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Andrew G. Talabere for the degree of Master of Science in Fisheries Science presented on November 21, 2002.

Title: Influence of Water Temperature and Beaver Ponds on Lahontan Cutthroat Trout in a High-Desert Stream, Southeastern Oregon

Abstract approved ____
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The distribution of Lahontan cutthroat trout *Oncorhynchus clarki henshawi* was assessed in a high-desert stream in southeastern Oregon where beaver *Castor canadensis* are abundant. Longitudinal patterns of beaver ponds, habitat, temperature, and Lahontan cutthroat trout age group distribution were identified throughout Willow Creek. Three distinct stream segments were classified based on geomorphological characteristics. Four beaver-pond and four free-flowing sample sections were randomly located in each of the three stream segments. Beavers substantially altered the physical habitat of Willow Creek increasing the depth and width of available habitat. In contrast, there was no measurable effect on water temperature. The total number of Lahontan cutthroat trout per meter was significantly higher in beaver ponds than free-flowing sections. Although density (fish/m^2) showed no statistically significant ($P < 0.05$) increase, values in beaver ponds were two-fold those of free-flowing sections. Age-1 and young-of-the-year trout were absent or in very low numbers in lower Willow Creek because of elevated temperatures, but high numbers of age-2 and 3 (adults) Lahontan cutthroat trout were found in beaver ponds where water temperatures reached lethal levels (>24°C). Apparently survival was greater in beaver ponds than free-flowing sections as temperatures approach lethal limits.

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Influence of Water Temperature and Beaver Ponds on Lahontan Cutthroat Trout in a High-Desert Stream, Southeastern Oregon

by

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Andrew G. Talabere, Author

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CHAPTER 1: INTRODUCTION

Water temperature is a critical habitat component that potentially limits the distribution of stream fishes (Peterson and Rabeni 1996; Dunham et al. 1999; Torgersen et al. 1999). Streams in the interior basins of western North America are characterized by high seasonal variation and large diurnal fluctuations in temperature (Dunham et al. 1999; Zoellick 1999; Ebersole et al. 2000). For example, streams in southwestern Idaho had diurnal fluctuations of approximately 10°C with daily maximum temperatures up to 29°C (Zoellick 1999). Behnke (1992) speculated that, because of their evolutionary history in high-desert environments, populations of interior rainbow (redband) trout *Oncorhynchus mykiss* spp. and Lahontan cutthroat trout *O. clarki henshawi* are adapted to high water temperatures. Although recent research suggests that some phenotypes of redband trout have elevated physiological function up to 24°C (Gamperl et al. in press), there is no evidence for increased thermal tolerance above 24°C. For Lahontan cutthroat trout, Meeuwig (2000) found growth and feeding rates are depressed at 24°C and critical swimming speed is negatively affected by large diel fluctuations (12°C to 24°C).

Variation in stream temperature can be affected on a diel and seasonal basis by human activities. In the Great Basin, human activities (e.g. livestock grazing, mining, road building) have reduced the riparian canopy cover (Platts and Nelson 1985; Minshall et al. 1989) on many streams. A loss of riparian vegetation exposes more of the stream surface to direct solar radiation and heating during the day (Brown 1969; Beschta 1997). Additionally, stream channels with reduced riparian vegetation integrity are susceptible to both lateral and vertical erosion during flood events (Platts et al. 1985). Lateral erosion generally increases the surface area and decreases the stream depth thereby potentially increasing the solar input and rate of stream heating (Beschta 1997). High desert streams subjected to intensive human activity and loss of riparian vegetation may have altered thermal regimes that restrict the distribution of trout to cooler headwater areas (Theurer et al. 1985).

For example, Lahontan cutthroat trout persist in highly fragmented headwater streams throughout the northwestern Great Basin. Historically, Lahontan cutthroat trout occupied an estimated 135,000 ha of lakes and 5800 km of streams (Gerstung 1986) in northern and western Nevada, northeastern California and southeastern Oregon (Coffin and Cowan 1995). The lacustrine populations have since declined from 11 to 2 and occupy approximately 0.4% of historic lake habitat. The highly fragmented fluvial populations (Dunham et al. 1997) now occupy approximately 11% of historic habitat (Coffin and Cowan 1995). Elevated water temperatures are a primary factor limiting the downstream distribution and possible expression of diverse life-history forms (Dunham et al. 1997; Jones et al. 1998). Lahontan cutthroat trout were listed in 1975 as threatened by the United States Fish and Wildlife Service (Office of Federal Register 40[1975]:29864).

Lahontan cutthroat trout in Willow Creek, southeastern Oregon, are restricted in distribution as a result of past land management practices. The lower sections of Willow Creek are degraded both physically and biologically, riparian vegetation is sparce, and water temperatures often exceed 26°C during the summer (Hanson et al. 1993; Jones et al. 1998). Efforts to recover stream habitat and riparian vegetation in Willow Creek began in the early 1970s and continue today under a grazing management plan that recognizes riparian vegetation and fish habitat as valuable resources (BLM 1990). Preliminary observations of responses to the recovery effort include an increase in riparian willow *Salix spp.* and expanded beaver *Castor canadensis* activity including more dams and impounded stream area.

Beaver ponds can drastically alter the quality and quantity of habitat available to fish in a stream ecosystem. For example, the expansion of beaver colonies across a 294 km^2 area in northern Minnesota increased total pond area from 2.5 km^2 in 1940 to 32.5 km^2 in 1986 (Johnston and Naiman 1990). By creating ponds and altering stream habitat over long periods of time (e.g. multiple decades or more), beaver can establish a mosaic of pond habitats in varying states of succession (Schlosser and Kallemeyn 2000). The diversity of habitats created across the stream landscape by beaver may provide spatial and temporal habitat complementation (*sensu* Dunning et al 1992) sufficient to support multiple life-history forms (Schlosser 1995; Fausch et al. 2002). Beaver ponds are present throughout Willow Creek, but the largest and deepest ponds occur in the lower sections, where the water temperatures approach lethal limits (Jones et al. 1998).

The presence of beaver ponds in high-desert streams has raised questions about possible affects on already elevated stream temperatures. Although no studies addressing beaver pond-temperature interactions have been published for high-desert streams, research from other geographic areas provides information that can be used to frame questions. In Wisconsin, McRae and Edwards (1994) compared water temperatures from sites dispersed among 21 beaver ponds in 4 streams; they found no consistent relationship between size and number of impoundments and the direction and magnitude of downstream warming in the summer. Thermal effects of individual beaver impoundments, even among those on the same headwater stream, were best understood on a site-specific basis in the context of local stream and ground water hydrology, riparian shading, and aspect (MacRae and Edwards 1994). In the central Sierra Nevada Mountains, Gard (1961) attributed the apparent cooling affect of a beaver pond to cold springs in the bottom of the pond. In a detailed study of groundwater patterns associated with a beaver pond in central Oregon, Lowry (1993) documented that the temperature of groundwater input below a beaver dam lagged approximately 3 months behind the in-channel water temperature; thereby providing a source of cool water in the summer and warm water in the winter.

The local alteration of groundwater flow documented by Lowry (1993) is consistent with other studies describing the effects of beaver dams on stream ecology (Naiman et al. 1988). For example, beaver dams also influence the flow of water, sediment, organic material, and nutrients (Naiman et al. 1986; Naiman et al. 1988). Alteration of stream processes (e.g. discontinuity of flow) associated with beaver dams raise two important questions concerning possible effects on the distribution and persistence of trout in high-desert streams: 1) What effect do beaver ponds have on the longitudinal temperature profile of a high-desert stream? 2) Do beaver dams/ponds influence the longitudinal distribution of trout in high-desert streams? (Figure 1).

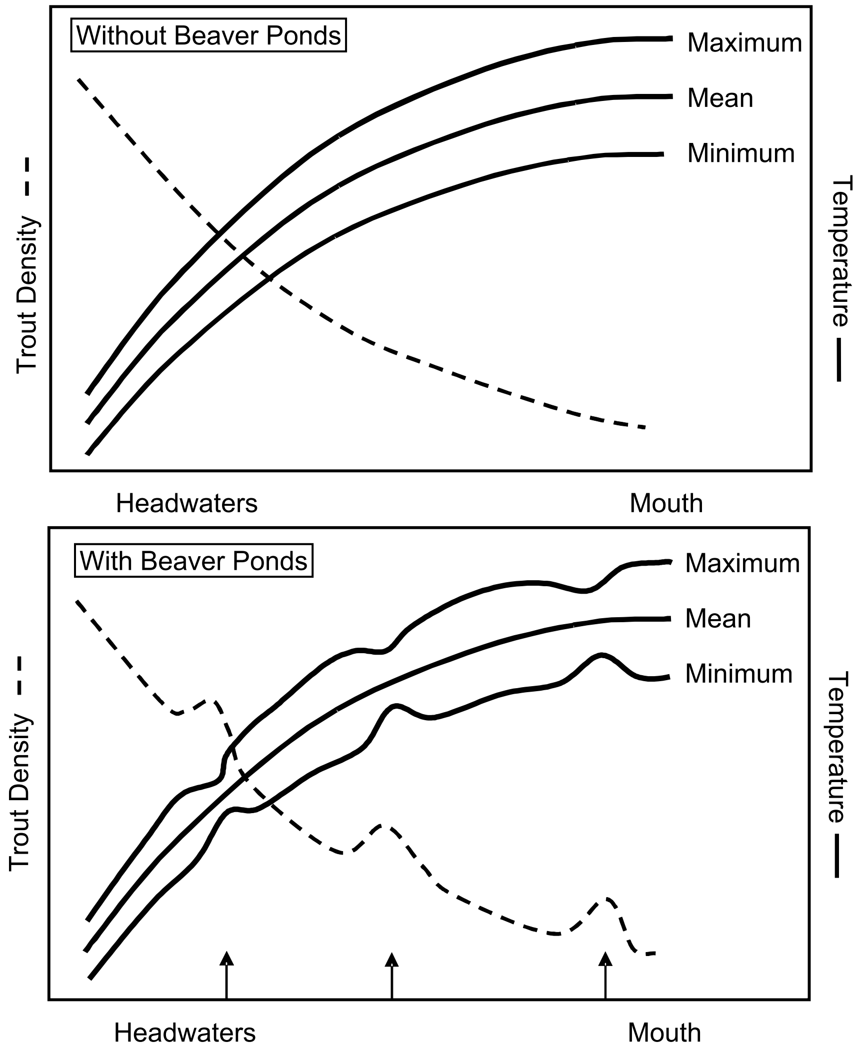

Figure 1. Conceptual diagram of decreasing trout abundance (---) with increasing stream temperature (–) and the hypothesized response of water temperature and trout density to beaver pond complexes (-).

The goal of this study was to examine the summer distribution patterns of an allopatric Lahontan cutthroat trout population in a beaver influenced high-desert stream. The specific research objectives were to: 1) incorporate beaver ponds into an examination of longitudinal patterns of habitat and temperature across reach and segment scales, and 2) determine the influence of beaver ponds on the longitudinal distribution and abundance patterns of Lahontan cutthroat trout age groups at the reach and segment scales.

CHAPTER 2: STUDY AREA AND METHODS

STUDY AREA AND BACKGROUND

This study was conducted during the summers of 1998 and 1999 along Willow Creek, a stream draining the eastern flank of the Trout Creek Mountains in southeastern Oregon. The Trout Creek Mountains are a series of north-south trending uplifted fault blocks at the northern extent of the Basin and Range Physiographic Province (Orr et al. 1992). Late Miocene basalt (Minor 1986) overlain with sheets of ash-flow tuff (Orr et al. 1992) comprise the main Trout Creek Mountain blocks. With a drainage area of 130 km^2, Willow Creek begins from springs at 2,150 m (above mean sea level) (Figure 3). The only perennial tributary (an unnamed stream) has source springs at 2,185 m and 2,010 m. Willow Creek flows more than 30 km north toward pluvial Coyote Lake before terminating at approximately 1,300 m. The upper portion of Willow Creek flows in a narrow basalt canyon. The basalt canyon abruptly ends at approximately 1,561 m (Figure 2) and Willow Creek then flows through ash-flow tuff for several kilometers before reaching the Valley floor of depositional gravels and fine-grain alluvium. Portions of lower Willow Creek have incised as much as 4 m into the valley floor.

