A Field Test of Effects of Livestock Grazing Regimes on Invertebrate Food Webs that Support Trout in Central Rocky Mountain Streams



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EXECUTIVE SUMMARY

This report summarizes the initial findings and progress for two large field studies conducted as part of a Ph.D. research project funded by the Natural Resources Conservation Service (NRCS), US Forest Service (USFS), Wyoming Department of Game and Fish (WYG&F), and Bureau of Land Management (BLM), investigating the role of invertebrate prey resources in supporting rangeland trout populations. Traditional range management to benefit trout has focused on maintaining instream habitat by preventing bank erosion, but this approach may be inadequate. Recent research worldwide has shown that trout derive half their food from terrestrial invertebrates that fall into streams from riparian vegetation (see Baxter et al. 2005 for a review). Much of the rest comes from aquatic insects, many of which feed on dead leaves from riparian vegetation. This means that healthy riparian vegetation is critical not only to bind banks and maintain pools and riffles, but also to support terrestrial invertebrates and provide food for aquatic insects that feed trout. In summary, sustaining healthy trout populations also requires sustaining habitat and food for their prey.

Our recent work in Wyoming is the first to demonstrate the link between better grazing management and increased trout populations via these invertebrates. We found that High-Density Short-Duration (HDSD, similar to intensive rotational grazing discussed in this report) grazing resulted in 2-3 times more riparian vegetation, twice the terrestrial invertebrates falling into streams, 3-5 times more terrestrial invertebrate biomass in trout diets, and also twice the trout biomass, compared to traditional season-long grazing (Saunders and Fausch 2007b). Given the potential for HDSD grazing management to double trout abundance, this applied science has important implications for management of rangeland trout streams. However, what is needed now to promote policy change is a broader evaluation of the relative effectiveness of the most

common grazing systems used by both private and public rangeland managers. The goal of this project is to understand the importance of terrestrial and aquatic invertebrates as a prey resource for rangeland trout, and whether prescribed grazing management can increase their availability by promoting streamside vegetation.

During summer 2007 we conducted a large-scale field comparative study on 16 rangeland streams in north-central Colorado. The objectives were to determine 1) whether prescribed grazing management increases the input of terrestrial prey to rangeland streams by promoting riparian vegetation, 2) whether terrestrial invertebrates are an important prey resource for brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) in rangeland streams, 3) whether intensive grazing management is associated with increased trout abundance, and 4) how these response variables compare in sites managed for livestock grazing versus sites grazed by wildlife only. To address these goals, we identified four sites with season-long grazing, four under simple rotational grazing, five under an intensive rotational grazing system, and three that were grazed by wildlife only.

During summer 2008 we conducted a large-scale field experiment in which riparian pastures were constructed and streamside vegetation was experimentally grazed under four different grazing treatments. The objectives were to 1) determine the effect of a single season's use of riparian vegetation by cattle, 2) test whether the amount of terrestrial invertebrates falling into streams and in trout diets are reduced by more intensive grazing, and 3) evaluate the relative importance of woody versus herbaceous riparian vegetation for supplying terrestrial invertebrate prey resources to rangeland trout streams. To address these goals we constructed four riparian pastures on each of four streams near Lander, WY (n = 16 pastures) and used cow/calf pairs to apply four grazing treatments to each stream in a randomized complete block design (streams served as blocks). Experimental treatments were: 1) a moderate grazing treatment leaving a 4 - 6 inch stubble height after grazing, 2) an intensive grazing treatment leaving a 2 - 3 inch residual stubble height after grazing, 3) the same intensive grazing treatment with additional removal of 66% of riparian shrubs within 10 m of the stream, and 4) a control treatment with no livestock grazing, but from which wildlife were not excluded.

During both summers, we measured streamside vegetation characteristics, sampled the invertebrates entering stream reaches and in the stream substrate, collected trout diets, and conducted fish abundance and biomass estimates at each site. This report presents results of the initial analysis of data collected during summer 2007 and outlines the experimental design used, and sampling conduced, during summer 2008.

Results of research conducted during summer 2007 show that intensive rotational sites had more aboveground herbaceous vegetation than season long or simple rotational sites. At all sites, graminoids contributed the most to the total biomass of aboveground vegetation. Furthermore, there was no evidence that sites managed for intensive rotational grazing had less vegetation biomass than sites grazed only by wildlife. The average maximum height of grasses forbs and shrubs, a measure of vertical vegetation structure, showed a similar pattern as the aboveground biomass. Vegetation tended to be tallest at sites managed for intensive rotation grazing and shortest at season long sites. Sites managed for season-long grazing received the greatest amount of vegetation removal (ca. 60%, measured in percent utilization) of the four systems studied. In contrast, sites managed for both intensive rotational and wildlife only grazing had relatively little vegetation use (10-20%), and significantly less than season long sites.

We sampled invertebrates falling into streams for six days during July and August 2007 using $\frac{1}{2}$ - m² pan traps. Overall, differences between the total biomass of invertebrates entering rangeland streams in north-central Colorado in July and August 2007 were primarily a result of reduced input of adult aquatic insect biomass entering streams during August, whereas differences in the total biomass of invertebrates entering streams under different grazing management systems were driven by biomass of terrestrial invertebrates entering sites. In general, sites managed for rotational grazing (both SRG and IRG) received more invertebrate biomass than sites managed for SLG. Although this pattern was consistent for the biomass of terrestrial invertebrates entering streams during July and August and for the biomass of adult aquatics entering streams during July, differences between sites were frequently not significant due to high variability in the input of invertebrate biomass among sites with each grazing system category. Unexpectedly, the biomass of terrestrial invertebrates entering streams managed for IRG was lower than that entering sites managed for either SRG or WO. Finally, the biomass of invertebrates entering streams not grazed by cattle was greater than that observed at sites managed for SLG, but statistically similar to sites managed for rotational grazing.

During July and August 2007 we collected diet samples from 20 trout per stream (120 – 350 mm fork length) to evaluate what invertebrate prey resources were important to trout in rangeland streams in northern Colorado. Overall, the biomass of invertebrate prey in trout diets was highly variable. With the exception of fish sampled at sites managed for Simple Rotational Grazing during August 2007, fish had more biomass of aquatic invertebrate prey in their diets than terrestrial prey. Throughout summer 2007 both the total and terrestrial invertebrate biomass in trout diets was greatest at sites managed for Simple Rotational Grazing. In contrast, at sites managed for Intensive Rotational Grazing trout tended to have less invertebrate biomass (both

aquatic and terrestrial) in their diet than fish at sites under the other three types of grazing management. The total invertebrate biomass in trout diets at sites under each of the four different types of grazing management reflected the biomass of terrestrial invertebrates in trout diets during both July and August 2007, but reflected the biomass of aquatic invertebrates only during July. Furthermore, the biomass of terrestrials in trout diets closely reflected the biomass of terrestrial invertebrate entering streams except for sites managed for IRG. The biomass of terrestrials in trout diets was less than would be expected based on the amount entering IRG sites, relative to sites under different grazing management. Finally, vertebrate prey items (fish, amphibians, and small mammals) were rare, being found in less than 5% of stomach samples, but are likely an important prey resource for those that consume them.

We estimated fish population parameters at each site during August using three-pass removal electrofishing conducted at night. Density and biomass of adult trout less than 350 mm was nearly two times greater at sites grazed with rotational grazing systems compared to sites grazed season-long, but these differences were not significant due to high variability in trout populations among sites in each grazing management category. Trout density and biomass at two of the three sites grazed by wildlife only were not significantly different from any of the sites where livestock grazing occurred. The third site in this group was excluded because habitat in adjacent reaches was badly degraded by season-long grazing, which likely influenced trout abundance and biomass in the study reach. Overall, trout density and biomass appeared to be strongly influenced by large mobile trout that are known to use habitat features at much larger scales than our study reaches.

Results to date indicate there are differences in aboveground vegetation biomass, input of terrestrial and adult aquatic invertebrates, and fish abundance and biomass among sites under

different grazing regimes. Sites managed for season-long grazing had consistently lower values for all measures analyzed thus far, and these differences were frequently significant except for fish population parameters. Unexpectedly, sites managed for intensive rotational grazing received less invertebrate input and trout inhabiting these sites had less invertebrate biomass in their diet than would have been predicted base on the biomass and structure of riparian vegetation. This was particularly true during the August sampling period. In general, sites managed for wildlife use only received similar amounts of terrestrial and adult aquatic invertebrate inputs as sites managed for rotational grazing (simple or intensive). Furthermore, fish at these sites consumed similar amounts of invertebrate prey (particularly terrestrial invertebrates) as fish at sites managed for livestock use, although there was considerable variation between sites under different grazing management. There was often high variability among sites within each management regime, likely due to differences in climate and vegetation throughout the study region, as well as phenology of vegetation and invertebrates at individual sites. In particular, fish abundance and biomass were highly variable among sites, perhaps due to movement by larger trout. Analysis of diets for fish of different sizes may reveal important differences among grazing systems. Additional analyses will focus on determining what site level factors (e.g., vegetation height, humidity, stream temperature, etc.) influence the availability of invertebrate prey resources and their use by trout, and developing targeted management recommendations for riparian grazing that supports this important food web subsidy.

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INTRODUCTION

Livestock grazing is one of the dominant land uses in the West, and can have strong negative effects on aquatic habitats if poorly managed. Currently, more than 850 million acres are grazed in the western U.S. (GAO 1988, NRCS 2002), on a mixture of publicly and privately owned grasslands, shrublands, forested regions, and riparian areas (Shiflet 1994). Throughout these vegetation types cattle influence ecological functions directly by trampling and compacting soils, defecating, and removing vegetation. These direct impacts can alter the productivity of the landscape, change vegetation community composition, and have cascading effects throughout terrestrial and aquatic food webs. In riparian areas, the boundary between terrestrial and aquatic habitats is especially sensitive to removal of vegetation and trampling that often causes bank erosion and degrades aquatic habitats.

Although riparian zones make up <1% of rangelands, cattle congregate in these areas to find forage, shade, and water (Armour et al. 1991), and when allowed to range freely can overgraze and trample stream banks, and reduce bank stability. This leads to channel erosion, increased turbidity, siltation of streambed gravel, decreased pool depths, and reduced habitat complexity (Platts 1981; Kauffman and Krueger 1984; Belsky et al. 1999), which can reduce growth and reproduction of trout, and ultimately trout abundance and production. As a result of the high potential for grazing to affect riparian areas and aquatic systems, the Bureau of Land Management (BLM), U.S. Forest Service (USFS), and the Natural Resources Conservation Service (NRCS) have identified better management of riparian grazing as a critical goal for the future (BLM 2000; USFS 2004; NRCS 2005) and an area where better understanding about the effect of livestock use is needed (Wyman et al. 2006).

Current Grazing Practices as they Affect Fish

Although it is generally accepted that fish need both food and cover resources to persist, current grazing management is primarily designed to protect stream bank stability and instream habitat. General guidelines used to manage riparian grazing include maintaining 40-50% of aboveground vegetative biomass to sustain plant roots that bind banks (Meehan 1991), and maintaining at least a 4-inch stubble height of grasses to prevent cattle from browsing substantially on riparian shrubs (Clary and Webster 1989; Clary and Kruse 2004). The guiding principle has been that maintaining this minimum level of riparian vegetation prevents bank erosion that fills in pools trout need for overwinter survival, and clogs riffles that provide trout spawning habitat and support aquatic invertebrates on which trout feed.

