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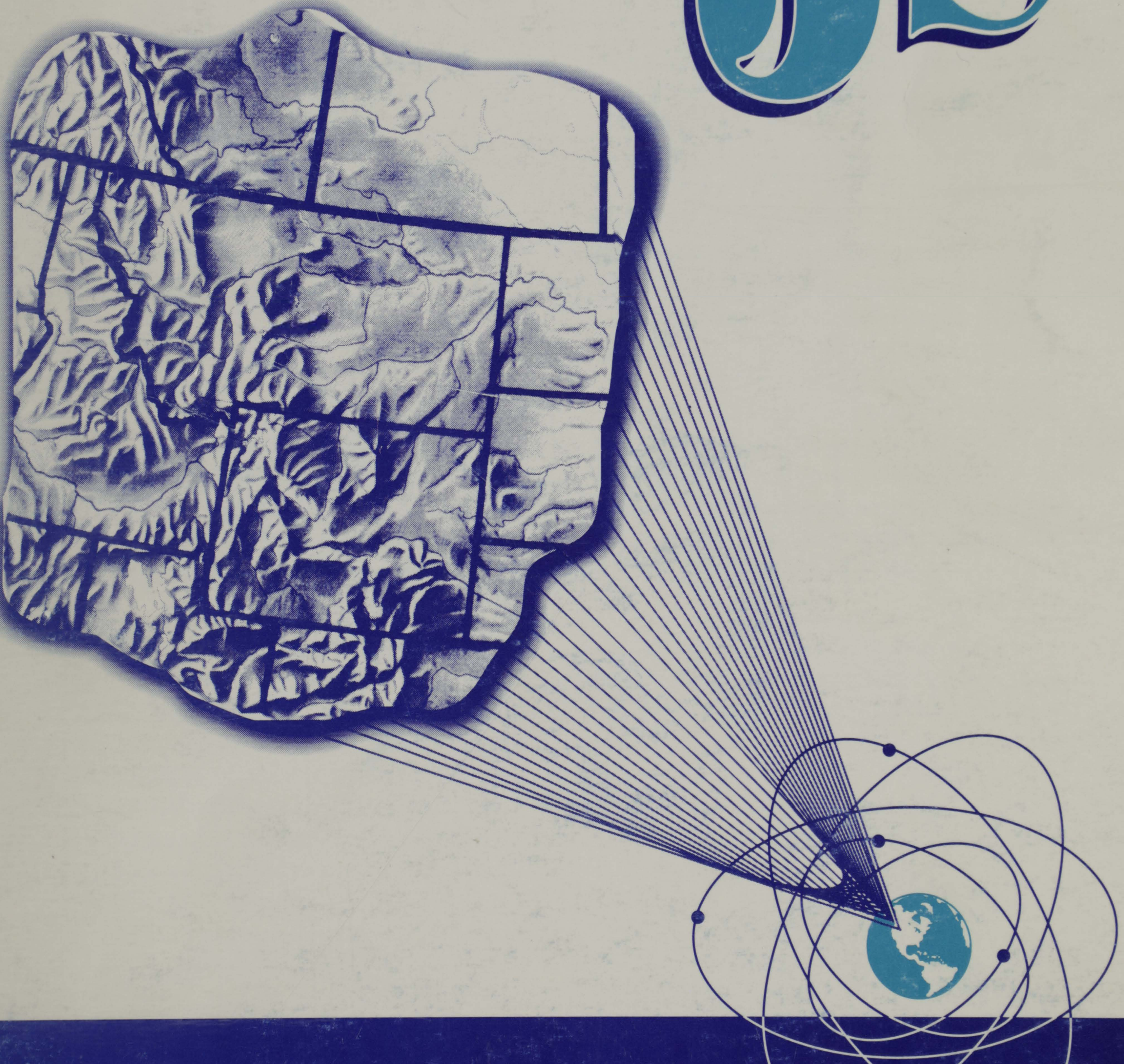

INTERMOUNTAIN JOURNAL OF SCIENCES

The Intermountain Journal of Sciences is a regional peer-reviewed journal that encourages scientists, educators and students to submit their research, management applications or viewpoints concerning the sciences applicable to the intermountain region. Original manuscripts dealing with biological, environmental engineering, mathematical, molecular-cellular, pharmaceutical, physical and social sciences are welcome.

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Three hard copies of the submitted manuscript, with copies of the "Guidelines and checklist for IJS referee " attached and forwarded to th appropriate Associate Editor. The Associate Editor retains one copy of the manuscript and guidelines for his/her review, and submits a similar package to each of two other reviewers. A minimum of two reviewers, including the Associate Editor, is required for each manuscript. The two other reviewers are instructed to return the manuscript and their comments to the Associate Editor, who completes and returns to the EIC a blue "Cover Form" and all manuscripts and reviewer comments plus a recommendation for publication, with or without revisions, or rejection of the manuscript. This initial review process is limited to 30 days.

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LITERATURE CITED

Dusek, Gary L. 1995. Guidelines for manuscripts submitted to the *Intermountain Journal of Sciences*. Int. J. Sci. 1(1):61-70.