Willow Creek is a terminal stream with no surface connection beyond the Coyote Lake basin. The four other perennial stream systems in the Coyote Lake basin are Whitehorse Creek, Fish Creek, Antelope Creek, and Twelvemile Creek. During years of average precipitation, Willow Creek has no surface connection to other stream systems in the basin. During the study period, mean discharge was 0.06 m^3/s. Discharge generally peaks in May or June at the height of snow-melt and tapers to minimum flow in September. Mean annual precipitation varies from 20 cm/year at the lower elevations to 73 cm/year at the higher elevations (OCS 2002). Precipitation at lower elevations is distributed throughout the year, but approximately two-thirds of the high-elevation precipitation falls as winter snow. Mean low-elevation air temperatures in the Coyote Lake basin vary from a January minimum of -1.1 °C (range: -35 – 18°C) to a July maximum of 19.4 °C (range: 0 – 42°C) (OCS 2002).

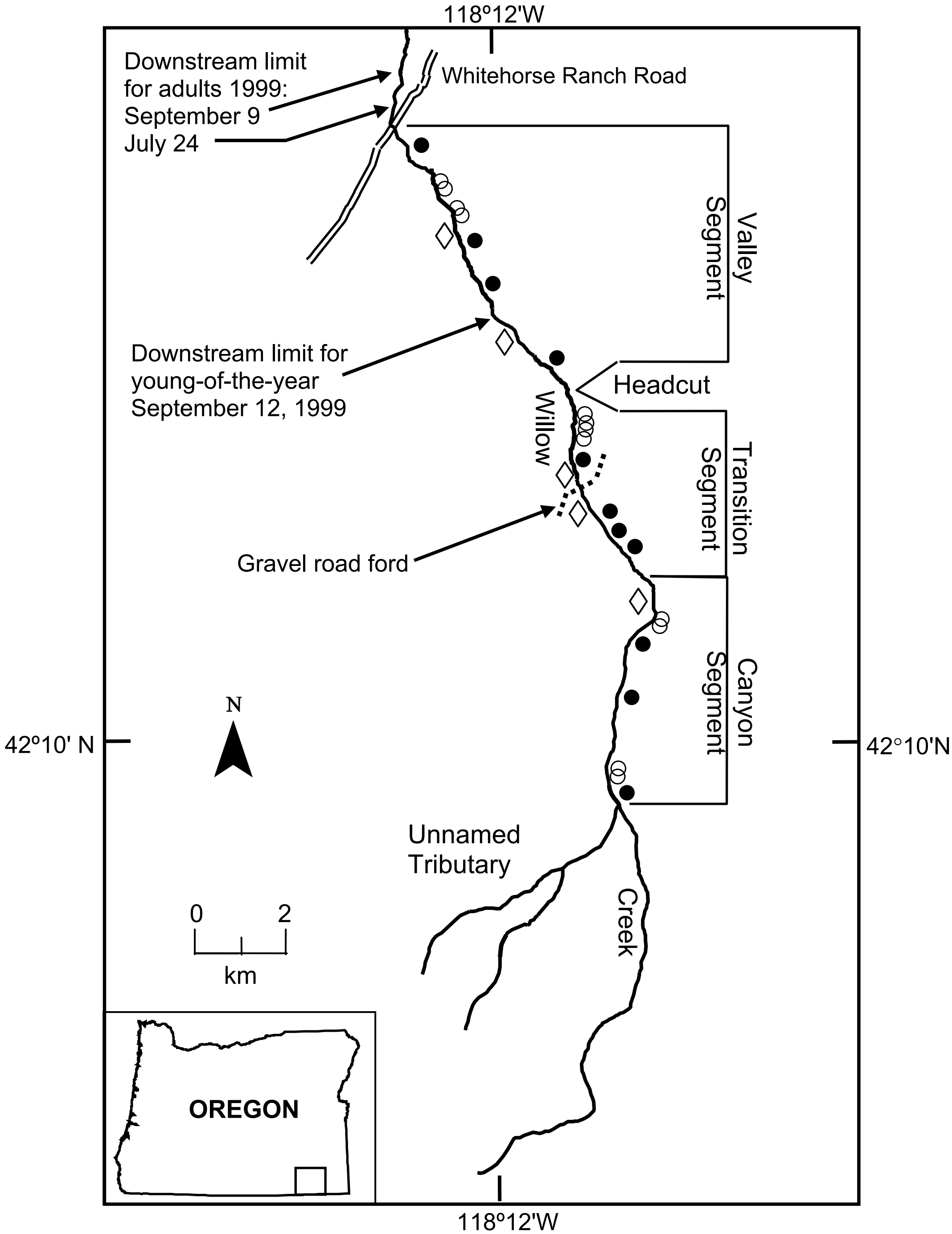

Figure 2. Willow Creek in Coyote Lake basin southeastern Oregon. Overlapping open circles (○) are study beaver ponds from the same beaver complex. Solid circles (●) are free-flowing study sections. The diamonds (◊) are locations of beaver ponds constructed between the July and September sampling periods.

The upland vegetation of Coyote Lake basin is dominated by sagebrush-bunchgrass communities (Franklin and Dyrness 1973). The upper elevations support mountain mahogany *Cerocarpus ledifolius*, quaking aspen *Populus tremuloides*, big sagebrush *Artemesia tridentata* spp., and native bunchgrasses (e.g. *Pseudoroegneria spicata, Festuca idahoensis, Achnatherum thurberianum*, and *Leymus cinereus*). In addition to big sagebrush and native bunchgrasses, the middle and lower elevations support exotic annual grasses (e.g. *Bromus tectorum, Salsola kali*, and *Sisymbrium loeselii*). Species of willow (e.g. *Salix exigua, Salix lucida, Salix boothii*, and *Salix scouleriana*), mountain alder *Alnus incana*, Wood's rose *Rosa woodsii*, sedges *Carex* spp., rushes *Juncus* spp., and big sagebrush were common riparian plant species. Black cottonwood *Populus balsamifera trichocarpa* is found in riparian zones of nearby streams (Whitehorse and Big Trout Creeks); its absence from Willow Creek may be the result of past land use (Evenden 1989).

The evolutionary history of Lahontan cutthroat trout in Coyote Lake basin is unclear. Current landforms preclude a hydrologic connection between Coyote Lake basin and all other naturally occurring Lahontan cutthroat trout populations in the Lake Lahontan basin. Behnke (1992) proposed that Lahontan cutthroat trout entered the Coyote Lake basin via headwater stream transfer from the Quinn River system (Nevada). Recent analysis of landforms and Pleistocene lake levels suggests the Coyote Lake basin was connected intermittently to Lake Lahontan via the Alvord Basin (Lindberg and Hemphill-Haley 1988;Reheis 1999). Regardless of the transfer mechanism, the cutthroat trout in Coyote Lake basin are pure Lahontan cutthroat trout, most closely related to the Quinn River group but genetically unique in accordance with their isolation (Williams 1991; Williams et al. 1992).

Similarly, the historical context for beaver in streams of Coyote Lake basin is uncertain. Peter Skene Ogden passed through the Trout Creek Mountains in 1828, but there was no mention of beaver activity in his journals (Williams 1971). In contrast, Ogden noted an absence of beaver in the Quinn River system and an abundance of beaver in the Humboldt River system (Williams 1971). Hanson et al. (1993) cited personal communications suggesting that the Oregon Game Commission translocated beaver into the adjacent McDermitt Creek (Quinn River) watershed in the 1930s. The abundance of beaver in streams of the Coyote Lake basin was described by Roy Naftzger after flying over the area in 1961 as "closely-strung strings of pearls, the 300 or so beaver ponds, often connected, one above the other, from the desert nearly to the top of the watershed" (letter from Roy E. Naftzger Jr., Whitehorse Ranch to Mary Hanson, Oregon Department of Fish and Wildlife, May 21, 1992). However, a stream survey by the Oregon Department of Fish and Wildlife in 1970 recorded the presence of only "…one or two inactive beaver dams…" (Hanson et al. 1993).

The Great Basin, and specifically Willow Creek, has a long history of intensive use by humans. Cattle, and to a lesser extent, sheep and feral horse grazing affected the Willow Creek watershed for decades before Whitehorse Ranch was established in 1869. Riparian vegetation has also been influenced by beaver trapping and dam removal; efforts to eradicate riparian vegetation occurred in the 1960s.

The U.S. Bureau of Land Management manages all of Willow Creek in, and upstream of, the study area. Beginning in 1989, cattle grazing was reduced and feral horses were relocated downstream of Whitehorse Ranch Road (BLM 1989). Angling for Lahontan cutthroat trout was closed for all streams in the Coyote Lake basin by the Oregon Department of Fish and Wildlife in May, 1990 (Hanson et al. 1993). Angling closures remained in effect until 2000. No anglers were observed during 1998 and 1999, and it was assumed that fish numbers were not affected by angling during this study. Lahontan cutthroat trout is the only species of fish in the Coyote Lake basin. The Pacific tree frog *Hyla regilla* and Great Basin spadefoot toad *Scaphiopus intermontanus* are the only other aquatic vertebrates (Chiller and Gomez 1999) (see Appendix A for a list of observed species).

METHODS

Sample Section Selection

This study was conducted on a 23 km long portion of Willow Creek between an unnamed tributary confluence and the Whitehorse Ranch Road (Figure 2). Willow Creek was initially divided into three stream segments based on distinct valley and channel geomorphology (Frissell 1986; Gregory et al. 1989) (Figure 2). The Canyon segment extended from the tributary junction downstream to the mouth of the canyon. This segment flows through a uniform basalt canyon. The Transition segment extended from the mouth of the canyon to the top of a 3-m high erosional headcut. The Valley segment extended from the headcut downstream to the Whitehorse Ranch Road.

Eight sample sections (four free-flowing and four beaver-pond) were randomly selected in each segment. Free-flowing stream sections were 30 wetted channel widths in length. Free-flowing sections located within 200 m of a beaver pond were discarded, and a new site was randomly selected.

Beaver complexes (i.e., three or more functioning contiguous dam/pond combinations) were located and mapped in June and August, 1999. The Canyon and Valley segments each had two beaver complexes, and the Transition segment had one complex. In the Canyon and Valley segments, two beaver-pond sections were randomly located in each of the two complexes. In the Transition segment, the four beaver-pond sections were randomly located in the only beaver complex. Beaver-pond sections extended upstream from the dam crest to either free-flowing stream (in the case of the upper-most beaver pond of a complex) or another dam. In some cases short stretches of free-flowing stream (less than one-half the beaver pond length) existed between a beaver pond and the next dam upstream; these stretches were included in the beaver-pond section.

Physical Habitat

In order to assess physical habitat, five evenly spaced transects were set perpendicular to the stream in each sample section. Wetted width, depth, and shade were measured at each transect. For free-flowing sections, a thalweg depth measurement was recorded at each transect. In addition, all pools in the free-flowing sections were counted, and length, width, and maximum depth were measured. In beaver-pond sections, depths were measured at five points along the transect; points were located at each bank and at three evenly spaced points, 25, 50, and 75% of the distance from one bank to the other. In addition, the maximum depth of each beaver-pond section was recorded. Riparian canopy density was measured at each transect in all sample sections using a densiometer (Platts

1987). A second shade measurement was taken at each transect using a clinometer to record the angle of either vegetative or topographic shade relief perpendicular to the stream.