Indeed, rapid increases in trout populations after cattle are fenced away from riparian zones indicate that grazing can have strong effects, but little is known about why these increases occur, leaving managers with little guidance for planning more sophisticated grazing management to benefit stream fish. Several demonstration projects in which cattle grazing was eliminated from riparian zones altogether showed large increases in abundance or biomass of trout within five years after complete rest (Keller and Burnham 1982; Knapp and Matthews 1996; see Meehan 1991 for review). However, full recovery of stream habitat, including revegetation and stabilization of banks, lateral scour that creates deep pools with overhead cover, cleaning of stream gravel needed for invertebrate production and trout spawning, and input of woody debris that creates habitat complexity, often requires more than these short periods to achieve.

Importance of Invertebrate Prey Resources

In addition to increasing instream habitat, improved grazing practices can also increase riparian vegetation biomass and increase invertebrate prey availability for trout directly through increased inputs of terrestrial insects, or indirectly through detrital inputs that increase secondary production of aquatic insects. Recent studies have shown that terrestrial invertebrate prey that come directly from riparian vegetation and fall, crawl, or blow into streams, in addition to those produced within the stream itself, are important for sustaining trout in streams (Kawaguchi et al. 2003; Baxter et al. 2004; see Baxter et al. 2005 for review). This prey resource has been shown to account for 50 - 85 % of trout diets during summer months (Utz et al. 2007) and provide about 50% of their annual energy budget (Kawaguchi and Nakano 2001; Baxter et al. 2005; Sweka and Hartman 2008).

We recently conducted a 2-year field comparative study in 10 western Wyoming trout streams to test the hypothesis that improved grazing management could increase the biomass of terrestrial invertebrates entering streams and sustain greater trout populations. This research showed that the input of terrestrial invertebrates to streams with riparian zones under a prescribed grazing system termed high-density short-duration grazing was more than double that for paired streams under season-long grazing (Saunders 2006; Saunders and Fausch 2007b). About half the biomass of trout diets in these streams during summer afternoon periods consisted of these terrestrial invertebrates, a finding consistent with other recent studies in Virginia, Alaska, New Zealand, and Japan (Edwards and Huryn 1995; Cloe and Garman 1996; Wipfli 1997; Kawaguchi and Nakano 2001). Furthermore, trout biomass in the five Wyoming streams under improved grazing management was also more than double that in the five paired streams under season-long grazing.

These findings, which indicate that trout populations in rangeland streams rely on terrestrial invertebrates as an important prey subsidy, are supported by a Japanese study that showed that when stream reaches were covered with mesh greenhouses that reduced input of terrestrial invertebrates, the larger trout emigrated and reduced trout biomass by half (Kawaguchi et al. 2003). Overall, this body of work indicates that riparian vegetation has important benefits by supplying invertebrates that contribute about half the energy needed to sustain trout populations in streams (see Nakano and Murakami 2001; Baxter et al. 2005). Furthermore, our research indicated not only that the amount of riparian vegetation overhanging streams was an important predictor of the input of terrestrial invertebrates on which trout feed, but also suggested that input of plant detritus that supports aquatic invertebrates may be an additional important function of riparian vegetation (Saunders 2006; Saunders and Fausch 2007b). These results imply that poorly managed riparian grazing is likely to have substantial effects on trout populations, not only by degrading instream habitat, but also by reducing or changing riparian vegetation that supplies invertebrate and detrital subsidies that support trout. Therefore, range managers will need to understand the mechanisms driving the availability of invertebrate prey, in addition to the processes that maintain instream habitat, in order to sustain healthy trout populations in streams managed for livestock grazing.

Goals and objectives

The purpose of this study is to evaluate the effects of additional commonly-used grazing systems on stream-riparian linkages that support trout, determine if the effects of prescribed grazing in another region of the southern Rocky Mountains are similar to those measured in west-central Wyoming, and ultimately to provide guidelines that resource managers can apply to

help sustain healthy trout populations while maintaining livestock production. To address these goals we conducted: 1) A large-scale evaluation of three commonly used grazing management systems (plus a "wildlife only grazing" control) in Colorado during summer 2007, and 2) A large-scale field experiment of four grazing treatments in Wyoming during summer 2008 to evaluate the effects of a single season of grazing on terrestrial-aquatic linkages. The specific research goals for these projects were:

2007 Comparative Field Study

- Conduct a large-scale field study of three commonly-used grazing systems in northern Colorado, and compare the effects of these different types of grazing management to sites that are grazed only by wildlife.
- Identify attributes of the riparian vegetation that are important for the supply of terrestrial invertebrate prey that sustain trout populations in rangeland streams.

2008 Field Experiment

- Conduct a large-scale field experiment to test the effects of four treatments of different grazing intensities and woody vegetation removal on terrestrial invertebrate subsidies to streams, and use of this resource by trout.
- Determine the effect of a single grazing season on terrestrial prey resources that support trout in rangeland streams.

Methods for 2007 Comparative Field Study

Study Sites

To address these goals, we conducted intensive study site reconnaissance throughout the North Platte and Colorado river drainages of northern Colorado and southern Wyoming, as well as initial site and resource inventories in additional southern Rocky Mountain regions. Study site reconnaissance began during summer 2006 and continued through the beginning of summer 2007. A list of candidate streams was compiled from conversations with US Forest Service. Bureau of Land Management, and Natural Resources Conservation Service employees, both fisheries biologist and range management specialists, as well as Wyoming Game and Fish Department and Colorado Division of Wildlife regional managers and other local land management groups. Additionally, several private ranch operations were approached based on the recommendations of others. Overall, we contacted individuals throughout northern Colorado and southern Wyoming including regions around the Arapaho, Routt, Medicine Bow, and White River National Forests, and then focused our reconnaissance efforts for 2007 in the Upper North Platte and Colorado river drainages in Colorado. A total of 66 streams were considered, of which 45 in this latter region were identified and field reconnaissance was conducted during summer 2006 and June 2007.

Study Site Selection Criteria – Sites were evaluated for study based on their suitability for conducting research, fisheries resources, and rangeland management. Because the effects of grazing on fish populations are believed to be most important in lower-gradient channels with extensive riparian zones, compared to steep channels with narrow riparian zones, all sites were selected in the former geomorphic channel and valley type. Moreover, we selected sites that had

similar histories of forest insect outbreaks and fire, to reduce these sources of variation. Finally,

sites were selected to maximize distance to changes in reach type and grazing management.

Suitable study reaches for pilot sampling were identified based on the following five criteria:

- 1) Small stream channel (1-7 m wide) with relatively low gradient (\leq 4%) and minimal modification by beavers.
- 2) Trout population at relatively high abundance, and with multiple age classes. Brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) are ideal, to maintain consistency.
- 3) Riparian vegetation consisting of primarily shrub and herbaceous species, with minimal tree overstory.
- 4) Riparian grazing managed under one of the following regimes:
 - a. *Intensive Rotational Grazing (IRG)*, where cattle density is managed to achieve concentrated use in targeted areas over short periods (range 3-14 days depending on pasture size). In this system, sites may be grazed multiple times in a year, but each grazing event lasts only a short duration,
 - b. *Simple Rotation Grazing (SRG)*, where cattle graze an individual pasture for approximately 40 days, and the order of pastures used changes in consecutive years. This system is similar to a deferred rotational grazing system,
 - c. *Season-Long Continuous Grazing (SLG)*, where cattle are allowed to remain in the pasture from "green up" through plant dormancy (defined as \geq 75 days), or
 - d. *Wildlife Only (WO)*, where livestock do not have access to the riparian zone but these areas are available to wild ungulate populations.
- 5) Distributed among private, state, and federal lands.

Sites Selected for the 2007 Field Comparative Study - Of the streams surveyed, 16 sites in the

Upper North Platte, Yampa, and Colorado river drainages were selected to compare the effects of these different grazing systems on vegetation characteristics, falling invertebrates, fish diets, and fish abundance and biomass (Figure 1). Though we surveyed a large number streams throughout the Upper North Platte River drainage, we found relatively few sites with high potential (see Appendix 1 in the 2008 Annual Report). Overall, there appeared to be more sites managed for simple rotational (SRG) and season-long grazing (SLG) that fit our selection criteria than other management types. Sites managed for intensive rotational grazing (IRG) and wildlife use only (WO) were rare. Sites grazed by wildlife only were particularly difficult to find and tended to

have lower potential for research as these sites were typically in the upper regions of the drainages or in relatively small parcels of land.

We selected three to five sites under each of the four grazing management types for study in 2007 (Table 1). Sites were located on a mixture of US Forest Service and private lands. A total of 16 sites were distributed between 14 streams in pastures that had been under consistent management for a minimum of 7 years. We identified five sites managed for IRG, four sites each under SRG and SLG, and three sites with grazing by wildlife only. Sites managed for wildlife grazing only were difficult to find because most constructed enclosures were too small to meet the goals of our research, or did not provide for the habitat requirements of fish of different ages (Bayley and Li 2008). As a result, we were able to find only three suitable sites for this treatment, and these tended to be either near the headwaters upstream from other sites selected, or located on small parcels of land surrounded by heavily grazed riparian zones.

At each location selected, a 200-m study reach was identified. Extensive sampling of riparian vegetation, terrestrial prey resources, fish diets, and fish abundance was conducted during summer 2007 in each study reach. The sampling methods, outlined below, were similar to those used in our previous research (Saunders 2006; Saunders and Fausch 2007b).

Vegetation sampling

Riparian vegetation measurements including clipped biomass, overhead cover, vegetation structure, community composition and ground cover, and estimates of utilization for both woody and herbaceous species were made to describe the streamside vegetation at each 200-m study reach. Most vegetation measurements were made during July at peak standing crop biomass, prior to plant maturation. Utilization of woody and herbaceous plants was estimated

during late August and early September. The standing crop of aboveground biomass of riparian vegetation was estimated by clipping all plants to ground level within four 0.25-m² circular plots placed at four randomly selected distances from the downstream end of the study reach, with the outer edge 1.5 m from the bankfull mark. Biomass was determined for each functional group separately (i.e., graminoids, forbs, and shrubs). Clipped vegetation was dried at 55°C for 48 hours, and weighed (nearest 0.1 g).

Utilization of herbaceous vegetation was estimated using two 1-m² exclosures constructed at each study reach. One exclosure was placed at a randomly selected distance from the downstream end of the study reach on each bank. Exclosures were constructed using cattle panel (12.7 x 19.5-cm mesh) that is efficient at excluding ungulate herbivores, but not small mammals or insect herbivores. Paired vegetation clippings (0.25-m² circular plots; one inside and one outside the exclosure) were collected in late August or early September. Vegetation samples were processed in the same manner as above. Exclosures were constructed before livestock had access to the pasture that contained the study reach in all but three cases. On the North Fork North Platte River and Shafer Creek (both SLG sites) cattle had access to the study site for three weeks before exclosures were built. We did not construct exclosures at the Lower Trout Creek study site (a SRG site) because the pasture containing our study site had received 35 of the 40 days of grazing.