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design and Layout ~ **Media Works, Bozeman, Montana** Printing ~ **Kwik Kopy Printing, Bozeman, Montana**

David C. Richards
Marni G. Rolston
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A COMPARISON OF SALMONFLY DENSITY UPSTREAM AND DOWNSTREAM OF ENNIS RESERVOIR

ABSTRACT

Ennis Reservoir on the Madison River, southwest Montana, has been linked with changes in macroinvertebrate and fish assemblages. We tested the hypothesis that life history, distribution, and abundance of the salmonfly (Pteronarcys californica *Newport) differ upstream and downstream of Ennis Reservoir. We sampled larvae, shed exuviae, and discarded wings of salmonflies in 1994 and 1995 upstream and downstream of the reservoir. Wolman pebble counts and estimation of substrate embeddedness were made at nine exuviae collection sites to determine habitat availability. Predation rate on adult salmonflies and crayfish densities also were examined. Salmonflies downstream of Ennis Reservoir were 6-8 X less abundant, significantly larger, and possibly required one less year as larvae to complete development compared to salmonflies upstream of the reservoir. Adult salmonfly abundance both upstream and downstream of Ennis Reservoir was 3.2 to 4.0 X higher in 1995 than 1994. Numbers of exuviae were correlated with substrate embeddedness suggesting that abundance was influenced by habitat availability. Predation accounted for 5 to 15 percent of adult salmonfly mortality. Crayfish were at least 6.6 X more abundant downstream of Ennis Reservoir.*

Key words: biomonitoring, competition, predation, *Pteronarcys californica,* river regulation, salmonflies, water quality

INTRODUCTION

River regulation deleteriously affects aquatic ecosystems worldwide. Impoundments can alter thermal regimes (Webb and Walling 1997), erosion and sedimentation rates (Ligon et al. 1995), hyporheic zones (Stanford 1998), riparian areas (Andersson *et al.* 2000, Friedman and Auble 1999), primary production (Benenati et al. 1998), macroinvertebrate assemblages (Cazaubon and Giudicelli 1999), and fish assemblages (Ligon *et al.* 1995, Peáz et al. 1999). The effect of Ennis Reservoir on the Madison River ecosystem is important to fishery and recreational management and is of concern to many. Ennis Reservoir was formed on the Madison River by the construction of Montana Power Company's top release Madison Dam, near Ennis, Montana, in 1907 (Fig. 1). Ennis Reservoir has been accumulating sediment since its construction and present water depths average 2.5 to 4 m. Sediment export during spring runoff has been diminished by flow regulation. Changes in Madison River sediment accumulation and its effects on macroinvertebrate habitat availability

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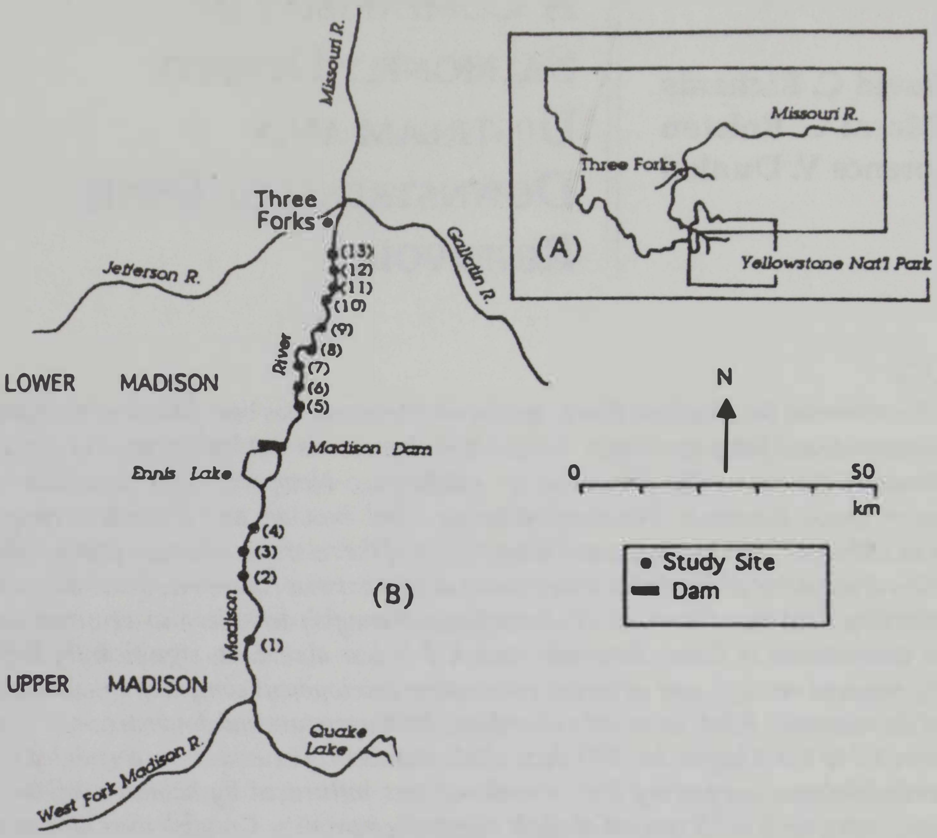