Stream discharge was measured once at the upstream and downstream boundary of each Willow Creek segment in both July and September, 1999. Depth was recorded, and a Marsh-McBirney® flow meter was used to measure velocity at 0.1 m intervals along a channel transect with uniform flow and substrate. A minimum of 12 depth and velocity readings were taken for each discharge estimate.

Temperature

The water temperature of each sample section was assessed using stationary temperature recorders (Onset® Hobotemp) and a hand-held temperature probe. One temperature recorder was placed at the center point of each sample section (a total of 24 recorders), and temperatures were recorded once every 60 minutes on the hour. Temperature recorders were positively buoyant and placed to maintain position at approximately 50% of depth in beaver-pond sections. In free-flowing sections, recorders were secured to substrate in the thalweg. A hand-held digital temperature probe was used to account for thermal heterogeneity by systematically searching the stream for discrete patches of water that varied by more than 3°C from the adjacent stream temperature (Ozaki 1988). The search area extended 100 m downstream and upstream of the section midpoint and in all cases extended beyond the section boundaries. Temperature recorders began recording at least 7 d before fish sampling in July and continued until after September fish sampling was complete.

Lahontan cutthroat trout

Lahontan cutthroat trout were sampled in July and September, 1999. Block nets were placed at each end of the sample section, and three passes were conducted with the backpack electrofisher. Lengths of all captured fish were measured to the nearest millimeter (fork length), and scales were collected from 30 randomly-selected fish in each of the three segments of Willow Creek during each sample period. Scale samples in each segment were divided among three size classes (<150 mm, 151- 200 mm, and >200 mm), and five fish were selected for each beaver-pond section and five for each free-flowing section in each size class. In addition, scales were collected from 262 Lahontan cutthroat trout captured by angling in all three segments. Young-of-the-year trout were noted where present, but they were not included in fish density analysis. However, fork lengths were measured for those individuals captured incidentally (no scales collected).

All electrofishing was completed while water temperatures were < 20°C (primarily between 0600 hours and 1100 hours). Trout were held in aerated buckets and released into the same beaver-pond or free-flowing section from which they were captured. The order in which sections were sampled was randomized to avoid site-by-time bias. Habitat surveys for each section were completed within 2 d of fish sampling. The approximate lower distribution limit of young-of-the-year trout was determined by spot shocking downstream from the lowest site where they were captured during regular sampling (Figure 2).

Data Summary and Statistical Analysis

Habitat data were summarized at the section and segment scale and by sample period. The 7-d average maximum temperature (7-day-maximum) was calculated for each day July 14 – 20, 1999 and September 4 – 10, 1999. Segment-level temperatures were calculated by averaging values from each section in the segment. Because Willow Creek can exceed recommended maximum temperatures for Lahontan cutthroat trout (22°C; (Dickerson and Vinyard 1999; Dunham 1999)), we calculated the mean hours above threshold temperatures (20°C, 22°C, 24°C, and 26°C) for individual sample sections during July 14 - 20, 1999 and September 4 – 10, 1999.

The age composition of fish captured in Willow Creek was estimated using an age-length key (Kimura 1977). The proportion of each age group was estimated in 10 mm length categories (50 - 300 mm), and then expanded by the total number of fish captured in each length category. Because the pooling of temporally separated sample populations may generate bias (Westerheim and Ricker 1978), age composition was calculated separately for July and September. Because   Jones et al. (1998) found no significant difference in size-at-age among Lahontan cutthroat trout in three segments of Willow Creek, the same age-length key was used for all segments in a sample period.

The total number of fish captured during three passes of electrofishing was used to estimate density (fish/m and fish/m^2) for each age group, section, segment, and sample period. Both linear and areal density measures were estimated in order to investigate the role of stream area in producing differences in fish abundance among sample sections (Snodgrass and Meffe 1998).

Analysis of variance was used to investigate differences in habitat characteristic means between beaver-pond and free-flowing sections within and among segments, and statistical relationships were further defined using the Tukey-Kramer multiple comparison test. The Mann-Whitney U test was used to test for differences in medians of fork lengths between section types and among segments. Differences in the distribution of fork lengths were tested with the Kolmogorov-Smirnov test. Significant differences in fish density among section types and segments were identified by ANOVA and the Tukey-Kramer multiple-comparison test. Associations between habitat characteristics and trout density were assessed using Pearson's product correlation. Test significance was set to $\alpha = 0.05$. All analyses were done using Number Cruncher Statistical Software (NCSS) (Hintze 1998).

CHAPTER 3: RESULTS

PHYSICAL HABITAT

Physical characteristics varied among stream segments (Figure 2). The Canyon segment was constrained by steep basalt rimrock walls. The mean gradient was 2.4%, and the segment was 5.9 km in length. The Transition segment was alternately constrained by valley walls of volcanic tuff and high alluvial terraces. Mean gradient in the segment was 1.2%, and the length was 5 km. The boundary between the Transition segment and the Valley segment was a 4-m high headcut. The Valley segment was constrained by high alluvial terraces. The mean gradient was 0.7%, and segment length was 11.4 km.

Water depth was greatest in Valley beaver ponds (Figures 3 and 4), and the difference was statistically significant ($P < 0.05$). Stream width of Canyon beaver-pond sections was significantly greater than Valley and Transition beaver-pond sections and all free-flowing sections (Figures 3 and 4; $P < 0.05$). Cross-sectional area of beaver-pond sections was not significantly different among segments (Table 1; $P < 0.05$), but the Canyon beaver-pond sections had significantly greater cross-sectional area than all free-flowing sections (Table 1; $P < 0.05$). Riparian shade also varied significantly by segment and habitat type. Shade cover for free-flowing sections was greater than beaver-pond sections. Shade cover decreased in a downstream direction; 56% (Canyon), 30% (Transition), and 28% (Valley) (Table 1; Figure 5).

Discharge (m^3/s) decreased through the study area in July (Figure 5). The largest decrease occurred in the Transition segment. In September, discharge decreased from 0.103 m^3/s in the Canyon segment to 0.004 m^3/s at the downstream boundary of the study area.

Table 1. Mean habitat values for beaver-pond and free-flowing sections in three segments of Willow Creek: Canyon, Transition, and Valley. All values are for July, except temperature, which differed significantly ($P < 0.05$) between July and September within each stream segment under the same section heading. Standard errors are in parentheses. Variables followed by an asterisk (*) differed statistically between beaver-pond sections and free-flowing sections (within row differences); values followed by the same symbol (†, #, or ^) are not statistically different ($P < 0.05$) among segments (within column differences).

	Beaver-pond Sections								Free-flowing Sections							
							7-Day-Maximum (°C)								7-Day-Maximum (°C)	
Segment	n	Mean Length (m)	Mean Surface Area (m^2)	Mean Width (m)	Mean Depth (m)	Mean Shade (%)	July	Sept.	n	Mean Length (m)	Mean Surface Area (m^2)	Mean Width (m)	Mean Depth (m)	Mean Shade (%)	July	Sept.
Canyon	4	44.3 (9.2)	218.9† (49.2)	4.9*# (0.3)	0.27† (0.04)	30*† (4.5)	16.3† (0.1)	14.1# (0.1)	4	76.5 (7.2)	220.1†,# (16.6)	2.9*† (0.3)	0.23† (0.02)	82*# (5.5)	16.2† (0.1)	14.0# (0.1)
Transition	4	58.3 (5.1)	148.9† (24.9)	2.5† (0.2)	0.33† (0.05)	20† (1.5)	21.1*# (0.03)	18.8† (0.1)	4	89.3 (3.9)	238.5† (17.3)	2.7# (0.2)	0.21† (0.01)	40† (9.9)	19.0*# (0.5)	16.6† (0.6)
Valley	4	71.5 (4.5)	180.7† (4.8)	2.6† (0.2)	0.46*# (0.02)	21† (3.1)	23.2^ (0.2)	18.3† (0.3)	4	55.5 (1.9)	109.6# (11.0)	1.9^ (0.2)	0.25*† (0.02)	25† (7.2)	22.3^ (0.6)	18.2† (0.7)

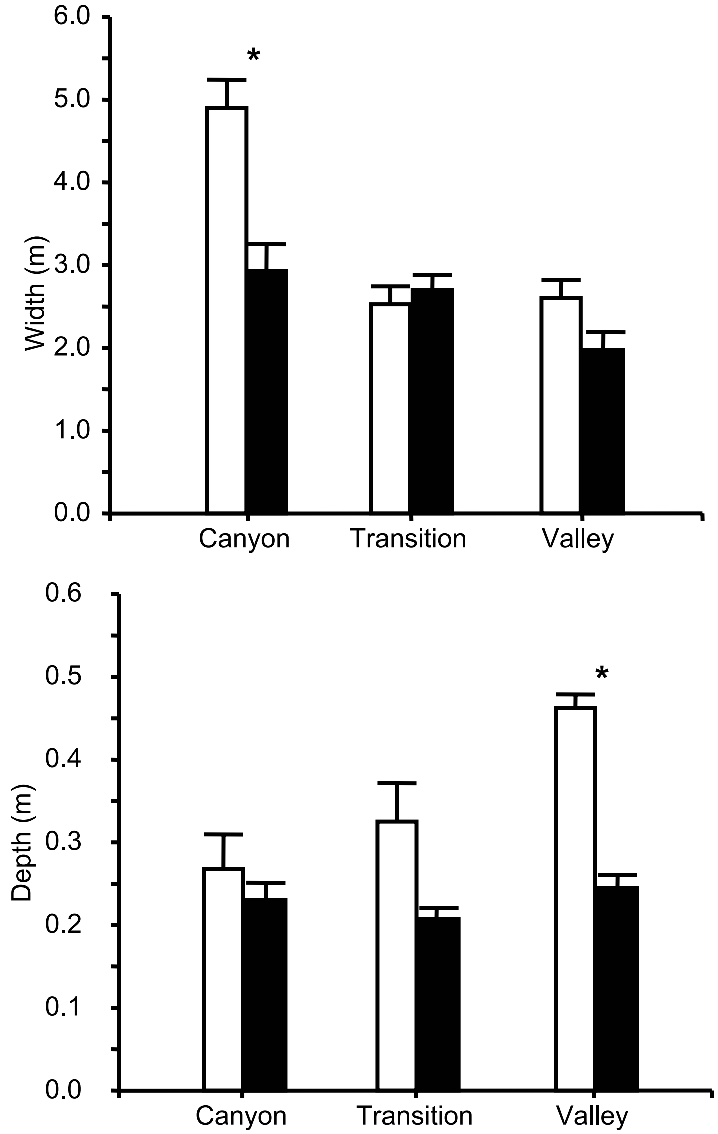

Figure 3. Means and standard error bars for wetted width and depth of beaver-pond (□) and free-flowing (■) sections of Willow Creek, Harney County, Oregon. Asterisks (*) indicate statistical difference ($P < 0.05$).