We estimated the amount of woody vegetation browse that occurred at each site between early June and late August. During early June we marked a total of 100 twigs on 20 different shrubs. To select the shrubs, we identified 10 randomly selected distances from the downstream end of the study reach on each side of the stream, and flagged the closest shrub. Five twigs on the periphery of each shrub were individually marked with a colored 10-cm cable tie and the

current year's growth was measured (nearest 1 mm; shrub species was also recorded). Current year's growth was identified as the distance from the annual growth scar to the base of the pseudoterminal bud. During late August or early September, twig length measurements were retaken to estimate tiller growth during the study period. Additionally, twigs were categorized as either unbrowsed, browsed (stripped or clipped), or dead. On three occasions fewer than 70 twigs were relocated. In these cases, browse of woody vegetation was estimated by recording the number of browsed and unbrowsed twigs on 100 tillers.

Hemispherical photographs were taken to document the total vegetative cover and to determine the relative contribution of different vegetation types to vegetation cover. Overhead vegetative cover was recorded at 10-m intervals along each reach, with random starting points (0-10 m). Digital photographs of overstory vegetation were taken using a Nikon D200 with an AF DX Fisheye-NIKKOR 10.5mm f/2.8G ED lens positioned 50 cm above the ground or stream surface. Images were taken each 2 m along a transect perpendicular to the channel that extended 4 m into the riparian zone on each bank. Percent overhead cover will be estimated from the digital images by placing an equally spaced 100-point sampling grid over the images, after the fisheye distortion had been corrected using program Capture NX (Nikon Corporation). Fisheye lenses tend to produce a large amount of barrel distortion and exaggerate the relative size of objects to conform to the format of the lens. As a result, objects near the center of the image appear larger than those at the edges, but they show less barrel distortion. By accounting for the convex curvature of the lens, image correction can produce images where objects have the proper vertical orientation. After the digital enhancement, each point of the sampling grid will be identified as either open (no vegetation) or as one of four vegetation types (grasses, forbs, shrubs, or trees). Additionally, at 1-m intervals along each transect where overhead vegetation

was photographed, the height (nearest 0.1 m) of the tallest graminoid, forb, and shrub was also recorded in the field using a range pole (nearest 10 cm).

During 16 July through 10 August 2007, we characterized plant communities by identifying all species present and estimating ground cover class by species along two 30-m Daubenmire transects placed 1.5 m from each stream bank. Transects started at a randomly chosen distance (1-169 m) from the downstream end to fit within the 200-m study reach, and followed the contour of the stream bank. Daubenmire transects consist of visually estimating ground cover classes for all plant species in 10 equally-spaced quadrats, each 20 cm x 50 cm (Stohlgren et al. 1998).

Invertebrate sampling

Inputs of terrestrial and adult aquatic invertebrates were measured in each reach using plastic pan traps filled with 5 cm of stream water, to which approximately 5 mL of unscented, biodegradable surfactant was added to reduce water surface tension (Mason and MacDonald 1982; Wipfli 1997; Nakano et al. 1999b). Initially, overhead vegetative cover was measured in each reach using a convex densiometer along the thalweg at 5-m intervals and classified as either high or low (> 35% or < 35% cover). Five clear pan traps (100 cm x 40.6 cm x 15.2 cm deep) were randomly allocated to locations in each 200-m reach in proportion to the size of these two strata of overhead cover. In addition, three of the five pan traps were randomly selected and deployed along the stream bank, and the other two were located mid-channel to sample both invertebrates that fall from vegetation along the stream banks and those that fall from overhead vegetation or as they are flying above the stream channel. Bottoms of pan traps were elevated between 12 and 17 cm above the water surface on PVC stands.

Invertebrates falling into study reaches were sampled during July and August when terrestrial inputs to temperate streams are greatest (Cloe and Garman 1996; Kawaguchi and Nakano 2001; Allan et al. 2003; Baxter et al. 2005; Saunders and Fausch 2007b). Falling invertebrates were collected for a 9-d period that was divided into three 3-d samples, to optimize sampling effort based on a variance analysis of samples collected during our previous research near Lander, WY (Saunders and Fausch 2007b). After each 3-d period, invertebrates in traps were sieved with a 250-µm net and preserved in 70% ethanol.

Invertebrates inhabiting the stream substrate were sampled in each reach on the same day that diet samples were collected from trout (see below). Benthic samples were collected during both July and August using a Hess Sampler with 250-µm mesh. At each site, a total of nine samples were collected directly above the upper most extent of the reach where electrofishing was used to collect fish for diet sampling. Six of the nine benthic samples were collected from two consecutive riffles (three from each riffle). Three additional samples were taken to sample additional sources of aquatic invertebrate prey items for trout (e.g., detritus beds and aquatic vegetation). Large debris was removed from the sample in the field, and the sample was stored in 70% ethanol.

Samples of drifting invertebrates were collected to test the specific hypothesis that the amount of terrestrial invertebrates drifting into the study reaches was equal to the amount drifting out. If this can be assumed, then the difference in input of terrestrial invertebrates among reaches will be due primarily to those falling in. Drift samples were collected from one site under each of the four types of grazing management during an afternoon in late August when terrestrial inputs to streams would be high. Samples were collected from Arapaho Creek (SRG), the lower site on the Canadian River (IRG), the North Fork North Platte River (SLG), and

Hinman Creek (WO). At each site, three drift nets (20 cm x 50 cm with 750-µm mesh) were placed at the top and bottom of the reach, and remained in place for 2 h. Nets were placed approximately 25%, 50%, and 75% of the distance across the wetted width of the channel and positioned so that the top of each net extended above the water surface to collect terrestrial invertebrates floating in the surface film. Measurements of water flow (taken at 60% water depth within the mouth of each drift net) were recorded at the beginning and end of the 2 h period to estimate the volume of water strained by each drift net. Samples were stored in 70% ethanol and returned to the lab for processing.

Sampling for fish diets and fish population characteristics

Stomach contents were collected from fish within each 200-m reach to estimate the biomass and proportion of terrestrial invertebrates in the diet of salmonids, to coincide with invertebrate sampling during July and August. Diet samples were collected by gastric lavage (flushing stomachs) from 20 fish captured by electrofishing between mid-afternoon and dusk (ca. 1500-1900 h), to measure gut contents just after the period of peak terrestrial invertebrate input (Elliott 1969; 1970; Young et al. 1997a; Nakano et al. 1999a; Hieber et al. 2003). Fish between 120 mm and 350 mm fork length (FL) were selected for diet sampling, because stomach samples cannot be efficiently flushed from smaller fish and because larger fish become piscivorous. Stomach contents were sieved through 333-µm mesh and preserved in 70% ethanol.

In addition to the afternoon sampling conducted at all sites in July and August, trout diets were also sampled at 6-h intervals for a 24-h period (starting at 0000 h) at all sites under IRG and SLG management. This sampling was conducted to assess whether an afternoon sample was representative of terrestrial invertebrate consumption throughout the day, and to estimate the

relative abundance of terrestrial and aquatic prey consumed by trout. At each site, 10 fish were sampled from four consecutive 50-m reaches (one reach during each period). Before release, fish were given a partial fin clip to avoid resampling.

To determine how terrestrial inputs influence fish populations, we estimated abundance and biomass of all fish (including cyprinids and catostomids) in each 200-m reach. Fish abundance was estimated using three-pass depletion electrofishing (Riley and Fausch 1995; Gowan and Fausch 1996) conducted at night (see Saunders and Fausch 2007b for details). Mass (nearest 0.1 g) and length (nearest 1 mm FL) were recorded for all trout (mass was recorded for cyprinids and catostomids >50 mm only). Biomass was estimated by multiplying population abundance by mean fish mass, and the finite population variance (Riley and Fausch 1995) was used to calculate variances for biomass estimates. High-output LED headlamps and hand held dive lights were used to illuminate the area electrofished. Two backpack electrofishing units (LR-24, SmithRoot Inc., Vancouver, WA) were used in wide streams to increase efficiency. Age-0 fish are not sampled efficiently by this method and were not measured. Abundance estimates were made in August when flow levels were sufficiently low for effective electrofishing. Removal estimates of capture probability and fish abundance were calculated using the Huggins closed population estimator in Program MARK (White and Burnham 1999), where the probability of recapture was set at zero (for removal estimates) and fish size was used as an individual covariate. Removal estimates were validated in 2006 (Saunders and Fausch 2007a) using standard mark-recapture methods (White et al. 1982) to address potential bias that results from reductions in detection probability between successive passes (Peterson et al. 2004; Rosenberger and Dunham 2005).

Invertebrate identification and biomass estimation

All invertebrates were stored in ethanol and later sorted to the taxonomic level necessary to identify those of terrestrial and aquatic origin (generally Family, see Saunders and Fausch 2007b for details). Biomass (nearest 0.0003 g) of invertebrates found in pan trap and drift samples was measured after samples were dried at 60°C for 48 h. Because water temperatures at the sites we sampled were higher, and the trout diets more complex, than those used to estimate rates of gastric evacuation under lab conditions (Elliott 1972; Windell et al. 1976; Elliott 1991; Hayward and Weiland 1998; Sweka et al. 2004), we could not accurately estimate the fish consumption of invertebrates using models available in the literature. Rather, biomass of prey items found in trout diets were estimated and reconstructed using published Length-Mass regressions assembled from the literature (Rogers et al. 1977; Smock 1980; Meyer 1989; Burgher and Meyer 1997; Benke et al. 1999; Johnston and Cunjak 1999; Sabo et al. 2002).

Stream habitat characteristics

Substrate composition and embeddedness, stream width, fish habitat (including pools, runs, and undercut banks), amount of large woody debris (LWD), water and air temperature, map gradient, and discharge were measured for each 200-m reach. Substrate composition was quantified by measuring the second longest dimension of 100 bed particles selected at 2-m intervals while walking along a zig-zag transect oriented at a 45° angle between stream banks (i.e., Wolman pebble count; Wolman 1954; Overton et al. 1997). Embeddedness was estimated as the percentage (nearest 10%) of each of these bed particles that was buried by fine sediments. Wetted and bankfull widths were measured at 10-m intervals. The dimensions of each pool and run (minimum and maximum depth, length, and width) were measured (nearest 0.1 m, except

nearest cm for depth), and the agent forming each pool was recorded. Additionally, the length and width (i.e., distance into the bank) of all undercut banks were measured (nearest 0.1 m). We defined undercut banks as depressions in the bank that had a width and height of greater than 20 cm, and extended along the stream bank for at least 30 cm. Large woody debris pieces, defined as those longer than 2 m and having at least one end diameter greater than 10 cm, were counted and each piece measured. The total length of pieces, and length inside the bankfull mark (nearest 0.1 m), as well as the minimum and maximum diameters (nearest 1 cm) of all LWD were measured.

HOBO WaterTemp Pro temperature loggers (Onset Computer Corporation, Pocasset, MA), programmed to record water temperature hourly from June through September, were deployed in the middle of each reach. Loggers were deployed in shaded locations that were not vulnerable to physical disturbance by grazing animals. HOBO ProV2 temperature and relative humidity loggers, programmed to record air temperature and relative humidity hourly from June through September, were placed inside a 4-inch PVC thermal shield and hung approximately 1 m off the ground in a shaded location near the center of each study reach, within 3 m of the stream bank. Stream gradient for a 500-m stream segment containing each study reach was estimated from U.S. Geological Survey 7.5-minute topographical maps. Discharge (m³/s) was estimated at each site in August during base flow using a Swoffer current meter (Model 2100, Swoffer Instruments INC., Seattle, WA) and the mid-section method (Murphy and Willis 1996).

