armour the channel and point bars. Numerical and stochastic models have confirmed the impact of 'hungry water' in which elevated flow stages and bank stabilization projects have elevated critical shear stress values (Singer and Dunne, 2004). These alterations have led to bed degradation and coarsening over time. Second, an increase in the supply of coarse-grained sediment (i.e. gravel) may have occurred over time. The most likely sources of gravel in the Colusa region include the channel banks and main stem contributions. The setback construction of the artificial levees above Colusa provides an opportunity for meandering and channel bank erosion to re-entrain gravels as the Sacramento River drains through the coarse-grained channel fill and point bar facies of the Pleistocene-aged Modesto and Red Bluff Formations (Helley and Harwood, 1985; Fischer, 1994). Additionally, gravel deposition may have increased in the Colusa reach because of flood flow diverted through the flood bypass (Colusa Wier) north of Colusa and subsequent loss of competence (Kresch, 1970; Singer and Dunne, 2004). Another situation that could provide potential increases in gravel load includes bed adjustments to high flows in regions of artificial levees. For example, Singer and Dunne (2004) noted that, in the Colusa region (and in areas of stabilized banks), elevated stages that would have expended energy on the channel banks, instead direct that energy on the channel bottom. This phenomenon has the effect of coarsening bed material and increasing bed slope.

To the south of Colusa, river confinement increases and the stream gradient decreases leading to more stable conditions (Gilbert, 1917; State of California, 1994). In addition, the fine-grained component (primarily clay) of the banks increases to the south (Singer and Dunne, 2001). The combination of these factors most likely is responsible for the fine sands that comprise the point bars in the Knights Landing area. Several samples in the Knights Landing area were too fine-grained to conduct dry, mechanical shaking grain-size distribution procedures (silt). Additionally, the majority of bars in this area contained evidence of high elevation deposition without well-defined point bars and resemble sand ‘banks’ as opposed to point bars (Figure 11). Harvey and Sing (1989) showed that vertical accretion of point bars along the Sacramento River occurs during rising and peak stages as the thalweg scours. During falling stages the point bar creases laterally thereby producing narrow, steep banks. \textit{C. hirticollis} would find these high relief bars unsuitable habitat because larvae are only found where water exists within several inches of the surface. In short, altered flows, channel stabilization, an increase in gravel load, and overall reduction in sediment supply has caused the grain size distribution of the bars to become bi-modal ranging from very coarse sand and gravel in the north to fine sands in the south. Neither mode, however, offers productive \textit{C. h. abrupta} habitat.

Knisley (2003) and Brust et al. (2006) indicated that \textit{Cicindela hirticollis} larvae only burrow in moist sand. Field experiments along Chesapeake Bay beaches showed that medium-sized sand (0.5–0.6 mm) favours the soil moisture and compaction conditions preferred by \textit{C. dorsalis}, a species of tiger beetle that co-occurs with \textit{C. h. hirticollis} (Fenster et al., in press). Therefore, although the reach north of Colusa to Red Bluff currently contains the
best remaining remnants of the original Sacramento River riparian corridor (State of California, 1994), anthropogenic alterations have produced grain size distributions unsuitable for the sediment compaction and moisture retention needed for C. h. hirticollis and C. h. abrupta functions. Deposition of mud on top of sand and a decrease in flow variability have encouraged vegetation growth (Dolan et al., 1974). Additionally, although the Sacramento River loses its tendency towards anabranching and braiding approximately 40 km north of Colusa, Brice (1977) documented an increase in vegetation of large islands upstream from Colusa as a moderating effect of Shasta Dam on peak flows. Finally, foot and vehicle traffic have contributed to sediment compaction to the detriment of habitat suitability.

This study, however, did not investigate other potential causes of extirpation. While a variety of natural factors, including parasites, predators, food limitation and climatic changes (particularly reduced rainfall) can limit tiger beetle populations, these have not been implicated in any widespread decline or extirpation (Knisley and Schultz, 1997; Pearson and Vogler, 2001). The effects of pesticides on tiger beetles have not been studied but could cause decline in beetle numbers near areas of heavy pesticide use, including along the Sacramento and Feather Rivers where intensive agricultural activity and pesticide use exist. It seems unlikely, however, that pesticides themselves could cause the widespread extirpation of C. hirticollis. Most of the listed and candidate tiger beetles and most other rare US species have declined as a result of human-induced disruptions and/or loss of habitat (Pearson et al., 2006). Natural succession or encroachment by invasive plant species have affected some species by eliminating open areas of habitat required by adult and larval tiger beetles (Knisley and Hill, 1992; Pearson et al., 2006).

In summary, along the Sacramento River between Colusa and the confluence with the Feather River, river modifications apparently have contributed to the apparent extirpation of C. h. abrupta. In particular, human activities have resulted in fewer, higher, steeper, coarser and/or more densely vegetated sand bars. Flow releases from two large dams cause existing point bars to experience flooding for longer periods than the pre-dam natural conditions and during different months than those in which they occurred prior to dam construction. These findings support the hypotheses of Knisley (2003) for C. h. abrupta and State of California (1994) for additional species that large dams (i.e. controlled water releases), levees and channel bank stabilization projects have contributed to the loss of key habitat elements.

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