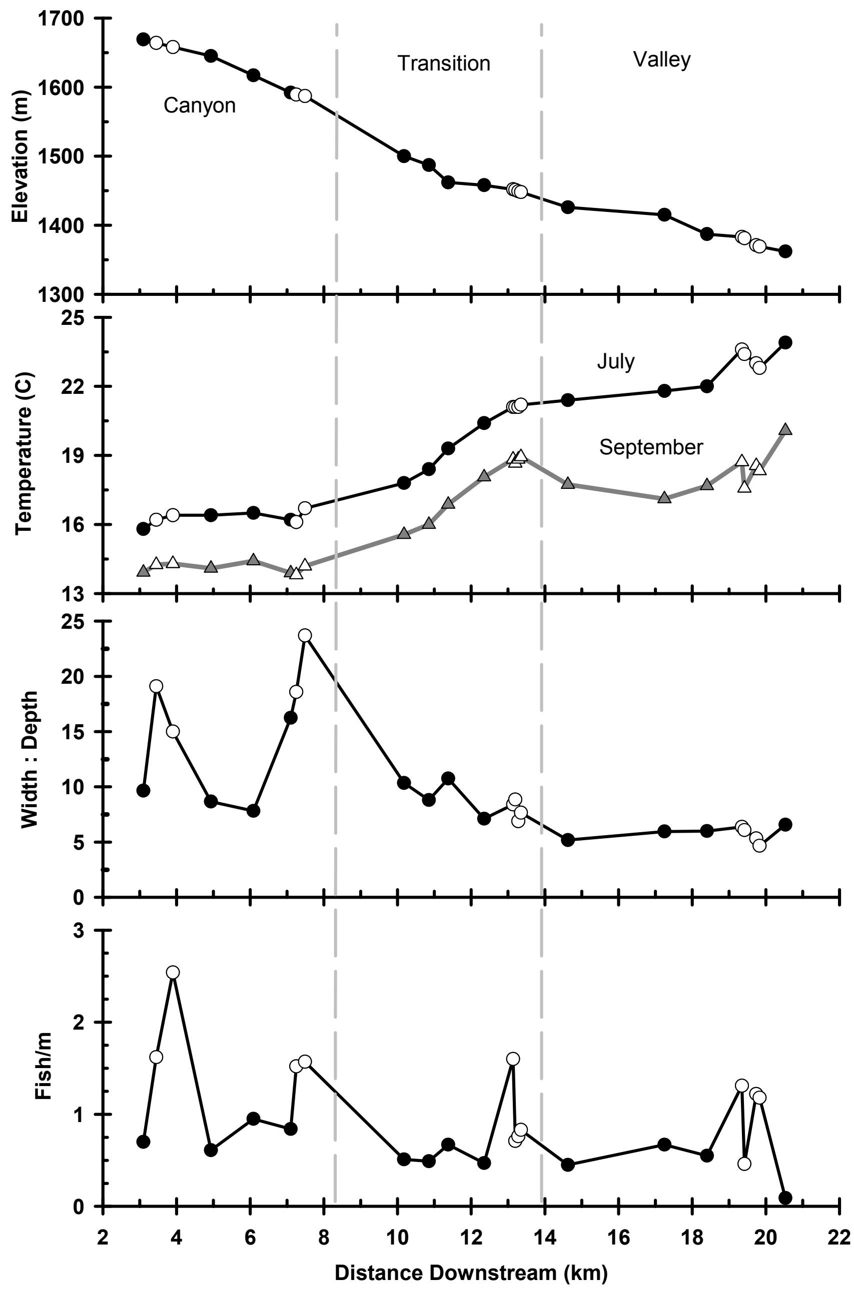

Figure 4. Longitudinal stream profile of elevation, 7-day maximum temperature, width:depth, and abundance of trout. Beaver-pond sections are open symbols (○, △) and free-flowing sections are closed symbols (●, ▲). Dashed vertical lines mark the segment boundaries.

TEMPERATURE

During the July sample period, stream temperature increased progressively downstream (Table 1; Figures 4 and 5). The 7-day-maximum temperature differed significantly among segments ($P < 0.05$) but differences between beaver-pond and free-flowing sections within segments were not statistically significant ($P > 0.05$). The maximum temperature recorded increased from 19°C in the Canyon segment to 24°C in the Transition, and 27°C in the Valley. The hours per day above threshold temperatures (22°C, 24°C, 26°C) varied between the Transition and Valley segments and among individual beaver-pond and free-flowing sections during the 7-day period of July 14-20, 1999 (Figure 6). The mean hours per day over 26°C in the Valley segment was 0.2; free-flowing sections were not statistically different from beaver-pond sections ($P > 0.05$). The mean hours per day over 24°C differed significantly between the Transition (mean = 0.1; SE = 0.2) and Valley (mean = 1.2; SE = 0.2) segments ($P < 0.05$). Beaver-pond sections were statistically different from free-flowing sections in the Transition segment ($P < 0.05$), but were not different in the Valley segment. Above 22°C, mean hours per day differed between the Transition segment (mean = 0.5; SE = 0.3) and the Valley segment (mean = 3.1; SE = 0.3) ($P < 0.05$). Beaver-pond sections did not differ from free-flowing sections ($P > 0.05$) within either the Transition or the Valley segments. Canyon segment temperatures did not exceed the 22°C threshold (Figure 4)

The 7-day-maximum temperatures for individual segments and sections were significantly lower in September than July ($P < 0.05$; Figure 3 and Table 1). The maximum temperatures for September were 19°C, 20.2°C, and 21.3°C for Canyon, Transition, and Valley segments, respectively. Temperatures in September did not exceed the 22°C threshold.

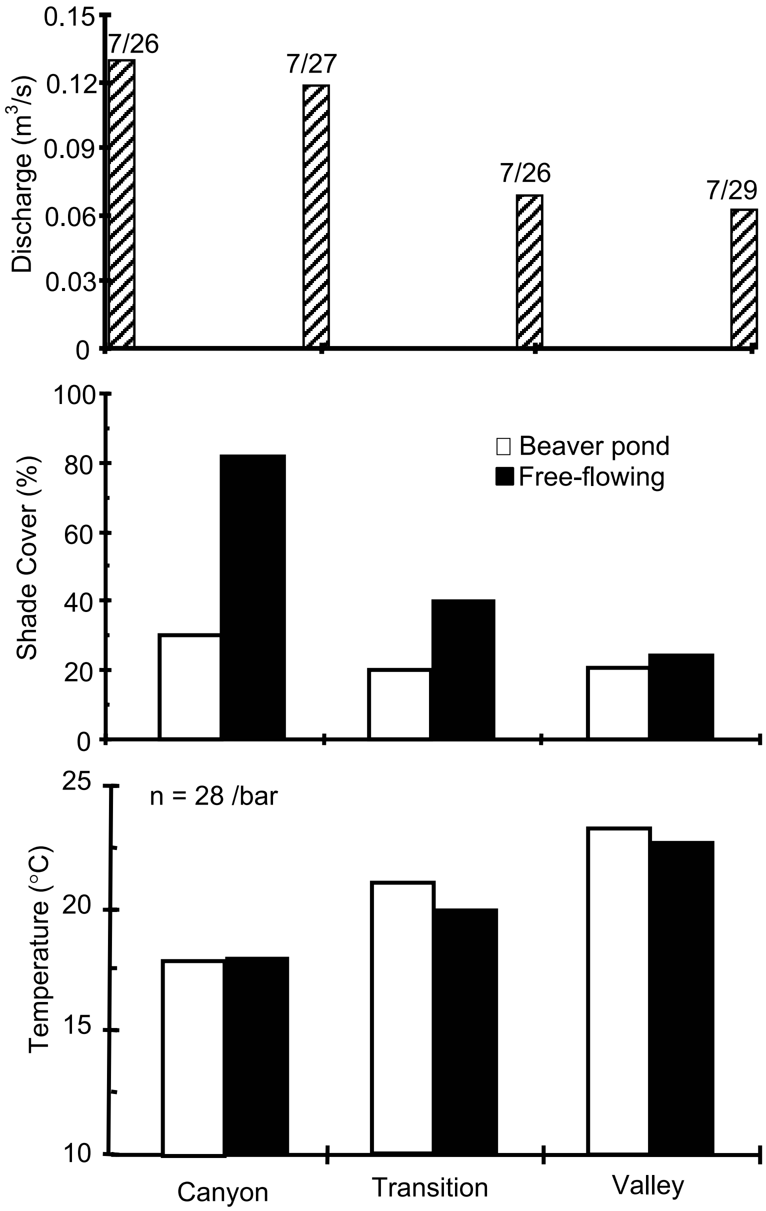

Figure 5. Discharge, mean shade, and mean maximum temperature from July. Discharge bars (▨) represent the inflow and outflow for each segment and are from a single discharge measurement taken on the date indicated above each bar. Mean maximum temperature is the average of the maximum temperatures for each of seven days (July 14 -20; n = 7) from each section (n = 4).

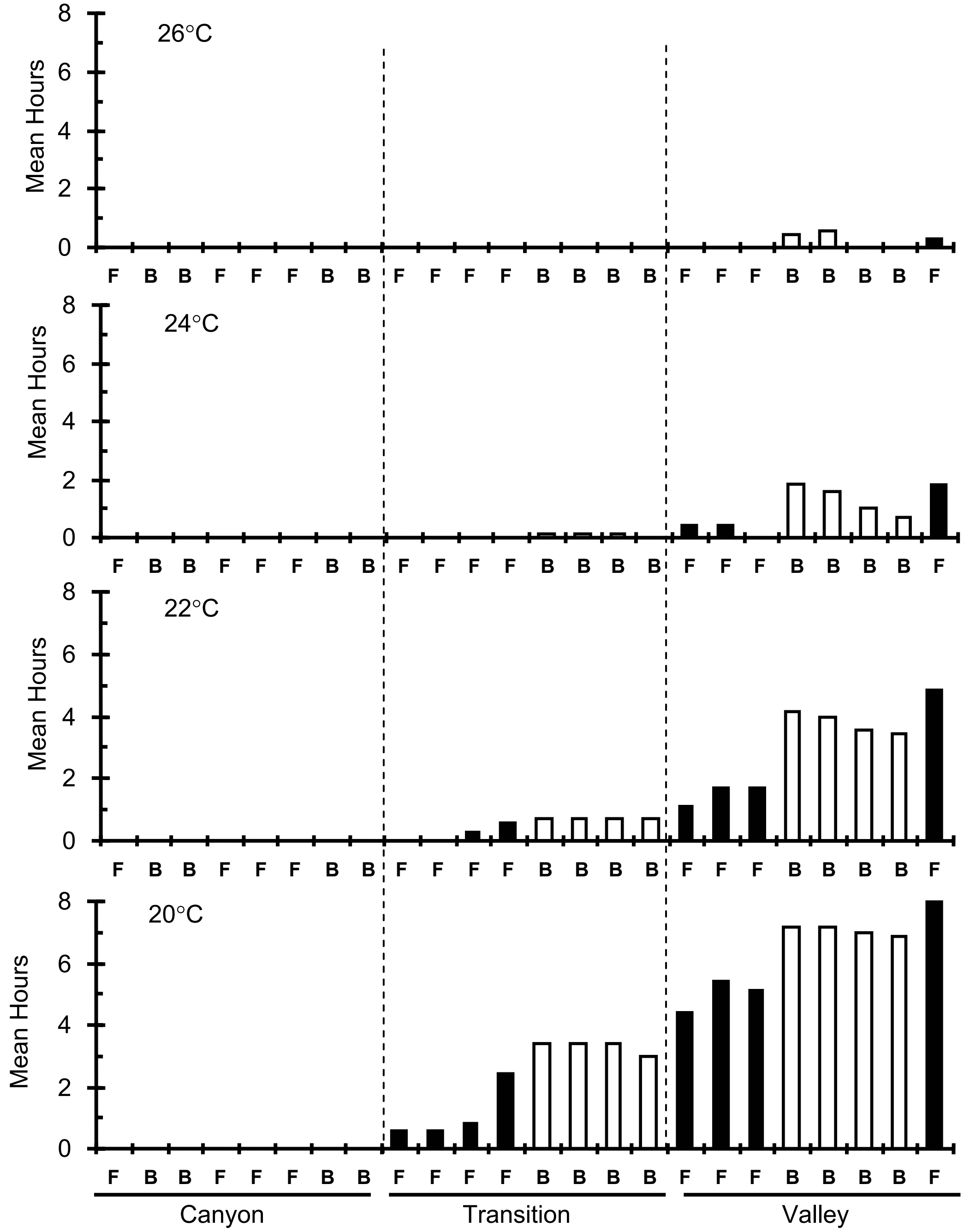

Figure 6. Mean hours/day that the water temperature exceeded 20, 22, 24, and 26°C in beaver-pond (B;□) and free-flowing (F;■) sections of the Canyon, Transition, and Valley segments of Willow Creek, Harney County, Oregon. Means were calculated from temperatures recorded at 1 h intervals from 14 – 20 July, 1999.