Sample processing and statistical analysis

During summer 2007, approximately 1700 invertebrate samples were collected from the 16 streams in the comparative study to investigate the effects of riparian grazing management on

aquatic food webs. To date 320 of the pan trap samples $(2/3^{rd})$ of the total number) and all 800 of the fish diet samples have been processed. Additionally, 100 vegetation samples were collected, dried, sorted to functional groups in the lab, and weighed. Currently we have processed 6 of 16 sets of hemispherical photographs take during August 2007 to quantify overhead cover.

Analysis of data for this report focused on vegetation biomass, the input of terrestrial invertebrates, biomass of aquatic and terrestrial invertebrates in trout diets, and trout biomass under the four different grazing systems. Analysis of variance (ANOVA) was used to investigate differences in aboveground vegetation biomass, prey input, fish diets, and fish biomass among the four grazing systems. In all analyses, sampling site was considered as a random effect and retained in the model if significant (at alpha = 0.05). Grazing system, sampling period (when more than one collection was made), fish size (for analysis of fish diets), and elevation were analyzed as fixed effects. Parameters for fish size and elevation were retained in the model only when significant. When either grazing system or month, and the interaction of these parameters, were non-significant, data were pooled across these parameters for analysis. Results presented in this report represent significant differences (alpha ≤ 0.05), unless otherwise indicated. When the interaction between grazing system and month was significant, we report the results for the four types of grazing management independently for July and August 2007.

Measurements of riparian vegetation, trout densities, and trout biomass generally met the assumption of normality required to conduct parametric statistical analysis (i.e. ANOVA). In contrast, data pertaining to the input of invertebrate biomass to streams and the biomass of invertebrates consumed by trout were transformed to reduce heterogeneous variance and improve normality. Invertebrate input data were transformed using natural logarithms, and the

biomass of invertebrates consumed by trout was transformed using the square-root. As a consequence, the results of statistical analyses and the effect sizes reported in the text reflect differences between treatments in the transformed scale, whereas figures show back-transformed estimates of treatment averages (and their standard errors) in the original (i.e., untransformed) scale. Standard errors for back-transformed data were estimated using the Delta Method (DeGroot and Schervish 2002).

Pending the processing of hemispherical photographs to estimate vegetation composition and overhead cover, a model selection framework (Anderson et al. 2001; Burnham and Anderson 2001; Burnham and Anderson 2002) will be used to identify important parameters influencing terrestrial invertebrate inputs, and trout diets and abundance. The goal of further analysis will be to identify specific attributes of the riparian area and streamside vegetation communities that influence the availability of terrestrial invertebrate prey resources, trout diets, and trout abundance.

Results and Discussion for 2007 Comparative Field Study

Riparian Vegetation

Sites that were managed for intensive rotational grazing and wildlife grazing only tended to have more riparian vegetation biomass than sites managed for either simple rotational or season-long grazing, but differences within vegetation functional groups were rarely significant due to high variability among sites within each grazing system (Figure 2). Overall, both the total aboveground vegetation biomass (combined mass of grasses, forbs, and shrubs) and the biomass of herbaceous vegetation (grasses and forbs) was different among grazing systems, and greatest at sites under IRG management and lowest at sites managed for SLG (ANOVA: $F_{Total} = 4.97$, P

= 0.02; $F_{Herbaceous}$ = 5.76, P = 0.01). Sites managed for IRG had, on average, 2.8 times more aboveground biomass of herbaceous vegetation than sites managed for SLG and 1.8 times more than sites managed for SRG (Least Squares Means comparison: P_{SLG} = 0.002, P_{SRG} = 0.02). Grasses contributed most to aboveground vegetation biomass at all sites, and differences among sites grazed by livestock were similar to those observed for herbaceous vegetation, though not as significant (ANOVA: F = 3.06, P = 0.07; Least Squares Means comparison: P_{SLG} = 0.01, P_{SRG} = 0.07). There was no evidence to suggest that sites managed for IRG had more grass, forb, or shrub biomass than sites grazed only by wildlife (Least Squares Means comparisons: P > 0.3). Intensive rotational and wildlife only sites also tended to have more biomass of forbs and shrubs, but these differences were not significant (ANOVA: F_{Forb} = 1.13, P = 0.4; F_{Shrub} = 0.65, P = 0.6).

Utilization of herbaceous vegetation was greatest at SLG sites and decreased with both increasing management effort (SLG to IRG) and exclusion of cattle from riparian areas (WO sites). Furthermore, utilization of herbaceous vegetation at WO sites was, on average, lower than at sites managed for cattle grazing, but these differences were not significant for sites managed under rotational grazing systems due to high variability among sites within each grazing regime (Figure 3). Utilization of grasses and forbs was similar within each of the four management regimes. The total utilization of herbaceous vegetation (a weighted average of the utilization of grasses and forbs) at sites managed for SLG was 3.2 times higher than sites managed for IRG and 5.9 times higher than at WO sites (ANOVA: F = 2.54, P = 0.1; Least Squares Means comparison: $P_{IRG} = 0.04$, $P_{WO} = 0.03$). Utilization at sites managed for SRG did not differ significantly from sites under other management types due to the relatively high variability among sites (Figure 3). At three sites, the 1-m² grazing exclosures used to estimate utilization could not be constructed before cattle were stocked in the pastures containing our study sites. At

two sites, both managed for SLG, exclosures were constructed after approximately three weeks of use, which would make these estimates conservative (i.e., had the exclosures been built earlier, utilization would have been even higher). At the Lower Trout Creek study site (SRG), we did not construct grazing exclosures because cattle had already been in the pasture for 35 days and would have remained there for only 5 more days.

The height of the tallest streamside vegetation within 4 m of the stream channel was greatest at sites managed for rotational grazing or grazed only by wildlife, reflecting the lower levels of utilization and greater aboveground vegetation biomass at these sites. In general, there was the least vertical vegetation structure among sites grazed by livestock at sites managed for season-long grazing and the greatest at sites managed for intensive rotational grazing (Figure 4). This pattern was significant for each vegetation functional group (ANOVA: $F_{Grass} = 5.3$, P = 0.01; $F_{Forb} = 4.65$, P = 0.02; $F_{Shrub} = 3.58$, P = 0.05). In general, the average height of the tallest grasses, forbs, and shrubs at sites managed for intensive rotational grazing were 1.9, 2.9, and 3.5 times greater, respectively, than at sites managed for season-long grazing. Furthermore, vertical vegetation structure of forbs and shrubs was similar among sites managed for rotational grazing and sites grazed only by wildlife (Least Squares Means comparisons: P > 0.3), but the maximum height of grasses was 1.6 times greater at sites managed for intensive rotational grazing than those used only by wildlife (Least Squares Means comparisons: P = 0.02).

Overall, data collected during summer 2007 indicated that sites managed for rotational grazing (both simple and intensive) had more aboveground vegetation biomass, and that this vegetation was taller, than sites managed for season-long use, and suggested that they also had more than under a simple rotational system. Furthermore, IRG sites had equal or greater aboveground biomass and vegetation height as sites that received no livestock use. These greater

amounts of vegetation associated with sites managed for intensive rotational grazing and wildlife only grazing may increase the amount of terrestrial invertebrates and adult aquatic insects entering streams by several mechanisms. Greater vegetation biomass and vertical vegetation structure at these sites may provide more food and cover for terrestrial invertebrates, thereby supporting greater densities, and a greater variety of common plant species may also support a greater diversity of terrestrial invertebrate species (Morris 2000; Soderstrom et al. 2001; Zurbrugg and Frank 2006). Additionally, increased structural complexity of riparian vegetation may increase the probability that terrestrial invertebrates fall into streams, and that adult aquatic insects remain near streams and so are also more likely to fall in (Baxter et al. 2005; Saunders and Fausch 2007b).

High variability in the biomass of aboveground vegetation among sites within grazing systems may have resulted from the distribution of our study sites, or site-specific grazing management. Estimates of aboveground vegetation biomass were used to describe the summer availability of food and cover resources for invertebrates, and thus do not reflect the total grazing pressure the riparian vegetation received by the end of the year. The amount of aboveground vegetation depends on both the potential for vegetation production at a site as well as the recent grazing history (i.e., whether a site has been grazed in the current year). Additionally, our study sites were distributed over a large area of north-central Colorado and thus have the potential to be influenced by regional weather patterns, different amounts of annual precipitation, and different vegetation communities. For example, sites distributed on the eastern and western sides of the Continental Divide are likely to have both different plant species and different weather patterns. Finally, variation between sites sampled within each grazing system resulting from differing livestock management (e.g., timing and duration of grazing or stock densities) or

wildlife densities would increase the variation in the amount and height of vegetation at replicate sites within each grazing system. Therefore, it is likely that a the combination of regional influences on vegetation, as well as differences in management strategies between land owners, limits our ability to detect statistically significant differences among grazing systems. Regardless, two general patterns were evident. Vegetation biomass and structural complexity increased with increasing management intensity. Additionally, attributes of the streamside vegetation were similar between sites managed for rotational grazing, particularly intensive rotational grazing, and sites managed for wildlife use only.

Sites managed for IRG and WO received less use (measured as percent utilization) than sites where cattle were present for more than 30 days. Sites where cattle were present season long (i.e., throughout the entire summer and fall) had both the highest percent utilization values and lowest amounts of aboveground vegetation biomass. Furthermore, estimates of utilization at sites managed for SLG may be conservative, because grazing exclosures at two of the four sites sampled were not constructed until after three weeks of used had already occurred. Differences in the percentage utilization of herbaceous vegetation across sites grazed by cattle may result from different stocking rates, or differing amounts of vegetation regrowth after cattle were removed from pastures. Under IRG, in particular, vegetation has a higher potential for regrowth because grazing bouts leave more of the growing season available for regrowth. In contrast, under SLG, any regrowth is likely to be regrazed later in the summer when cattle focus on riparian areas due to drying of upland vegetation.

The similarity in vegetation between sites where grazing is managed intensively and sites located in a riparian exclosures or allotments that have been ungrazed by cattle for more than 20 years suggests that healthy vegetation can be achieved if grazing management is tailored to fit

the riparian system. However, the grazed and ungrazed systems could appear to be very different after plant defoliation occurs, depending on the timing of grazing. For example, riparian zones grazed after the active growing season is over are likely to have less vegetation biomass for the remainder of the summer than sites where no grazing occurs. The timing of these grazing events could have strong effects on invertebrate production or input to streams depending on insect phenology and the influence of vegetation removal on invertebrate use and activity in riparian areas.

Falling Invertebrate Input

Total invertebrate biomass falling into streams during 2-16 July and 9-16 August 2007 was greatest at sites ungrazed by livestock (WO) and those managed for simple rotational grazing (SRG), and lowest at sites grazed season-long (SLG; Figure 5). With the exception of sites managed for SRG, the total invertebrate biomass entering streams tended to be less during August than during July, but this difference was not significant due to high variability in invertebrate input between sites (ANOVA: $F_{month} = 0.59$, P = 0.4). Sites managed under SLG received, on average, less invertebrate biomass during summer 2007 than other sites (ANOVA: $F_{Graxing system} = 5.57$, P = 0.005), but pairwise differences were significant when compared to sites managed for SRG and WO only (Least Squares Means comparisons: $P_{SRG} = 0.02$, $P_{WO} = 0.05$). On average, sites managed for SRG, IRG, and WO received 3.3, 1.5, and 2.8 times more total invertebrate biomass, respectively, during summer 2007 than sites managed for SLG. Unexpectedly, sites managed for SRG received, on average, twice as much invertebrate biomass as sites managed for IRG (Least Squares Means comparisons: P = 0.1). In general, sites managed for WO received more invertebrate biomass than SLG sites, but no differences could be detected compared to sites managed for rotational grazing (Least Squares Means comparisons: P > 0.22).

The amount of terrestrial invertebrate biomass entering streams was similar during July and August 2007 and was greatest at sites managed for SRG and WO (Figure 6A). Terrestrial invertebrate biomass entering sites was similar during July and August (ANOVA: $F_{month} = 0.69$, P = 0.4) except for sites managed for SRG, which received, on average, 2.9 times more terrestrial invertebrate biomass during August than July. The general pattern in the total invertebrate biomass entering sites was driven more by the input of terrestrial invertebrates than adult aquatic insects. Sites managed for SRG, IRG, and WO received, on average, 5.4, 1.7, and 3.4 times more terrestrial invertebrate biomass, respectively, than sites managed for SLG (ANOVA: $F_{system} = 5.57$, P = 0.005; Least Squares Means comparisons: $P_{SRG} = 0.001$, $P_{IRG} = 0.2$, $P_{WO} = 0.02$). Furthermore, sites managed for SRG and IRG (Least Squares Means comparisons: $P_{SRG} = 0.34$, $P_{IRG} = 0.15$).

In contrast to patterns for terrestrial invertebrates entering streams, the input of adult aquatic insects was similar across sites, but greater during July than during August 2007 (Figure 6B). In general, sites received 3.7 times more biomass of adult aquatic insects during July than August (ANOVA: $F_{month} = 11.14$, P = 0.006). Although the biomass of adult aquatic insects falling into streams during summer 2007 did not differ among grazing systems (ANOVA: F_{system} = 0.77, P = 0.5), sites managed for IRG and WO tended to receive more adult aquatic insect biomass during July 2007 than sites managed for either SLG or SRG (Least Squares Means comparisons: P = 0.17 - 0.4, see Figure 6B). In general, biomass of adult aquatic insects entering streams during August 2007 was consistently low across all sites sampled.
Overall, differences in the total biomass of invertebrates entering rangeland streams in north-central Colorado in July versus August 2007 were primarily a result of reduced input of adult aquatic insect biomass entering streams during August. In contrast, differences in the total biomass of invertebrates entering streams under different grazing management systems were driven by inputs of terrestrial invertebrates. In general, sites managed for rotational grazing (both SRG and IRG) received more invertebrate biomass than sites managed for SLG. This pattern was consistent for the biomass of terrestrial invertebrates entering streams during July and August and for the biomass of adult aquatics entering streams during July, but differences between sites were frequently not significant (at alpha of 0.05) due to high variability in the input of invertebrates entering streams managed for IRG was lower than that entering sites managed for either SRG or WO. Finally, the biomass of invertebrates entering streams not grazed by cattle was greater than that observed at sites managed for SLG, but no differences could be detected compared to sites managed for rotational grazing.

These consistent patterns were present even though we were unable to detect significant differences in the aboveground biomass of herbaceous or woody vegetation among most grazing systems (see above). Furthermore, sites receiving the lowest levels of invertebrate inputs (i.e., Intensive Rotational Grazing sites) had the highest amounts of aboveground vegetation and the greatest vertical vegetation structure of all sites. Two potential mechanisms may be responsible for this paradox. First, simple metrics of aboveground vegetation production and stream-side vegetation height may be insufficient to predict invertebrate inputs from riparian areas to streams. In contrast, invertebrate subsidies may be dependent on particular attributes of the riparian vegetation, and not simply the absolute amount of vegetation. Secondly, the flux of

invertebrates to streams is likely to be highly variable, both through time and spatially, as a result of local weather influences, insect phenology throughout the summer, and an interaction of these two processes which drive insect development and delivery to streams.

Comparisons with published literature show that streams in northern Colorado received similar amounts of terrestrial invertebrate subsidies as streams in other regions of the world. Though inputs of terrestrial invertebrates to northern Colorado streams were less than observed in streams passing through deciduous forests in the eastern U.S. (Cloe and Garman 1996), terrestrial inputs were similar to those observed in Scotland (Bridcut 2000) and a deciduous forest in northern Japan in dry years (Baxter et al. 2005). Furthermore, the terrestrial invertebrate input entering grassland streams in northern Colorado was greater than that measured for grassland streams in Japan (Kawaguchi and Nakano 2001), and New Zealand (Edwards and Huryn 1995; Edwards and Huryn 1996). In fact, rangeland streams in northern Colorado under season-long and simple rotational grazing received 2.2 and 12 times more terrestrial invertebrate biomass than streams grazed by livestock in New Zealand (Edwards and Huryn 1995). In contrast to what we found in Wyoming during 2005 (Saunders and Fausch 2007b), the biomass of terrestrial invertebrates entering streams under three of the four grazing systems studied did not show any strong seasonality. Only at sites that were managed for SRG was invertebrate input greater during August than July, as was found in Wyoming. Again, analysis of additional samples that are currently being sorted is needed to test these effects.

Invertebrate Biomass in Trout Diets

The biomass of both terrestrial and aquatic invertebrates in trout diets during the afternoon was highly variable during July – August 2007, but fish at sites managed for SRG

tended to have more invertebrate biomass in their diets than fish at other sites. During July 2007, fish at SRG sites had the greatest total invertebrate biomass in their diets and fish at WO sites had the least (Figure 7), but even this difference was not significant because of high variability in fish diets both within each site and among sites under the same grazing management (both in diet composition and biomass consumed). Trout at sites under SLG and IRG management had similar amounts of invertebrate biomass in their diet, and the amount of invertebrate biomass in trout diets at these sites was intermediate to that measured at SRG and WO sites. Furthermore, during July this pattern was consistent for both the terrestrial and aquatic invertebrate biomass in trout diets (Figure 8). During August, trout at SRG sites again had the greatest invertebrate biomass in their diets, with more than 3.2 times more total invertebrate biomass in their diet than trout at sites under any other grazing management, and this difference was significant (ANOVA: $F_{month x, system} = 7.18, P = 0.0001$). Furthermore, during August 2007 fish at sites managed for IRG had less invertebrate biomass than fish at sites under either SLG or WO management, although these differences were not significant due to high variability in trout diets. In general, during summer 2007 the trout sampled (length range: 110 - 365 mm) consumed few vertebrate prey items. Only 23 of 507 diets collected (only 4.5%) contained vertebrate prey remains. Small fish, primarily salmonids, cyprinids (minnows), and catostomids (suckers), were the most prevalent vertebrate prey item, but small mammals and amphibians were also found.

During both July and August 2007 trout at sites managed for SRG had more terrestrial invertebrate biomass in their diets than trout at sites under other types of grazing management, but this difference was significant only during August (Figure 8A). The biomass to terrestrial invertebrates in trout diets increased between July and August at half the sites sampled (SRG and WO sites), while it remained constant (SLG sites) or decreased (IRG sites) at other sites

(ANOVA: $F_{month x system} = 6.11$, P = 0.0004)). However, pairwise comparisons for sites under the same grazing management between July and August were significant only for sites managed under SRG and WO (Least Squares Means comparisons: $P_{SRG} < 0.001$, $P_{WO} = 0.02$). During July, we were unable to detect any significant difference in the biomass of terrestrial invertebrates in trout diets at sites with different grazing management, even though trout at sites managed for SRG had, on average, more than 2.8 times more biomass in their diets than fish at sites under SLG, IRG, or WO management. In contrast, during August, the same comparison was significant, as fish at SRG sites had, on average, 6.3, 22.5, and 4.4 times more terrestrial invertebrate prey than trout at sites managed for SLG, IRG, and WO grazing, respectively (Least Squares Means comparisons: $P_{SRG} = 0.03$, $P_{IRG} = 0.003$, $P_{WO} = 0.08$).

In general, trout at sites under each of the four types of grazing management had similar amount of aquatic invertebrate biomass in their diets, but trout had more aquatic invertebrate biomass in their diets during July than August (Figure 8B). Of the aquatic invertebrate prey in trout diets during summer 2007, 42% were adult aquatic insects, 41% were juvenile and pupa macroinvertebrates, and 17 % were other aquatic invertebrates (e.g., snails, bivalves, and annelids). On average, trout consumed 1.8 times more aquatic invertebrate biomass during July than August 2007 (ANOVA: $F_{month} = 22.97$, P < 0.0001). In contrast to July diets when trout had similar amounts of aquatic invertebrate biomass in their diets across the 16 sites sampled, during August, fish at sites managed for IRG had less aquatic invertebrate biomass in their diets. For example, trout at sites under SLG, SRG, and WO management had 4.3, 3.7, and 2.4 times more aquatic invertebrate biomass in their diets than trout at sites managed for IRG (Least Squares Means comparisons: $P_{SLG}= 0.01$, $P_{SRG}= 0.02$, $P_{WO}= 0.2$).

At SLG and IRG sites, which were considered the most contrasting grazing systems, we collected diet samples intensively for a 24-h period (N = 324 total). In general, trout had more aquatic invertebrate biomass in their diets over the diel period than terrestrial invertebrate biomass (Figure 9). At night (i.e., 0000h), trout at sites managed for SLG had a similar amount of terrestrial invertebrate biomass in their diets as fish at sites under IRG management, but during the day they had, on average, 10 times more terrestrial biomass in their diets (ANOVA: $F_{system} = 23.72, P < 0.0001$). Similarly, fish at SLG sites also had, on average, 2 times more aquatic invertebrate biomass in their diets than did trout at sites managed for IRG (ANOVA: $F_{system} = 12.95, P < 0.0003$). Terrestrial invertebrate biomass tended to increase throughout the day at sites under both types of grazing management, although trout at IRG sites may have been feeding on terrestrials later as evident by the midnight biomass peak (Figure 9A). In contrast, the biomass of aquatic invertebrates in trout diets followed different patterns at IRG and SLG sites (Figure 9B). The amount of aquatic invertebrate biomass in trout diets at IRG sites was relatively low at 0000 h, 0600 h, and 1800 h with the peak occurring at 1200 h, whereas the biomass of aquatic invertebrates in trout diets at SLG sites was consistently high during the 0000 h, 0600 h, 1800 h sampling periods and lowest at 1200 h.