The diel temperature cycle on July 14, 1999 (day with second highest daily maximum temperature) was not substantially different between adjacent beaver-pond and free-flowing sections in the same segment (Figure 7). Hourly temperature recordings are synoptic among all sections. The minimum temperature in the Canyon segment was 12.6°C for the beaver-pond section and 12.5°C for the free-flowing section. Canyon segment maximums were identical at 18.2° C. For the Transition segment, minimums were 14.5°C and 14.9°C for beaver-pond and free-flowing sections respectively. Transition segment maximums were 24.1°C for the beaver-pond section and 23.24°C for the free-flowing section. In the Valley segment, the minimum temperature was equal for both the beaver-pond and free-flowing section at 16.9°C. The maximum in the beaver-pond section was 25.95 °C and the free-flowing section had a maximum temperature of 26.7°C.

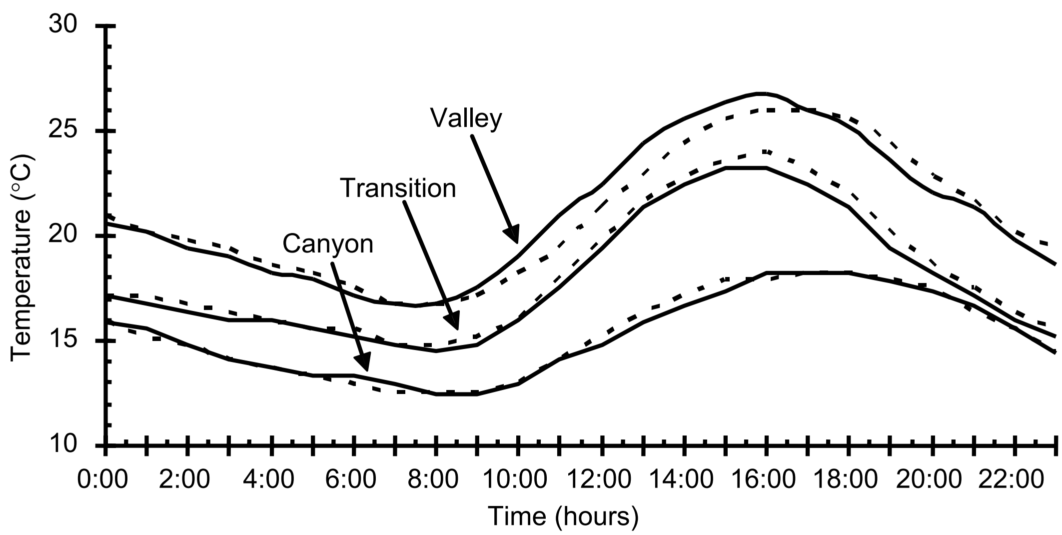

Figure 7. Diel temperature pattern of Willow Creek, Harney County, Oregon, for July 14, 1999; the day with the highest recorded water temperature (26.7°C) where data were available for all segments. Each dashed line (- - -) represents one beaver-pond section and each solid line (—) represents one free-flowing section in each of the Canyon, Transition, and Valley segments. Within-segment sections are adjacent and at the downstream end of the segment.

LAHONTAN CUTTHROAT TROUT

Age and Length Analysis

Scale samples were analyzed from 333 Lahontan cutthroat trout to determine length-at-age and to assess growth from July to September. Three age groups of Lahontan cutthroat trout were identified from scale analysis (Table 2; Figure 8). Because there was uncertainty in aging many of the largest trout, all fish larger than 250 mm were grouped together as age-3 and older. In July, trout aged from scales accounted for 14% of the total 1,378 Lahontan cutthroat trout captured during the period. The composition of scale samples was 16% age-1, 59% age-2, and 25% age-3+. Lahontan cutthroat trout captured in September were also placed in three age groups. Trout aged from scales accounted for 13% of the total 1,099 Lahontan cutthroat trout captured in September. The composition of scale samples was 30% age-1, 46% age-2, and 24% age-3+. .

The lengths of aged fish differed significantly among age groups in the same sample period, but comparisons of lengths between sample periods within the same age yielded mixed results (Table 2). In July, the median length of age-1 fish was significantly less than that of age-2 ($P < 0.001$) and of age-3 ($P < 0.001$). Similarly, the distribution of lengths differed significantly among age-1 and ages two and three ($P < 0.001$). All comparisons of lengths among age groups differed significantly within the same sample period ($P < 0.001$). For age-1 fish, the median length was not significantly different between July and September (Table 2; $P = 0.06$). The median lengths for age-2 fish differed significantly between July and September (Table 2; $P < 0.001$). Age-3 fish were not significantly different in length between July and September (Table 2; $P = 0.65$).

Table 2. Fork length means and SE and medians and range for age-1, age-2, and age-3+ Lahontan cutthroat trout aged from scales.

Age Group	n	Fork Length Mean (mm)	SE	Median (mm)	Range (mm)
			July		
1	31	104	3.8	112	58 – 132
2	112	163	2.5	158	122 – 220
3+	48	219	3.5	222	172 – 290
			September		
1	43	115	3.2	118	72 – 152
2	65	177	2.7	176	136 – 230
3+	34	220	5.2	220	160 – 274

Lahontan Cutthroat Trout Size Distribution Patterns

Lahontan cutthroat trout median lengths and length distributions differed among some sections and segments in July. In the Canyon segment there was no significant difference between beaver-pond and free-flowing sections in median length (Figure 9; P = 0.08) and the distribution of lengths was insignificant (P = 0.0503). For the Transition segment, there was no difference in median length between beaver-pond and free-flowing sections (P =0.15), but the length distribution was significant (P = 0.001). In the Valley segment, the median length and distribution differed significantly between beaver-pond and free-flowing sections (Figure 9; $P < 0.001$).

In September, significant differences in median fish lengths between beaver-pond and free-flowing sections were evident for the Canyon segment (Figure 9; P = 0.004) and Valley segment ($P < 0.001$), but not for the Transition segment (P = 0.15). The distribution of fish lengths were significantly different between beaver-pond and free-flowing sections for all segments; Canyon (P = 0.007), Transition (p = 0.004), Valley ($P < 0.001$) (Figure 9).

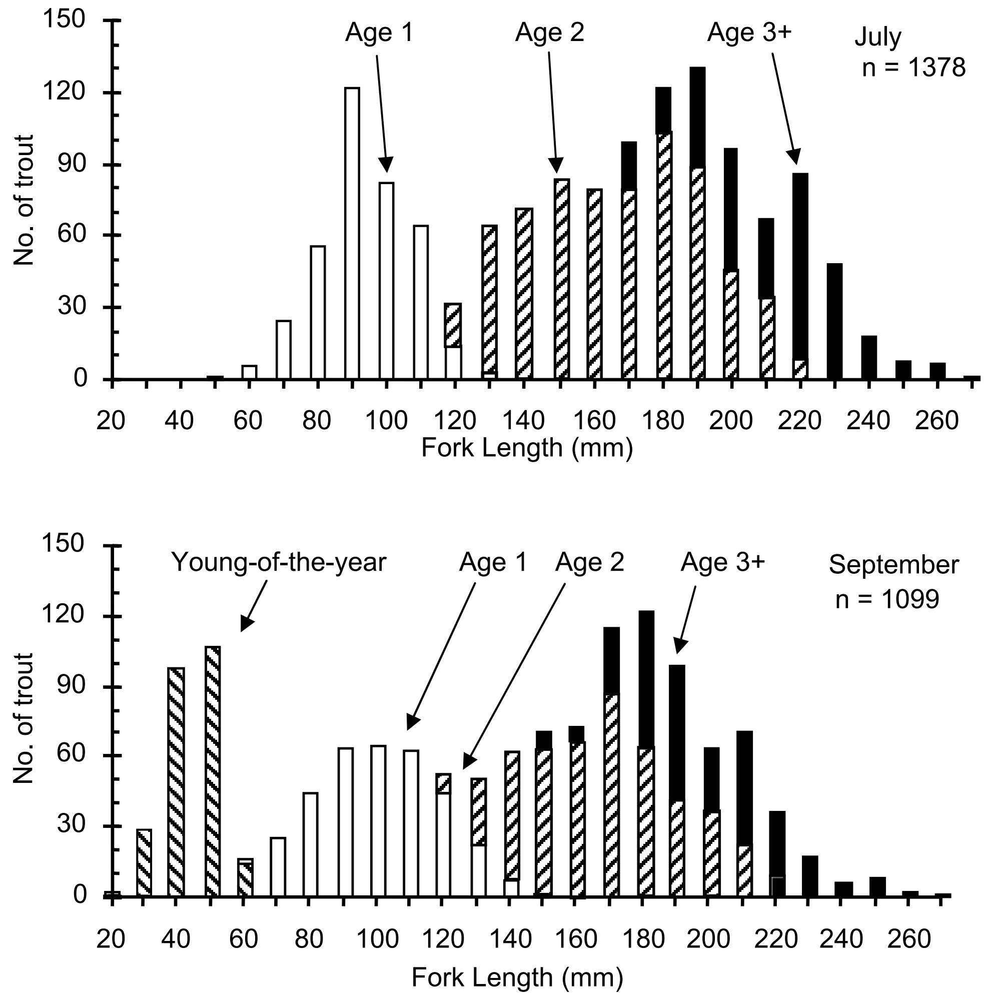

Figure 8. Length frequency histograms of Lahontan cutthroat trout from Willow Creek, Harney County, Oregon in July and September, 1999. Age distributions were calculated using an age-length key and scale analysis of 191 fish for July and 142 fish for September. Scales were not collected from young-of-the-year trout (<75 mm), and they were not included in the age-length key.

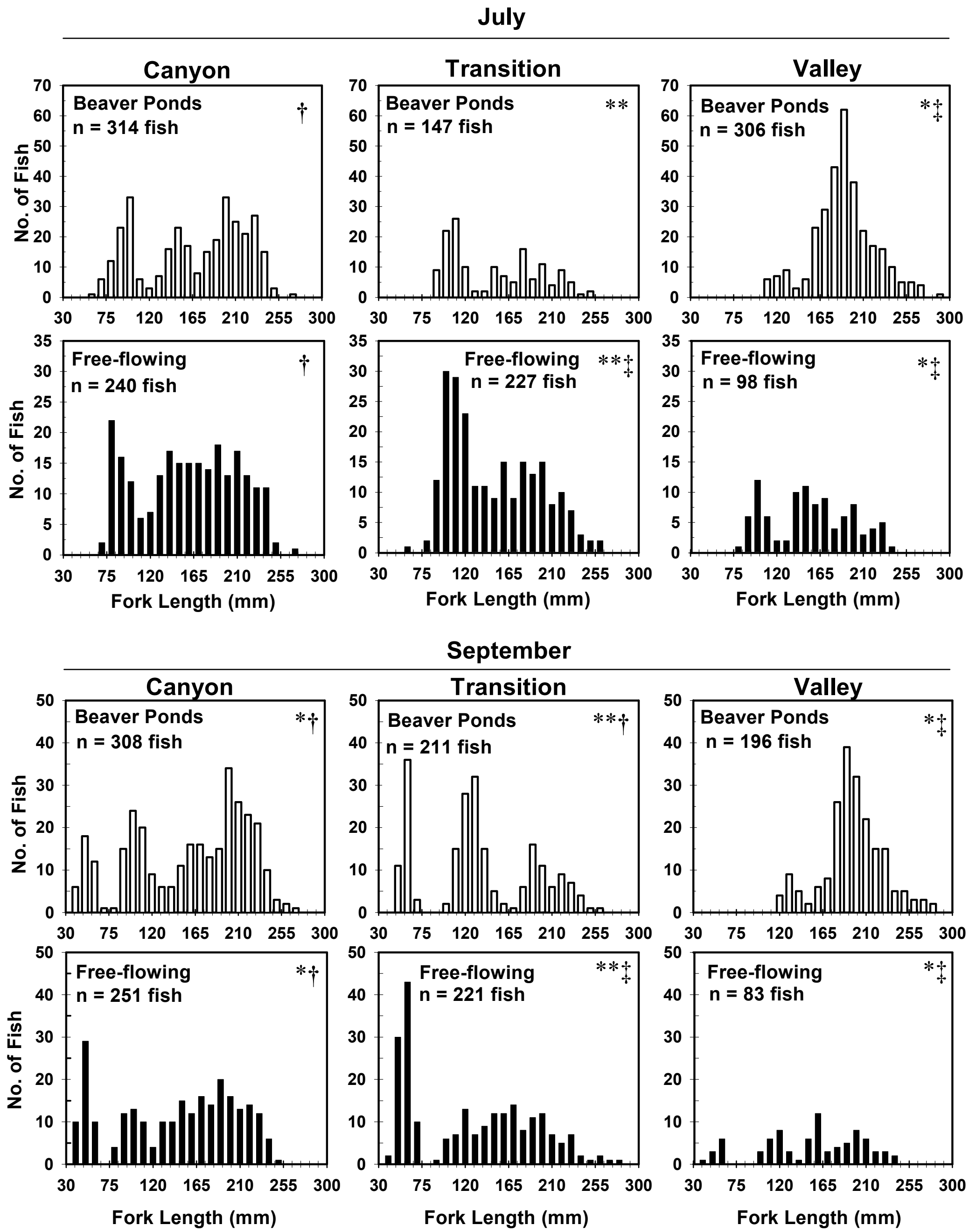

Figure 9. Length of Lahontan cutthroat trout captured in beaver-pond (□) and free-flowing (■) sections from three segments of Willow Creek, Harney County, Oregon, July and September, 1999. Asterisks indicate significantly different medians (*) or distributions (**) between beaver-pond and free-flowing sections within the same segment and month. Daggers indicate significantly different medians (†) or distributions (‡) between the same section type, within the same segment, between months. Young-of-the-year (< 75 mm) were not included in comparisons of medians and distributions.

Measures of Lahontan Cutthroat Trout Abundance

Lahontan cutthroat trout mean linear-denstiy (trout/ m) differed significantly among segments in July for age-1 ($P = 0.005$) and age-3+ ($P = 0.046$), but not for age-2 ($P = 0.12$) (Figure 10). Age-1 trout linear-density was approximately four and five times higher in the Transition and Canyon segments respectively than in the Valley segment. Age-3+ trout linear-density in the Canyon segment was more than twice that of the Transition segment.

The linear-density of Lahontan cutthroat trout was significantly higher in beaver-pond sections than free-flowing sections. For example, age-1 linear-denstiy was significantly higher in beaver-pond sections than free-flowing sections of the Canyon and Transition segments (Table 3). Beaver-pond sections did not have significantly more fish-per-meter than free-flowing sections in the Valley segment. Among age-2 trout, the linear-density in beaver-pond sections was significantly higher than free-flowing sections in the Canyon and Valley segments ($P < 0.05$), but not in the Transition segment ($P > 0.05$). Similarly, age-3+ Lahontan cutthroat trout linear-density was significantly higher in the Canyon and Valley segment beaver-pond sections ($P < 0.05$).

In September, the beaver-pond sections of the Canyon segment had significantly higher linear-density Lahontan cutthroat trout than the free-flowing sections for age-1, age-2, and age-3+ (Table 3; $P < 0.05$). Linear-density in the Transition and Valley segments did not differ significantly between beaver-pond and free-flowing sections.

Lahontan cutthroat trout areal-density (trout/ m^2) in July, differed significantly among segments for age-1 ($P = 0.009$), but not for age-2 ($P = 0.33$) and age-3+ ($P = 0.28$) (Table 3). Age-1 areal-density was four times greater in the Transition segment than in the Valley segment; the Canyon segment was not significantly different from either the Transition or Valley segments. For September areal-density, segment level differences were significant ($P = 0.04$) for age-2 between the Canyon segment and the Transition segment. Within segment differences between beaver-pond and free-flowing sections were significant for age-1 Lahontan cutthroat trout in the Transition segment ($P < 0.05$) and age-3+ in the Valley segment ($P < 0.05$). In both instances, the beaver-pond sections had four times as many fish per square meter as the free-flowing sections.

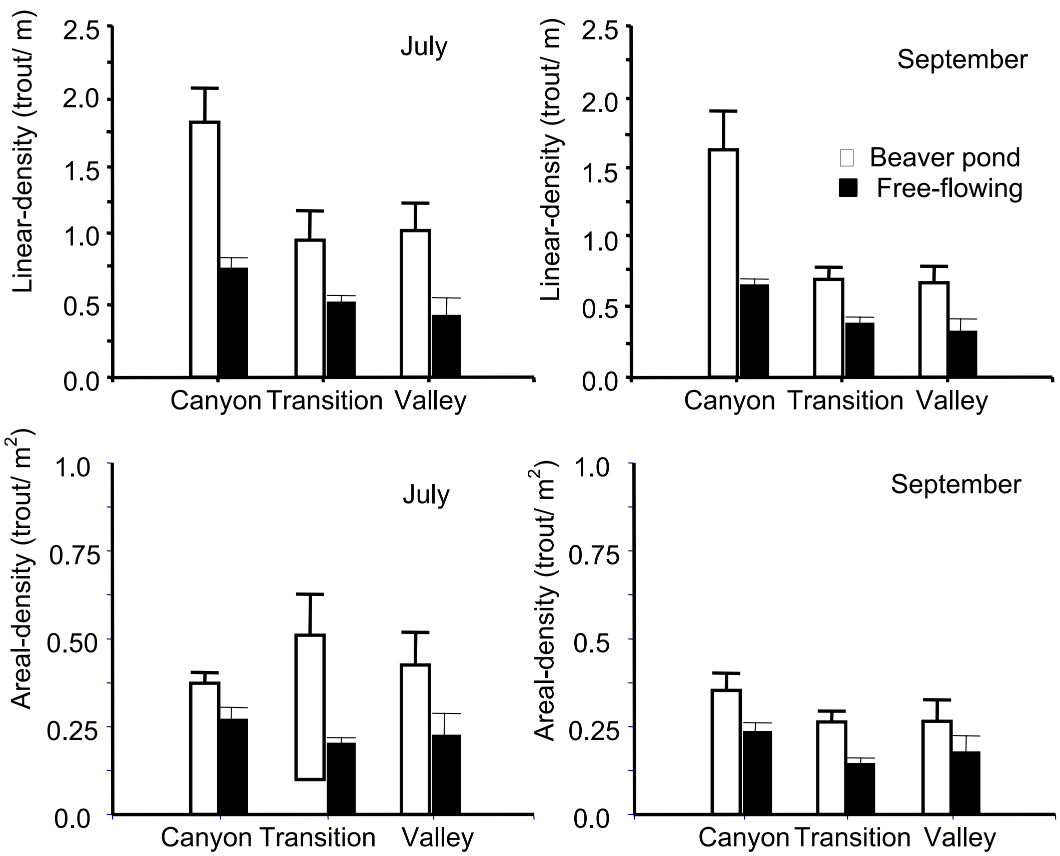

Figure 9. Mean Lahontan cutthroat trout per meter and per square meter of stream in July and September, 1999 in Willow Creek, Harney County, Oregon. Bars represent standard errors.

Total linear-density in July was significantly different among segments ($P <$ 0.001), with the Canyon beaver-pond sections having more fish than any other segment-section combination (Figure 10). Total areal-density in July was not significantly different among segments ($P = 0.13$). In September, total linear-density differed significantly among segments ($P < 0.001$). The beaver-pond sections of the Canyon segment had more than twice the linear-density as the next highest section (Transition beaver-pond sections) and more than five times the lowest linear-density value in the Valley segment free-flowing sections (Figure 10). Although segment was a significant factor for areal-denstiy in September ($P = 0.03$), the only significantly different ($P < 0.05$) segment-section combinations were Canyon beaver-pond (mean = 0.35) and Transition free-flowing (mean = 0.15) sections.

Lahontan Cutthroat Trout-habitat Relations

The approximate downstream limit for young-of-the-year Lahontan cutthroat trout on September 9, 1999 was located in the Valley segment (Figure 2). The average maximum water temperature for the seven days prior to sampling was 17.3°C. The downstream limit for adult Lahontan cutthroat trout (age-1 and older) was identified on July 24 and September 9, 1999 just downstream of the study area boundary. The approximate 7-day-maximum temperature ending July 23, 1999 for the adult downstream limit was 23.6°C. For September 9, 1999, the approximate 7-day-maximum temperature was 19.6°C. Age-2 and age-3 trout were captured in all 28 sections, and age-1 trout were captured in all sections except one beaver-pond and one free-flowing section, both in the Valley segment.

Lahontan cutthroat trout-per-meter decreased with increasing temperature in beaver-pond ($r = -0.52$, $P = 0.02$) and free-flowing ($r = -0.71$, $P = 0.01$) sections. Investigated by age group and section type, Lahontan cutthroat trout per meter was negatively correlated with temperature in free-flowing sections for all age groups (Table 4). For beaver-pond sections, age-1 trout per meter decreased significantly with increasing temperature, and the relationship of temperature to trout per meter for age-2 and age-3+

was marginal (Table 4). Lahontan cutthroat trout per square meter was not correlated to temperature.

The effect of increasing water temperature on Lahontan cutthroat trout was expressed differently among age groups and was influenced by the section type. The density (fish/m) of age-2 and age-3+ trout in beaver-pond sections remained relatively constant even though water temperature increased significantly in a downstream direction (Figure 11). In contrast, the density (fish/m) of age-1 Lahontan cutthroat trout decreased dramatically as the temperature exceeded 22°C (Figure 11).

None of the other measured habitat variables show a consistent relationship to fish per meter, either as individual age groups or as total fish per meter. Measured habitat variables that have a significant correlation with Lahontan cutthroat trout per meter are also correlated (positively or negatively) with temperature. For example, mean width (Table 1) for both section types combined, was positively correlated with fish per meter for all three age groups ($r > 0.54$, $P < 0.007$). However, mean width is also negatively correlated with temperature ($r = -0.58$, $P = 0.003$) and positively correlated with cross-sectional area ($r = 0.71$, $P < 0.001$).