Overall, the biomass of invertebrate prey in trout diets was highly variable during summer 2007. Except for fish sampled at sites managed for Simple Rotational Grazing during August 2007, fish had more aquatic invertebrate prey in their diets than terrestrial prey items. Throughout summer 2007, both the total and terrestrial invertebrate biomass in trout diets was greatest at sites managed for Simple Rotational Grazing. In contrast, at sites managed for Intensive Rotational Grazing, trout usually had less invertebrate biomass (both aquatic and terrestrial) in their diet than fish at sites under the three other types of grazing management. The

total invertebrate biomass in trout diets at sites under each of the four different types of grazing management reflected the biomass of terrestrial invertebrates in trout diets during both July and August 2007, but only reflected the biomass of aquatic invertebrates during July. Furthermore, the biomass of terrestrial invertebrates in trout diets closely reflected the biomass of terrestrials entering streams with the exception of sites managed for IRG where the biomass of terrestrials in trout diets was less than expected, relative to sites under different grazing management, based on the amount entering these sites.

Trout inhabiting sites managed for Intensive Rotational Grazing had unexpectedly little invertebrate biomass in their diets compared to trout at sites under SLG, SRG, or WO management. Furthermore, consumption of vertebrate prey items cannot account for the low level of invertebrate prey in trout dies at IRG sites, as trout at these sites did not consume more vertebrate prey items than fish at sites under different grazing management. At this point it is unclear why trout at these sites consumed less prey. It is possible that the invertebrate biomass in trout diets at these sites is an artifact of the sampling methods used or the distribution of sample sites. Four of the five sites managed for IRG (those located north-east of Walden, CO) were each sampled once during 6 - 14 July and 12 or 15 August 2007. As a result, it is possible that weather conditions or correlated insect phenology among these sites could result in similarly low invertebrate availability at these sites by chance alone. Four of five sites are located close to each other, increasing the probability of such correlations. For example, a relatively short period of cool and calm weather during 12-15 August (i.e., only 4 days) could have resulted in reduced terrestrial prey availability at four of the five sites managed for IRG.

High variability in the biomass of prey in trout diets and the composition of trout diets limited our ability to detect statistically significant differences among grazing systems for all but

the most extreme difference (e.g., > 5 times different). High variability in trout diets may result from variability in the prev resource due to insect phenology and local weather conditions that drive the flux of invertebrates to streams. Furthermore, the development of dominance hierarchies among fish that occupy the same habitat is likely to allow a few large fish to usurp the best prey resources. Therefore, during periods when terrestrial prey are available, a few fish may consume large quantities of terrestrial invertebrates and essentially ignore aquatic invertebrates, while smaller fish which are forced to use prev resources other than terrestrial invertebrates may position themselves at feeding stations where they are more likely to encounter drifting aquatic invertebrates or may actively pick them from the substrate. Though we did not record which fish were collected from the same habitats, our data do indicate that some fish primarily fed on terrestrial invertebrates, while others had almost exclusively aquatic prey items in their diets. Furthermore, of the aquatic prey items found in trout diets, many were cased caddisfly larvae and snails which rarely enter the drift. This suggests that fish occupying the same habitat may be both using different prey resources and foraging differently. Thus, it may be important to understand the mechanisms that result in a diverse assemblage of invertebrate prey resources, which may allow trout of different sizes to coexist in the same habitat by decreasing intraspecific competition.

Fish Populations and Biomass Estimates

Density and biomass of adult trout less than 350 mm was greatest at SRG and IRG sites (Figure 10), but these differences also were not significant due to high variability among sites within grazing regimes. The trout in Floyd Creek (an IRG site) had migrated out of Steamboat Lake to spawn and were not resident fish, so this site was not included in the analysis of trout

density and biomass. Although both trout density and biomass were nearly two times greater at sites under rotational grazing systems compared to sites grazed season long, these differences were not significant. Trout density and biomass at sites receiving no livestock grazing (Wildlife Only) were not significantly different than any of the sites where livestock grazing occurred. One site under this WO regime, Grizzly Creek, was also excluded. Trout densities and biomass were very low there, probably due to many years of intense grazing that had caused degraded stream habitat in stream reaches adjacent to the study reach.

Large trout, mostly brown trout greater than 350 mm, were present at all sites and strongly influenced estimates of total trout biomass, particularly at sites grazed season-long where the majority of the trout were small. These large trout tend to be highly mobile and have large home ranges (Young et al. 1997b; Young 1999), which are needed to find adequate prey resources (typically other fish, not invertebrates) and meet their habitat needs. Therefore, it is less likely that these fish are dependent on either *in situ* invertebrate production or terrestrial invertebrate subsidies at the scale of our study reaches. Rather, they are likely influenced by landscape (i.e., riverscape) scale factors, and may be found only temporarily in any given habitat while they take advantage of specific resources located there. As a result of their movement behavior, we did not include these few large trout in our estimates of fish density or biomass at any of our sites.

Conclusion

Results to date indicate that there are differences in aboveground vegetation biomass, input of terrestrial and adult aquatic invertebrates, biomass of invertebrate prey in trout diets, and fish abundance and biomass among sites under different grazing regimes. However, these

differences were not always significant due to high variability among sites under the same grazing system. Sites managed for season-long grazing (SLG) consistently had the lowest values for all measures analyzed thus far, except trout diets sampled during August. In contrast, sites managed for rotational grazing (either SRG or IRG) tended to have the greatest values for all response variables. Unexpectedly, sites managed for IRG received low terrestrial invertebrate input during July and August compared to sites under SRG or WO grazing management sampled. Moreover, on average, fish at these sites had less invertebrate biomass in their diets during August than fish at other sites, even though these sites had more riparian vegetation with greater structural complexity than other sites. This suggests that input of adult aquatic insects and terrestrial invertebrates may depend on both the amount and character of streamside vegetation as well as local weather conditions that influence the transport of invertebrates from vegetation to streams.

There was often high variation in invertebrate input and in trout diets among sites within each management regime, likely due to differences in climate and vegetation throughout the large study region, as well as differences in phenology of vegetation and invertebrates at individual sites. Fish abundance and biomass was also highly variable among sites, perhaps due to movement by larger trout. Additional analyses of these data may help provide a mechanistic understanding of the factors driving the input and use of invertebrate prey resources by trout in rangeland streams. First, analysis of diets for fish of different sizes within each stream may allow understanding how dominance hierarchies influence fish diets (e.g., perhaps only the largest fish usurp most of the terrestrial invertebrates). Second, it is possible that more can be learned by estimating total consumption by all trout within study sites, as the product of diet times fish abundance. Third, we plan to use a model selection framework (Burnham and

Anderson 2002) to choose among multiple candidate models of response variables like invertebrate input and trout diet as a function of additional independent variables (covariates) like vegetation structure, humidity within the riparian zone, and stream temperature. This is important because vegetation, invertebrates, and fish in streams under the same grazing system can vary depending on other environmental characteristics.

Methods for 2008 Field Grazing Experiment

To experimentally test the effects of riparian grazing and loss of woody riparian vegetation on terrestrial prey subsidies to trout streams we conducted a large-scale field experiment during summer 2008. The objectives of this experiment were to: 1) evaluate the effect of a single season of grazing (i.e., the grazing pressure that a riparian area experiences during one growing season), 2) to test whether increased grazing intensity reduces the input of terrestrial invertebrates and the use of this prey resource by trout to a greater extent than either moderate grazing intensity or no cattle grazing (wildlife grazing only), and 3) to compare the effects of a single season of riparian grazing to riparian conditions that may result from a prolonged period of poor grazing management that reduces woody vegetation.

To address these objectives, we constructed small (1 - 2 ha) riparian pastures and used grazing by cow/calf pairs (rather than mowing) to manipulate riparian vegetation. This experiment was conducted on The Nature Conservancy's Red Canyon Ranch and US Forest Service allotments on adjacent streams near Lander, WY where previous research was conducted during summers 2004 – 2005 (see, Saunders 2006).

Experimental design

We conducted our experiment on streams with healthy riparian areas. We selected streams that had robust herbaceous and woody riparian vegetation and that had little bank erosion. We applied the vegetation removal treatments to reduce this vegetation to lower levels, rather than selecting streams with a long history of continuous grazing and applying "reduced use" or "rest" treatments in hopes of increasing vegetation to higher levels. This experimental design allows for greater control over riparian vegetation conditions, greater treatment differentiation, and the comparison of woody and herbaceous vegetation removal. To achieve these initial conditions we selected streams which have been managed for intensive rotational grazing consistently since the late 1980's. As a result, riparian vegetation and invertebrate communities resulting from our experimental treatments reflect a single season of riparian use and may not be similar to conditions where riparian areas have been heavily grazed and are provided short term rest (i.e., 1 - 5 growing season) or where grazing management is changed to allow for improved riparian vegetation conditions.

Four experimental treatments were designed to evaluate riparian conditions which would result from cattle grazing of riparian vegetation or livestock exclusion.

- *Treatment 1:* Moderate grazing treatment designed to maintain a residual stubble height of 4 6 inches (10 15 cm) of herbaceous vegetation.
- *Treatment 2:* Intensive grazing treatment designed to maintain a residual stubble height of 2 3 inches (5 7.5 cm) of herbaceous vegetation.
- *Treatment 3:* Intensive grazing plus removal of woody vegetation treatment. Initially, 66% of the woody vegetation was removed from within 10 m of both sides of the

channel. Subsequently, cattle were stocked to maintain a residual stubble height of 2 - 3 inches as in Treatment 2.

Treatment 4: Control treatment where livestock were fenced away from the riparian area for the duration of the experiment.

Treatments 1 and 2 were designed to evaluate the effects of cattle grazing during a single growing season. Treatment 3 was designed to simulate riparian conditions that may result from prolonged season-long grazing. Treatment 4 simulates riparian conditions in small scale riparian cattle exclosures. Each treatment was designed for rapid implementation to minimize the amount of time during which cattle were present, and was applied after annual high water levels subsided to minimize physical alteration of the riparian and aquatic habitat. Thus, experimental treatments were designed to test the effects of vegetation removal by livestock on the availability of invertebrate prey resources for trout, and not the effects of stream bank degradation resulting from cattle grazing. We constructed 16 riparian pastures, 4 on each of 4 different streams, and applied each of the 4 treatments (see above) to pastures in a randomized, complete block design with streams representing blocks (Table 3).

Pasture construction and treatment application

Riparian pastures were constructed on Red Canyon Creek, Cherry Creek, Pass Creek and Beaver Creek (see, Saunders 2006 for a map and description of study area). Study reaches were chosen to have similar riparian vegetation and stream characteristics and to be free of current beaver activity. In one site on Red Canyon Creek where beaver began to construct a dam, we removed dams and discouraged establishment on two occasions during the experiment. The

lengths of study reaches enclosed by riparian pastures were designed to support at least 50 adult trout (species present and age 1+ densities were determined during 2005, see Saunders 2006). Each pasture also included a 25-m long buffer at both the upstream and downstream ends of the study reach. At Red Canyon Creek, riparian pastures enclosed 250 m of stream, whereas at Cherry, Pass, and Beaver creeks, riparian pastures enclosed 200 m of stream. Additionally, riparian pastures were separated by at least 100 m of stream (except in one case on Red Canyon Creek where only 75 m was possible) to serve as a treatment buffer and ensure that the invertebrate drift entering study reaches was similar. Lateral fences connecting upstream and downstream cross fences (i.e., those perpendicular to the flow) were placed at least 25 m from the channel. The experimental pastures were constructed with three-strand electric fences energized with 2 solar electric fence energizers (Model S17 Solar, Gallagher USA, Kansas City, MO).