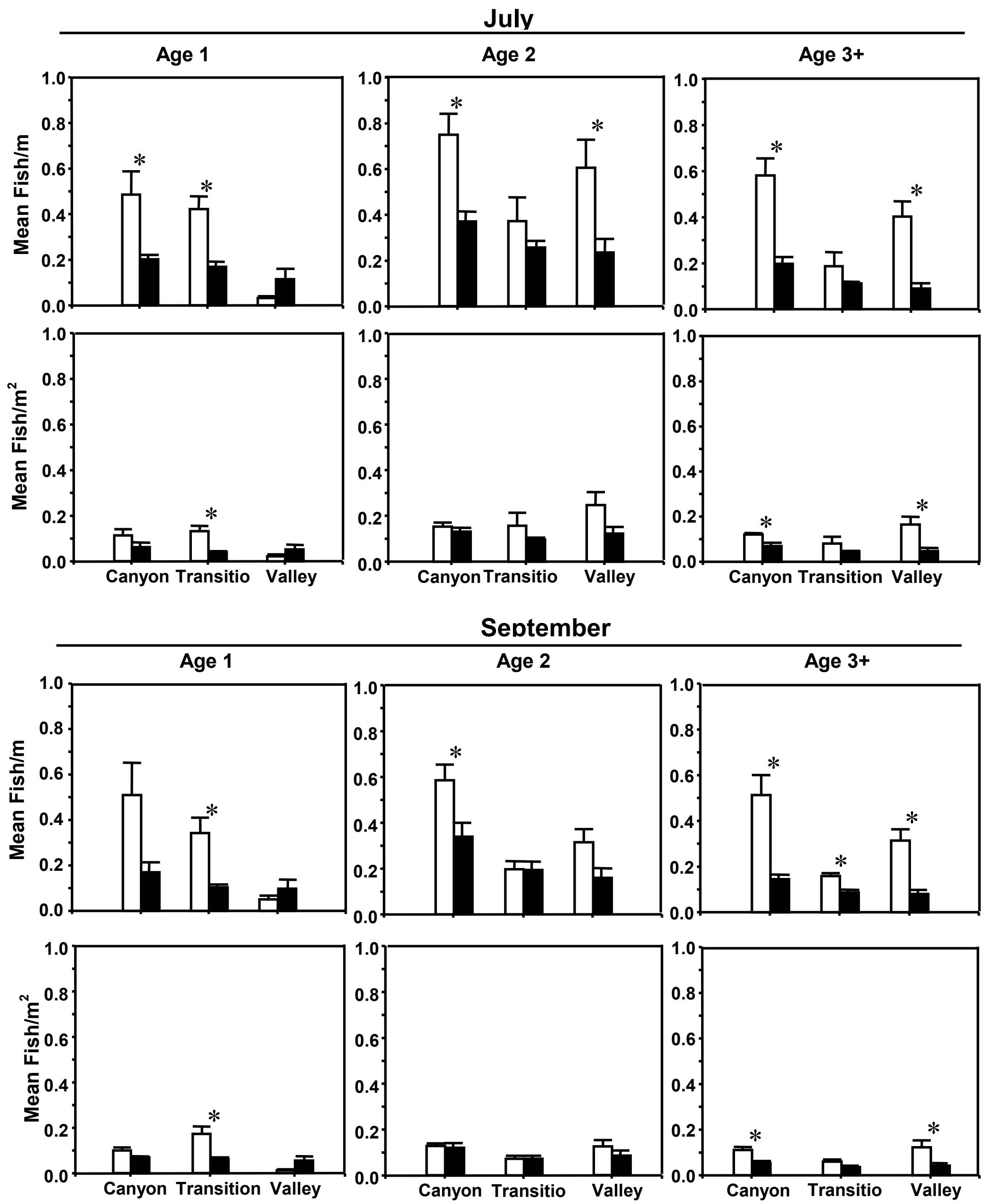
July
Age 1
Age 2
Age 3+
Mean Fish/m
Mean Fish/m²
1.0
0.8
0.6
0.4
0.2
0.0
Canyon Transitio Valley
Canyon Transitio Valley
Canyon Transition Valley
September
Age 1
Age 2
Age 3+
Mean Fish/m
Mean Fish/m²
Canyon Transition Valley
Canyon Transitio Valley
Canyon Transitio Valley

Table 3. Means of Lahontan cutthroat trout per meter and Lahontan cutthroat trout per square meter in beaver-pond and free-flowing sections for ages 1, 2, and 3+. Values are from July and September, 1999 in three segments of Willow Creek: Canyon, Transition, and Valley. Standard errors are in parentheses.

	Beaver-pond Sections						Free-flowing Sections					
	Mean trout per meter (fish/m)			Mean trout per square meter (fish/m^2)			Mean trout per meter (fish/m)			Mean trout per square meter (fish/m^2)		
Segment	Age 1	Age 2	Age 3+	Age 1	Age 2	Age 3+	Age 1	Age 2	Age 3+	Age 1	Age 2	Age 3+
						July						
Canyon	0.49	0.75	0.58	0.10	0.15	0.12	0.20	0.37	0.20	0.07	0.13	0.07
	(0.10)	(0.09)	(0.07)	(0.01)	(0.02)	(0.01)	(0.02)	(0.04)	(0.03)	(0.004)	(0.02)	(0.02)
Transition	0.42	0.37	0.19	0.17	0.16	0.08	0.17	0.26	0.11	0.06	0.10	0.04
	(0.06)	(0.10)	(0.06)	(0.03)	(0.06)	(0.03)	(0.02)	(0.03)	(0.01)	(0.01)	(0.10)	(0.01)
Valley	0.03	0.61	0.40	0.01	0.25	0.17	0.12	0.24	0.09	0.06	0.12	0.05
	(0.01)	(0.12)	(0.07)	(0.01)	(0.06)	(0.03)	(0.05)	(0.06)	(0.02)	(0.02)	(0.03)	(0.01)
						September						
Canyon	0.51	0.59	0.51	0.11	0.13	0.11	0.17	0.34	0.15	0.06	0.12	0.05
	(0.14)	(0.68)	(0.09)	(0.03)	(0.01)	(0.01)	(0.04)	(0.59)	(0.02)	(0.02)	(0.02)	(0.01)
Transition	0.34	0.20	0.16	0.13	0.07	0.06	0.10	0.2	0.09	0.04	0.07	0.04
	(0.07)	(0.03)	(0.01)	(0.02)	(0.01)	(0.01)	(0.01)	(0.04)	(0.01)	(0.004)	(0.01)	(0.01)
Valley	0.05	0.32	0.31	0.02	0.13	0.12	0.09	0.16	0.08	0.05	0.09	0.04
	(0.02)	(0.06)	(0.05)	(0.01)	(0.03)	(0.03)	(0.04)	(0.04)	(0.02)	(0.02)	(0.02)	(0.01)

Table 4. Correlation matrix of eight habitat variables versus Lahontan cutthroat trout per meter in beaver-pond and free-flowing sections of Willow Creek. Values are Pearson correlation coefficients, bold indicates correlation >0.50, and asterisks indicate significance ($P <$ 0.05)

	Lahontan cutthroat trout per meter							
	Beaver-pond Sections				Free-flowing Sections			
Variable	Age-1	Age-2	Age-3+	Total	Age-1	Age-2	Age-3	Total
7 - Day - Maximum (°C)	**− 0.74***	− 0.18	− 0.34	**− 0.52**	**− 0.63***	**− 0.61***	**- 0.71***	**− 0.71***
Maximum Temperature (°C)	**− 0.76***	− 0.22	− 0.37	**− 0.55**	**− 0.59***	**− 0.64***	**− 0.74***	**− 0.71***
Maximum Depth (m)	− 0.12	0.12	0.21	0.08	− 0.07	− 0.21	− 0.13	− 0.17
Mean Depth (m)	**− 0.54**	− 0.19	− 0.12	− 0.36	0.01	− 0.002	0.18	0.06
Mean Width (m)	**0.54**	0.40	**0.66***	0.66*	**0.66***	0.45	0.25	0.50
Width : Depth	0.49	0.38	0.49	0.56	0.45	0.32	0.11	.033
Cross-sectional Area (m^2)	0.24	0.18	0.48	0.36	**0.75***	**0.57**	0.46	**0.65***
Shade (%)	0.47	**0.60***	**0.56***	0.69*	**0.53**	**0.63***	**0.71***	**0.69***

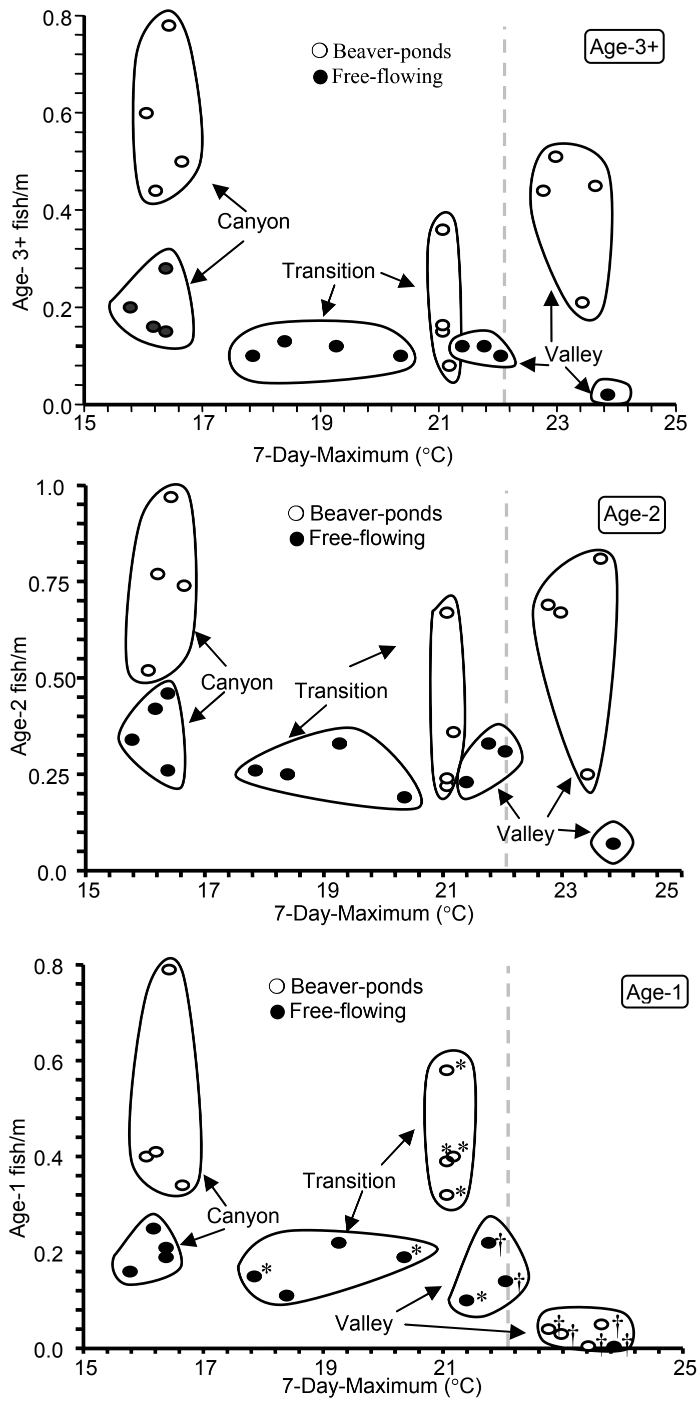

Figure 11. Scatter plots of age-1, age-2, and age-3+ Lahontan cutthroat trout per meter and temperature for the July sampling period. Study sections are clustered by section type and segment. Young-of-the-year were absent from sample sections in July (*) and both July and September (†) as indicated on the Age-1 panel. The vertical dashed gray lines denote the suggested daily maximum temperature of 22°C (Dunham 1999).

CHAPTER 4: DISCUSSION

Beavers substantially altered the physical habitat of Willow Creek and as a result, have apparently influenced Lahontan cutthroat trout distribution. In contrast, water temperature in Willow Creek was not influenced by beaver activity. The magnitude of habitat change was dependent on longitudinal location and geomorphic controls characteristic of each stream segment. The response of Lahontan cutthroat trout density to increasing water temperatures was influenced by beaver ponds. Other research on the affects of beaver ponds on fish distribution and species richness also found that beaver ponds interact with the local geomorphology and watershed position to influence fish assemblages (Snodgrass and Meffe 1998; Schlosser and Kallemeyn 2000).

Four factors interact to influence the distribution of Lahontan cutthroat trout in Willow Creek: 1) beaver pond morphology, 2) the beaver pond location within segments, 3) water temperature, and 4) the location of potential barriers (associated with geomorphic response and beaver activity) to Lahontan cutthroat trout movement. At the segment scale, beaver ponds were influenced by channel form more than the valley form. For example, beaver ponds in the Canyon segment were wide and relatively shallow despite their location in a narrow valley. In contrast to beaver ponds in upland valleys were narrow and deep (Johnston and Naiman 1987), beaver ponds in this segment of Willow Creek were found in wide aggraded areas associated with alluvial fans.

The beaver ponds in the Transition segment reflected the morphology of the narrow and moderately incised channel and were deepest in flooded meander-bend pools that had been scoured prior to impoundment. Although remnants of numerous beaver complexes were evident in the Transition segment, the majority of abandoned complexes appeared to have little influence on channel structure. Beaver-pond sections in the Transition segment were located mostly inside a fenced cattle exclosure and just upstream of a 4-m high headcut that acted as a barrier to upstream fish movement.

The narrow deeply incised channel of the Valley segment laterally constrained beaver pond widths similar to the Transition segment. In contrast to the Transition segment, beaver dams in the Valley segment had greater height creating deep ponds that extended farther upstream. Several abandoned beaver complexes were located in the

Valley segment; some of which appeared to have a continued influence on channel structure. The Valley segment beaver-pond sections were located in an area of expanding beaver activity and active channel migration. Although undocumented, personal observation suggests the combination of dam height and diffuse flow around and through the dams may result in seasonal blockage of at least upstream movement by Lahontan cutthroat trout in the Valley segment.

Lahontan cutthroat trout linear-density was highest in the Canyon segment. Several factors may explain the high number of trout. First, the Canyon segment was the least affected by human activity. The basalt rimrock precludes access to the canyon for much of the length; there was minimal evidence of cattle grazing and the riparian vegetation was very dense. Tait et al. (1994) reported a significant decrease in juvenile steelhead trout *O. mykiss* density with increasing exposure to solar radiation in high desert streams of central Oregon. Similarly, cover provided by riparian shade and woody inputs are common positive variables in models predicting the presence, density, and biomass of salmonids (Fausch et al. 1988). Second, water temperature in the Canyon segment does not exceed 20°C at anytime during the year. Lahontan cutthroat trout show no impairment to swimming ability, feeding, or growth at temperatures below 22°C (Meeuwig 2000). Third, the combination of dense riparian cover in the free-flowing sections, reduced overhead cover and increased habitat area in the beaver-pond sections, and overall cool water temperatures may result in elevated survival rates for Lahontan cutthroat trout. For example, beaver ponds in the Canyon segment are wide with extensive shallow edge habitat often associated with overhanging terrestrial or emergent aquatic vegetation. Complex low velocity edge habitat is considered a resource necessary for young-of-the-year cutthroat trout (Moore and Gregory 1988; Bozek and Rahel 1991). The edge habitat of a beaver pond may reduce the energetic cost of foraging by young-of-the-year and provide a growth advantage over riffle edge habitat (Rosenfeld and Boss 2001). Beaver ponds may also convey growth advantages to both juveniles and adults because of greater variety in choice of depths and velocities for feeding and resting (Fausch 1984; Spina 2000).

Lahontan cutthroat trout linear-density in the Transition segment dropped to about one-half that of the Canyon segment in the beaver-pond sections and two-thirds of the free-flowing sections. Discharge and riparian shade cover both decreased substantially in the Transition segment, and the 7-day-maximum temperatures increased to levels associated with impairment of swimming and growth in Lahontan cutthroat trout. A likely explanation for the loss of water may be the transition out of the shallow layer of gravel and cobble substrate in the Canyon segment (an uplifted fault block) to the deep depositional alluvium and gravels overlaying the dropped fault block of the basin floor (Valley segment). Reductions in stream volume and increased solar exposure have been documented to increase the rate of stream heating (Brown 1969; Beschta 1997).

The linear-density of age-2 and age-3+ Lahontan cutthroat trout declined substantially from the Canyon to the Transition segment in both the beaver-pond and free-flowing sections. In contrast, the abundance of age-1 trout remained relatively unchanged. The physical habitat (e.g. depth, cover) of the Transition segment beaver ponds may be unsuitable for high numbers of adults. Relatively shallow ponds with insufficient cover for adults may release juveniles from competitive pressures and increase their survival (Bozek et al. 1994; Spina 2000). Higher temperatures in the Transition segment may force trout to move or risk reduced fitness (Warren and Liss 1980). On the other hand, if high temperatures were responsible for the low numbers of adult (ages 2 and 3+) Lahontan cutthroat trout, then similarly low numbers of juveniles (age-1) would be expected. Without a mechanism restricting the movement of juveniles, this scenario is unlikely especially since adults may have higher tolerance to temperature extremes (Brett 1971). The barrier falls immediately downstream of the Transition segment beaver ponds (Transition/ Valley segment boundary) prevented fish that moved downstream over the falls from returning to the beaver ponds.

In the Valley segment, the downstream extent of Lahontan cutthroat trout varied among age groups. For example, age-1 abundance values in the Valley segment ranged from the lowest in the study (0 fish/m) to the second highest (0.22 fish/m) for free-flowing sections. The age-1 abundances in each of the beaver-pond sections were the lowest for age-1 trout in Willow Creek (Figure 11). Similarly, no young-of-the-year Lahontan cutthroat trout were observed in the Valley segment during July sampling (Figure 11). In contrast, ages-2 and 3+ fish were found in all sample sections of the Valley segment. In streams across the range of Lahontan cutthroat trout in northern Nevada, the distribution of large (> 100 mm standard length) and small (≤ 100 mm) fish overlapped (Dunham et al. 1999).

The unequal distribution of adult, juvenile, and young-of-the-year Lahontan cutthroat trout implies that the Valley segment may be acting as a sink (*sensu* Pulliam 1988) for adults moving downstream from above the head-cut barrier. No young-of-the-year trout were observed in the Valley segment or in Transition segment sections within 2 km the barrier during July sampling. During September sampling, young-of-the-year were captured in all sample sections upstream of and including the first free-flowing section in the Valley segment downstream of the headcut. This suggests that no successful recruitment occurred within the Valley segment.

Although the spawning distribution of Lahontan cutthroat trout in Willow Creek is unknown, temperatures in the Valley segment suggest a high mortality rate for eggs spawned in the Valley segment. The suggested temperature range for incubating cutthroat trout eggs is 4.4 – 12.8°C (Bell 1986) and the recommended optimum is 10°C (Hickman and Raleigh 1982). Based on other salmonid species, the upper thermal limits for eggs averages about 15°C (Beacham and Murray 1990). Water temperatures in the Valley segment of Willow Creek during the estimated time of egg incubation (April – June) exceeded 15°C sporadically beginning April 13 and exceeded 15°C for 11consecutive days in mid-May. In addition, observations during high spring flows, of adult Lahontan cutthroat trout attempting to jump the headcut barrier without success further suggests that the Valley segment is a sink.

Although there appeared to be no recruitment in the Valley segment, the beaver ponds support abundances of age-2 and 3+ Lahontan cutthroat trout equal to beaver ponds in the Canyon segment. In contrast, the free-flowing section of the Valley segment with temperatures comparable to the beaver-pond sections had the lowest abundance of age-2 and 3+ fish. Temperatures in the beaver-pond sections and the furthest downstream free-flowing section in the Valley segment regularly exceeded 22°C (Figure 11), the temperature at which feeding and swimming become impaired. Fish metabolism increases as temperature increases, but at temperatures between 22°C and 24°C, Lahontan cutthroat trout stop feeding and swimming performance becomes impaired (Dickerson and Vinyard 1999; Mueewig 2000). Smith and Li (1982) found that juvenile steelhead trout shifted to higher velocity water as temperature increased. They attributed this shift to higher food intake requirements being satisfied with higher drift rates in the faster water. In contrast, Lahontan cutthroat trout in the Valley segment beaver ponds were observed mid-afternoon resting on the pond bottom in water exceeding 24°C (as measured with a temperature probe).

The downstream distribution of Lahontan cutthroat trout in Willow Creek extends beyond what would be predicted based on the known distributional limits of Lahontan cutthroat trout from 30 streams in northern Nevada (Dunham et al. 1999). They suggested that much of the variation in their model may result from local interactions of topography and climate, creating conditions that restrict or extend Lahontan cutthroat trout distribution. Although the presence of beaver ponds in lower Willow Creek appeared to extend the downstream distribution of Lahontan cutthroat trout, the influence of the barrier in preventing upstream movement of fish out of the Valley segment may also contribute to the extended distribution and high density in the beaver ponds.

The downstream distribution of adult Lahontan cutthroat trout in the sample sections remained unchanged from the July to the September sample periods. However, trout abundance (fish/ m) decreased significantly between the two sample periods. The decrease in abundance in the beaver ponds of the Valley segment was larger than the decreases observed between July and September for the Transition and Canyon segments (neither of which were significant decreases). Although no data were collected specifically to address this change, possible explanations include higher natural mortality rates in the Valley segment beaver ponds, movement out of the ponds, and stress induced mortality from electrofishing. A higher mortality rate may be the result of added stress from high temperatures or reductions may have resulted from angling. As stated in the Methods, angling was closed during the study and assumed to have had no effect. Notes taken during electrofishing indicate only four mortalities out 305 captures in the Valley beaver-pond sections.

This study of Willow Creek has provided valuable information about the influence of beaver ponds on the distribution of Lahontan cutthroat trout in Willow Creek. The data clearly show the capacity of Willow Creek to support Lahontan cutthroat trout was increased by beaver ponds. Furthermore, data suggest that beaver ponds may provide a survival advantage to Lahontan cutthroat trout where their distribution is limited by temperature. However, the increased survival of Lahontan cutthroat trout in the Valley-segment beaver ponds does not translate into increased fitness. The combination of high temperatures interferring with recruitment and the barrier preventing upstream movement, results in Lahontan cutthroat trout in the Valley segment not contributing to the population in Willow Creek.

Willow Creek is a highly dynamic stream adjusting to changes in land management implemented in 1989. The high level of beaver activity combined with significant erosion and sloughing of vertical banks has altered the channel location and structure at numerous points along Willow Creek. Beaver have accelerated some aspects of stream recovery by flooding and saturating the soil adjacent to ponds. This has effectively drowned many upland species (e.g. sagebrush) and converted large areas to more typical riparian species (e.g. willow and sedges). Additionally, beaver ponds have trapped sediment and in some cases completely filled in aggrading what was an incised channel a decade ago. The rapid changes occurring in Willow Creek highlight the uniqueness of this system and the beneficial effect beavers have had in the recovery of Willow Creek. The continued monitoring of changes in the Willow Creek system and new efforts to monitor the effects of beavers in other high-desert streams will increase our knowledge and broaden our understanding of the role beavers play in arid-land streams.

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APPENDICES

Appendix C. Section type (BP = beaver-pond section; FF = free-flowing section), stream segment, date sampled, and whether or not young-of-the-year were observed for longitudinally ordered sample sections.

Section #	Sample Section Type	Stream Segment	Date Sampled		Observed Young-of-the-year	
			July	September	July	September
1	FF	Valley	7/13/99	9/01/99	No	No
2	BP	Valley	7/16/99	9/02/99	No	No
3	BP	Valley	7/15/99	9/02/99	No	No
4	BP	Valley	7/20/99	9/07/99	No	No
5	BP	Valley	7/20/99	9/10/99	No	No
6	FF	Valley	7/14/99	9/02/99	No	No
7	FF	Valley	7/21/99	9/04/99	No	No
8	FF	Valley	7/21/99	9/07/99	No	No
9	BP	Transition	7/26/99	9/14/99	No	Yes
10	BP	Transition	7/22/99	9/08/99	No	Yes
11	BP	Transition	7/22/99	9/08/99	No	Yes
12	BP	Transition	7/26/99	9/14/99	No	Yes
13	FF	Transition	7/23/99	9/08/99	No	Yes
14	FF	Transition	7/27/99	9/10/99	Yes	Yes
15	FF	Transition	7/26/99	9/11/99	Yes	Yes
16	FF	Transition	7/21/99	9/09/99	No	Yes
17	BP	Canyon	7/28/99	9/15/99	Yes	Yes
18	BP	Canyon	7/28/99	9/15/99	Yes	Yes
19	FF	Canyon	7/28/99	9/15/99	Yes	Yes
20	FF	Canyon	7/27/99	9/14/99	Yes	Yes
21	FF	Canyon	7/16/99	9/03/99	Yes	Yes
22	BP	Canyon	7/17/99	9/04/99	Yes	Yes
23	BP	Canyon	7/17/99	9/03/99	Yes	Yes
24	FF	Canyon	7/14/99	9/03/99	Yes	Yes