Treatments were applied to pastures (i.e., cattle were stocked) sequentially (Red Canyon and Cherry creeks) or to two pastures at a time (Beaver and Pass creeks) during July 2008. We ended the experiment during mid-September 2008, 6 - 9 weeks after cattle had been removed from the last pasture on each stream. Treatments 1 and 2 were applied by stocking 15 - 25 cow/calf pairs and 1 bull in each pasture. In pastures where we removed woody vegetation (i.e., Treatment 3), we left every third riparian shrub within 10 m of each streambank and cut all others to ground level and removed them from the pasture. Trees were rarely encountered in riparian pastures, but a few aspen and lodgepole pine that had diameter < 3 in (7.5 cm) and were within 10 m of the channel were treated as shrubs. All larger trees were left. After all woody vegetation had been removed, cattle were stocked to achieve the 2 - 3 in residual stubble height treatment. Cattle remained in each pasture for 2-4 d, except on Red Canyon Creek where pasture

size and production of herbaceous vegetation were greater and cattle remained for 9 - 11 days (see Table 3). Due to the time required to construct experimental pastures and the availability of cattle, the experimental treatments were completed later in Red Canyon and Pass creeks. This resulted in the duration of the experiment being about 20 d shorter in these streams (Table 3). However, both the midterm and final samples of invertebrate inputs and trout diets were conducted during the same two-week period each, with the two lower-altitude streams (Cherry and Red Canyon) being sampled the first week.

Sampling methods specific to 2008 field experiment

To evaluate the effect of riparian grazing on terrestrial invertebrate subsidies to trout, we measured riparian vegetation, input of terrestrial invertebrates and adult aquatic insects to streams, use of invertebrate prey resources by trout, and trout abundance, both before and after the experiment. Additionally, vegetation height, input of invertebrates to streams, and trout diets were measured three weeks after cattle had been removed from the last pasture (i.e., during a mid-term sampling period). Sampling procedures were similar to those used during 2007 (see Methods for 2007 Comparative Field Study above). In order to minimize the disturbance to aquatic habitat and avoid influencing trout behavior, all sampling, especially that which required handing fish, was conducted using the least intrusive means possible. For example, when it was necessary to access a study reach at multiple locations to collect samples, we avoided walking in the stream or close to the banks between sampling locations.

Streamside vegetation – Riparian vegetation was sampled both to determine when grazing treatments had been achieved (i.e., stubble height monitoring) and to evaluate the effects of grazing treatments on streamside vegetation attributes that may influence the flux of

invertebrates to streams. Aboveground vegetation biomass, vegetation height, and vegetation cover over the channel were quantified both before treatment application and at the end of the 6-week experiment. To quantify vegetation overhanging the channel before applying grazing treatments, hemispherical photographs were take in the center of the channel and at the bank full mark on both banks at 10-m intervals in each study reach. Additionally, vegetation structure (overhead cover and vegetation height) was measured within 4 m of the channel at the end of the experiment using the same hemispherical photograph and vegetation height sampling methods used during 2007 (see above). At the end of the experiment, utilization of herbaceous vegetation was estimated from two 1-m² cattle exclosures (see description above) located at randomly selected distances from the downstream end of the study reach and placed within 3 m of the channel. Exclosures were located in portions of the riparian zone dominated by herbaceous vegetation because we were not attempting to estimate browse of riparian shrubs.

To describe vegetation use throughout each riparian pasture, as well as to monitor vegetation regrowth throughout the duration of the experiment, three permanent transects were located along each sampling reach. At each site, transects were located at randomly selected distances from the downstream end of the sampling reach such that one transect was located in each 50-m stretch of the sampling reach (65-m stretches in the 200-m sampling reaches in Red Canyon Creek). Transects were centered on the channel and extended perpendicular to the thalweg into the riparian pasture for 30 m or until the pasture fence was encountered. The maximum height of grasses, forbs, and shrubs was measured at 1.5 m intervals on each transect. Vegetation height was measured prior to grazing, immediately after cattle were removed, at two week intervals during the experiment, and at the end of the experiment.

Invertebrate input – The input of terrestrial invertebrates and adult aquatic insects to study reaches was measured as in the 2007 observational study (see above). To quantify the biomass of invertebrates entering streams, six pan traps were deployed in each study, three each in bank and channel positions. Pan trap locations were determined base on the amount of high and low vegetation cover, as in previous research. Two 3-d samples were collected before applying grazing treatments, 3 weeks after cattle were removed, and after the experiment was terminated. Sampling at the beginning and end of the experiment was conducted before estimating fish abundance to avoid disturbing riparian vegetation and invertebrates before invertebrate samples were collected. The location of each pan trap remained consistent for the duration of the experiment, except when water levels dropped and exposed the substrate beneath pan traps. When this occurred, pan traps were relocated to the nearest comparable location.

Trout diets – During each 6-d period when invertebrate input was being measured (i.e., before, during, and at the end of the experiment), stomach samples from 15 trout were collected using gastric lavage. The initial and final diet sampling was conducted at least 5 d before conducting fish abundance estimates to avoid influencing trout feeding behavior, while attempting to avoid causing fish to move out of study reaches as a result of frequent exposure to electrofishing. As in previous research, we attempted to collect diet samples from trout of 120 – 350 mm fork length to target trout that were primarily insectivorous and large enough to sample efficiently. Trout were collected using a backpack electrofishing unit. Electrofishing began 25 m from the downstream end of the sampling reach and extended no further than 15 m below the pasture fence. On the occasion that we were unable to collect 15 individuals, we resampled the reach once the following day. Fish sampled on the first occasion were given a partial fin clip to avoid resampling. After diet samples were collected, trout were held in live wells for 2 h before

being released to the location where they were originally collected. Any mortality that resulted from the diet sampling process was recorded. In addition, to minimize the amount of electrofishing conducted and disturbance caused by working in the study reaches, we attempted to collect trout only from habitats likely to hold fish (e.g., pools and runs) and avoided walking in the stream as much as possible.

Fish abundance estimation – Fish abundance and biomass, both salmonid and nonsalmonid, were estimated before applying grazing treatments during July, and at the end of the experiment during August. Fish abundance was estimated using three pass removal electrofishing conduced at night (see above). During the initial estimate, fish were held for three hours in live wells after processing and released near their original location in the study reaches. However, they were not released within 25 m of the ends of the reach to minimize movement out of our study reaches after electrofishing.

Habitat and temperature measurements – To evaluate whether, or to what extent, experimental grazing treatments altered the amount and quality of habitat for trout, we measured aquatic habitat before and after the experiment. We measured the dimensions of all pools, runs, undercut banks, and coarse woody debris, as well as classifying bed substrate, using methods described above for the 2007 comparative study. Discharge was measured at the end of the experiment to describe differences among study reaches along each stream. Air and water temperatures were recorded hourly at each study reach during the experiment using Hobo temperature loggers (see above). Water temperature loggers were deployed at the downstream end of each pasture, where the fence crossed the stream (i.e., 25 m below the study reach). Air temperature/relative humidity loggers were deployed in 4 inch PVC thermal shields (see above) along the stream in the center of each riparian pasture (i.e., in the center of each study reach).

Sample collection and processing

During the summer 2008 field experiment we collected 160 vegetation clippings, 576 pan trap samples, and 720 trout diet samples. Additionally, we took approximately 740 hemispherical photographs to quantify over-story vegetation above study reaches and in the adjacent riparian areas. To date we have dried and weighed all the vegetation clippings, and processed all the trout diet samples and 28% of the pan trap samples. Currently we are continuing to process pan trap samples, estimate the biomass of invertebrates in trout diets using length measurement recorded for each invertebrate consumed, and will soon begin processing hemispherical photographs. Our goal is to finish processing all samples and photographs by December 2009 and prepare the final report and manuscripts for publication by spring 2010.

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Tables

Table 1. — Characteristics of physical habitat in the 16 study sites in northern Colorado. Data were collected at five sites managed for Intensive Rotational Grazing (IRG), four sites managed under Simple Rotational Grazing (SRG), four sites managed under Season-Long Grazing (SLG), and three sites grazed by Wildlife Only (WO, see text). Trout species present (BNT: brown trout, BKT: brook trout, RBT: rainbow trout, CUT: cutthroat trout) are listed in order of abundance. Stocking rate of cattle in pastures is reported as hectares per animal unit month (AUM).

Site name	Location	Land ownership ^a	Elevation (m)	Map gradient (%)	Trout species	Stocking rate (ha / AUM) ^b		
Intensive Rotational Grazing								
Lower Canadian	Lat: 40°37'58" N Lon: 106°01'45" W	Private	2,564	1.2	BNT, RBT			
Upper Canadian	Lat: 40°38'32" N Lon: 106°02'21" W	Private	2,555	2.6	BNT			
Michigan	Lat: 40°37'42" N Lon: 106°06'27" W	Private	2,580	1.0	BNT, RBT			
Illinois	Lat: 40°32'01" N Lon: 106°13'22" W	Private	2,564	1.4	BNT			
Floyd	Lat: 40°47'53" N Lon: 106°59'16" W	Private	2,458	1.2	BKT, RBT, CUT			
		Simple Ro	tational Grazing	Ş				
Arapaho	Lat: 40°24'32" N Lon: 106°23'28" W	USFS	2,683	1.4	BNT			
Northern Rock	Lat: 40°23'58" N Lon: 106°12'47" W	USFS	2,751	2.2	ВКТ			

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Table 1-- continued

Site name	Location	Land ownership ^a	Elevation (m)	Map gradient (%)	Trout species	Stocking rate (ha / AUM) ^b
Southern Rock	Lat: 40°02'10" N Lon: 106°39'27" W	USFS	2,600	1.4	BNT	
Lower Trout	Lat: 40°16'00" N Lon: 107°03'38" W	Private	2,343	2.8	BNT, BKT, RBT, CUT	
		Season	Long Grazing			
North Fork North Platte	Lat: 40°52'56" N Lon: 106°32'59" W	Private	2,591	1.2	BNT, BKT	
Shafer	Lat: 40°51'49" N Lon: 106°33'00" W	Private	2,576	2.4	BNT, BKT	
East Fork Troublesome	Lat: 40°11'26" N Lon: 106°13'30" W	USFS	2,475	0.8	BNT	
Newcomb	Lat: 40°35'43" N Lon: 106°36'05" W	USFS	2,656	1.2	BNT, BKT	
		Wild	llife Only			
Hinman	Lat: 40°46'07" N Lon: 106°48'57" W	USFS	2,375	1.4	BKT, RBT	0
Upper Trout	Lat: 40°13'45" N Lon: 106°06'00" W	USFS	2,508	3.2	BKT, CUT	0
Grizzly	Lat: 40°'26"10 N Lon: 106°29'00" W	Private	2,554	1.2	BNT	0

^a Sites were on lands owned privately, or by the U.S. Forest Service (USFS) or Bureau of Land Management (BLM).

^b Stocking rate data were requested from management agencies and ranch managers, but are still pending.

Table 2. — Characteristics of physical habitat in the 16 study sites in northern Colorado under four different types of grazing management (see text). Mean substrate diameters (Mean D) were determined using Wolman pebble counts (see text). The two most prevalent substrate types are given in order of abundance. The mean percent embeddedness (% Embedded) was estimated for all substrate particles \geq 15 mm collected during pebble counts. Mean summer water temperature was calculated from hourly water temperatures recorded during July and August 2007.

			Substrate			
Site Name	Bankfull width (m)	Dominant ^a	Mean D (mm)	% Embedded	Mean summer temperature (°C)	Pool and run area (m²)
Intensive Rotational Grazing						
Lower Canadian	5.4	Pebble / Cobble	49	19	b	397
Upper Canadian	5.2	Pebble / Cobble	48	41	16.3	463
Michigan	13.0	Cobble / Pebble	76	18	16.4	1490
Illinois	8.3	Pebble / Fine	42	35	17.5	1114
Floyd	2.0	Fine / Pebble	15	37	15.7	311
		Simple Ro	otational Gra	zing		
Arapaho	3.1	Cobble / Pebble	73	15	b	173
Northern Rock	3.0	Cobble / Fine	55	24	11.2	175
Southern Rock	6.3	Pebble / Fine	42	24	16.6	997

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Table 2-- continued

Substrate								
Site Name	Bankfull width (m)	Dominant ^a	Mean D (mm)	% Embedded	Mean summer temperature (°C)	Pool and run area (m²)		
Lower Trout	7.2	Cobble / Pebble	108	12	15.3	391		
Season Long Grazing								
N.F. North Platte	5.0	Pebble / Gravel	28	48	15.9	907		
Shafer	4.6	Pebble / Cobble	50	13	10.5	622		
East Fork Troublesome	7.3	Cobble / Pebble	78	45	b	971		
Newcomb	11.2	Pebble / Fine	45	36	14.9	895		
Wildlife Only								
Hinman	6.6	Cobble / Pebble	78	21	13.5	441		
Upper Trout	6.4	Cobble / Fine	101	36	14.1	541		
Grizzly	8.5	Pebble / Fine	28	27	18.4	1154		

^a Substrate categories are based on the Wentworth classification (Wentworth 1922).

^b No temperature data were available for 2007.

Table 3. — Characteristics of the experimental pastures and physical habitat in the 16 study sites in central Wyoming. Four experimental grazing treatments were applied to each stream in a randomized complete block design (see text). Trout species present (BNT: brown trout, BKT: brook trout, RBT: rainbow trout) are listed in order of abundance. The two most prevalent substrate types are given in order of abundance. Experiment duration identifies the period after application of experimental grazing treatments (i.e., after cattle were removed from experimental pastures), until the final pan trap sampling commenced. Grazing duration indicates the number of days of cattle grazing that was needed to achieve treatment stubble height in riparian pastures.

Stream	Position	Treatment	Location	Trout species	Elevation (m)	Dominant Substrate ^a	Experiment Duration	Grazing Duration (d)
Cherry	1	Intensive	Lat: 42° 40' 35" N Lon: 108° 39" 49" W	BNT	5613	Pebble, Cobble	11 July – 10 Sep (61 d)	2
Cherry	2	Control	Lat: 42° 40' 30" N Lon: 108° 39" 54" W	BNT	5635	Pebble, Cobble	-	-
Cherry	3	Intensive + Removal	Lat: 42° 40' 26" N Lon: 108° 39" 59" W	BNT	5648	Pebble, Cobble	14 July – 10 Sep (58 d)	2
Cherry	4	Moderate	Lat: N42° 40' 06" N Lon: 108° 40" 14" W	BNT	5710	Cobble, Pebble	14 July – 10 Sep (59 d)	1.5
Red Canyon	1	Moderate	Lat: 42° 40' 09" N Lon: 108° 39" 26" W	BNT	5671	Fine, Pebble	4 August – 10 Sep (38 d)	11
Red Canyon	2	Intensive + Removal	Lat: 42° 40' 03" N Lon: 108° 39" 23" W	BNT	5685	Fine, Pebble	2 August – 10 Sep (40 d)	9
Red Canyon	3	Control	Lat: 42° 38' 35" N Lon: 108° 38" 15" W	BNT	5852	Pebble, Fine	-	-
Red Canyon	4	Intensive	Lat: 42° 40' 26" N Lon: 108° 38" 12" W	BNT	5876	Pebble, Fine	2 August – 10 Sep (40 d)	9

Table 3—continued

Stream	Position	Treatment	Location	Trout species	Elevation (m)	Dominant Substrateª	Experiment Duration	Grazing Duration (d)
Pass	1	Moderate	Lat: 42° 37' 47" N Lon: 108° 45" 56" W	RBT, BKT	7277	Cobble	3 August – 17 Sep (45 d)	2
Pass	2	Intensive + Removal	Lat: 42° 37' 41" N Lon: 108° 45" 52" W	RBT, BKT	7306	Cobble	4 August – 17 Sep (45 d)	2.5
Pass	3	Intensive	Lat: 42° 37' 27" N Lon: 108° 45" 32" W	BKT, RBT	7430	Cobble	4 August – 17 Sep (45 d)	2.5
Pass	4	Control	Lat: 42° 37' 21" N Lon: 108° 45" 22" W	BKT, RBT	7446	Cobble	-	
Beaver	1	Intensive	Lat: 42° 37' 46" N Lon: 108° 43" 34" W	ВКТ	7963	Cobble, Pebble	17 July – 17 Sep (63 d)	3
Beaver	2	Moderate	Lat: 42° 33' 51" N Lon: 108° 43" 42" W	ВКТ	7978	Cobble, Pebble	17 July – 17 Sep (63 d)	2
Beaver	3	Control	Lat: 42° 33' 54" N Lon: 108° 43" 53" W	ВКТ	8001	Cobble, Pebble	-	-
Beaver	4	Intensive + Removal	Lat: 42° 33' 57" N Lon: 108° 44" 04" W	ВКТ	8029	Cobble, Pebble	23 July – 17 Sep (56 d)	3

^a Substrate categories are based on the Wentworth classification (Wentworth 1922).

Figures

Figure 1 — Map of the study area in Jackson, Routt, and Grand counties, Colorado showing sites sampled during summer 2007. Red circles show sites that were under intensive rotational grazing (IRG) management, purple circles show sites under simple rotational grazing (SRG) management, blue circles show sites under season-long grazing (SLG) management, and yellow circles show sites grazed only by wildlife (WO). Sites in Routt County were located in the Yampa River drainage. Sites in Grand County were in the Colorado River drainage. Sites located in Jackson County were in the North Platte River drainage.



Figure 2 — Average aboveground dry biomass of riparian vegetation at sites under four different types of grazing management. Data represent estimates from 16 riparian areas located in the northern Colorado. Clippings used to estimate vegetation biomass were collected in late August or early September 2007. Biomass was estimated from clippings taken from 0.25-m² circular frames placed along the stream bank. Error bars show ± 1 SE. Different letters indicate significant differences between sites based on pairwise comparisons after ANOVA.



Figure 3 — Average percent utilization of herbaceous riparian vegetation at sites under four different types of grazing management. Data represent estimates from 15 riparian areas located in northern Colorado (estimates could not be made for one Simple Rotation Site, see text). Vegetation clippings used to estimate biomass were collected in late August or early September. Biomass was estimated from clippings taken from 0.25-m^2 circular frames placed both in and next to 1-m^2 grazing exclosures constructed along the stream bank. Error bars show \pm SE. Different letters indicate significant differences between sites based on pairwise comparisons after ANOVA.



Figure 4 — Average height of the tallest vegetation within 4 m of the channel at sites under four different types of grazing management. Data represent estimates form 16 riparian areas located in northern Colorado. Vegetation height was measure systematically at each study site during August 2007. Error bars show \pm 1 SE. Different letters indicate significant differences between sites based on pairwise comparisons.



Figure 5 — Total invertebrate input to 16 streams in northern Colorado under four different types of grazing management. Estimates of invertebrates input come from pan trap collections during 2 - 16 July and 9 - 16 August 2007. Error bars show ± 1 SE, which represents the variation in the amount of invertebrate input among sites within each type of grazing management. Values reflect estimates computed using log transformed data which were subsequently back-transformed to show the average input of invertebrate biomass on the original (i.e., untransformed) scale. Standard errors were estimated using the Delta Method (see text).


Figure 6 — Terrestrial and adult aquatic invertebrate input to 16 streams in northern Colorado under four different types of grazing management. Estimates of invertebrates input come from pan trap collections during 2 - 16 July and 9 - 16 August 2007. Error bars show ± 1 SE in both panels, which represents the variation in the amount of invertebrate input among sites within each type of grazing management. Values reflect estimates computed using log transformed data which were subsequently back-transformed to show the average input of invertebrate biomass on the original (i.e., untransformed) scale. Standard errors were estimated using the Delta Method (see text).



Figure 7 — Total invertebrate biomass in trout diets for 16 streams in northern Colorado under four different types of grazing management. Invertebrates in trout diets were collected from 20 fish using gastric lavage during 6 – 19 July and 6 – 26 August 2007. Stomachs were sampled between 1400 and 1600 h. Error bars show \pm 1 SE in both panels, which represents the variation in the amount of invertebrate input among sites within each type of grazing management. Values reflect estimates computed using square-root transformed data which were subsequently backtransformed to show the average biomass of invertebrate in trout diets on the original (i.e., untransformed) scale. Standard errors were estimated using the Delta Method (see text). Different lower case letters above estimates indicate statistical significance ($\alpha = 0.05$).



Figure 8 — Terrestrial (A) and aquatic invertebrate biomass (B) in trout diets for 16 streams in northern Colorado under four different types of grazing management. Invertebrates in trout diets were collected from 20 fish using gastric lavage during 6 – 19 July and 6 – 26 August 2007. Stomachs were sampled between 1400 and 1600 h. Error bars show \pm 1 SE in both panels, which represents the variation in the amount of invertebrate input among sites within each type of grazing management. Values reflect estimates computed using square-root transformed data which were subsequently back-transformed to show the average biomass of invertebrate in trout diets on the original (i.e., untransformed) scale. Standard errors were estimated using the Delta Method (see text). Different lower case letters above estimates indicate statistical significance ($\alpha = 0.05$). The Lower case letter with an asterisk indicates statistical significance for $\alpha = 0.1$.



Figure 9 — Terrestrial (A) and aquatic invertebrate biomass (B) in trout diets over a 24 h period for 8 streams in northern Colorado under either Intensive Rotational or Season-Long grazing management. Invertebrates in trout diets were collected from 10 fish using gastric lavage during 6-26 August 2007. Error bars show ± 1 SE in both panels, which represents the variation in the amount of invertebrate input among sites within each type of grazing management. Values reflect estimates computed using square-root transformed data which were subsequently backtransformed to show the average biomass of invertebrate in trout diets on the original (i.e., untransformed) scale. Standard errors were estimated using the Delta Method (see text). Different lower case letters above estimates indicate statistical significance ($\alpha = 0.05$).



Figure 10 — Trout density (A) and biomass (B) for age-1 and older fish <350 mm estimated in late summer 2007 at 15 streams in northern Colorado. Estimates from Floyd Creek were considered an outlier and not included in the analysis (see text). Population estimates were conducted using three-pass nighttime removal electrofishing. Error bars show \pm SE in both panels, which represents the variability among sites under a given grazing system.