Figure 1. *Madison River and study sites. Legend of sample locations: 1) McAtee Bridge; 2) Varney Bridge; 3) Eight-Mile Hole; 4) Burnt Tree; 5) Beartrap; 6) Split-Rock (Beartrap Canyon); 7) West-side Parking Lot; 8) Duke's Rock; 9) Norris Bridge; 10) Black's Ford; 11) Roadcut; 12) Grey Cliffs; 13) Cobblestone.*

have not been published. Because Ennis Reservoir is relatively shallow, summer temperatures in the Madison River downstream are often greatly elevated from pre-dam conditions. Changes in the Madison River's thermal regime have been documented to affect aquatic macroinvertebrate assemblage changes, including stonefly (Plecoptera) densities (Fraley 1978), downstream of Ennis Reservoir.

Stoneflies are an important food source for trout and are important to the biological functioning of rivers and streams. However, the life cycles and ecology of many Plecoptera are poorly known (Hassage 1990). The salmonfly (*Pteronarcys californica* Newport) is the largest (40 to 60 mm in length) stonefly in western North America (Poole 1981). Salmonfly larvae (nymphs) are detritivorous shredders (Cummins *et al.* 1973, Short and Maslen 1977) and feed on both allochthonous and autochthonous coarse particulate organic matter (CPOM) (Fuller and Stewart 1979). Because of its body size and role in reducing CPOM to fine particulate organic matter (FPOM), it is an important link in the aquatic food web (Cummins *et al.* 1973, Short and Maslin 1977).

Salmonfly larvae typically have 3 to 4 year life cycles in western rivers, depending on water temperatures (Branham and Hathaway 1975, Merrit and Cummins 1984). Larvae usually occur in patches with age-segregated distributions (Elder and Gaufin 1973, Poole 1981, Freilich 1991) and prefer large, fast, well-oxygenated rivers with unconsolidated (unembedded) cobble and boulder substrates (Elder and Gaufin 1973). Salmonflies are currently used as indicators of water quality in state and federal monitoring programs, particularly for non-point sedimentation impacts (Barbour *et al.* 1999). Because impoundments often alter thermal regime and sediment characteristics, we predicted that life history and abundance of salmonflies would be altered downstream of Ennis Reservoir.

Body weights of larval salmonflies have been used to estimate year class strength (Branham and Hathaway 1975). Fraley (1978) reported that salmonfly adults below Ennis Reservoir were 13 percent smaller than those upstream of Ennis Reservoir. This difference was attributed to higher nymphal metabolic rate resulting from elevated water temperatures below the reservoir.

Crayfish sometimes prey on *Pteronarcys* species (Moore and Williams 1990) and also may compete with salmonflies for limited, unembedded cobble habitat where their ranges overlap. Also, predation on adult salmonflies in the Madison River riparian area has not been documented.

We conducted a survey of salmonflies in the Madison River and tested the hypothesis that life history, distribution, and abundance of salmonflies differ above and below Ennis Reservoir. We also tested the specific hypothesis that abundance of salmonflies is correlated with substrate embeddedness and we report observations of predation on adult salmonflies and possible competition with crayfish.

STUDY SITE

The Madison River is a medium-sized, 5th order river (Fig. 1). The upper portion of the Madison River, upstream of Ennis Reservoir, flows mostly through Tertiary basin fill and is comprised of a heterogeneous mixture of cobbles, gravel, sand, silt, and clay. Directly downstream of Ennis Reservoir, the Madison River cuts through Archean, high-grade metamorphic rock to form the Beartrap Canyon. Below the Beartrap Canyon, the Madison River again flows through Tertiary basin fill, similar to the upper Madison River (Alt and Hyndman 1986)

The upstream portion of the Madison River is typically of moderate gradient with well-developed riffle-run habitat and predominant cobble substrate. For about 3 km upstream of Ennis Reservoir, the river braids into numerous channels and substrate size decreases. In the Beartrap Canyon, the river flows through boulder-filled rapids, many of which were formed by rockslides within the narrow canyon. Below Beartrap Canyon, the lower portion of the Madison River re-establishes a cobble-riffle morphology, with increased inputs of fine sediments resulting from the canyon's geologic parent materials.

MATERIALS AND METHODS

Larval Collections

Salmonfly larvae were sampled using a standard D-net with a 1 mm mesh. Live (wet) weights were recorded from the upstream ($n = 241$) and downstream ($n = 203$) portions of the river with a Pesola™ spring scale (0.05 g) in May 1995. We also recorded the number of crayfish caught in our samples. We created a histogram of weight distributions of salmonflies from these samples to delineate size and year classes. It was difficult to determine the sex of very small (<0.5 g) larvae in the field; therefore, half of the larval salmonflies less than 0.5 g were considered female and half were considered male. Male and female pre-emergent larval weights in both the upper and lower portions of the Madison River were statistically compared using Student's *t*-test

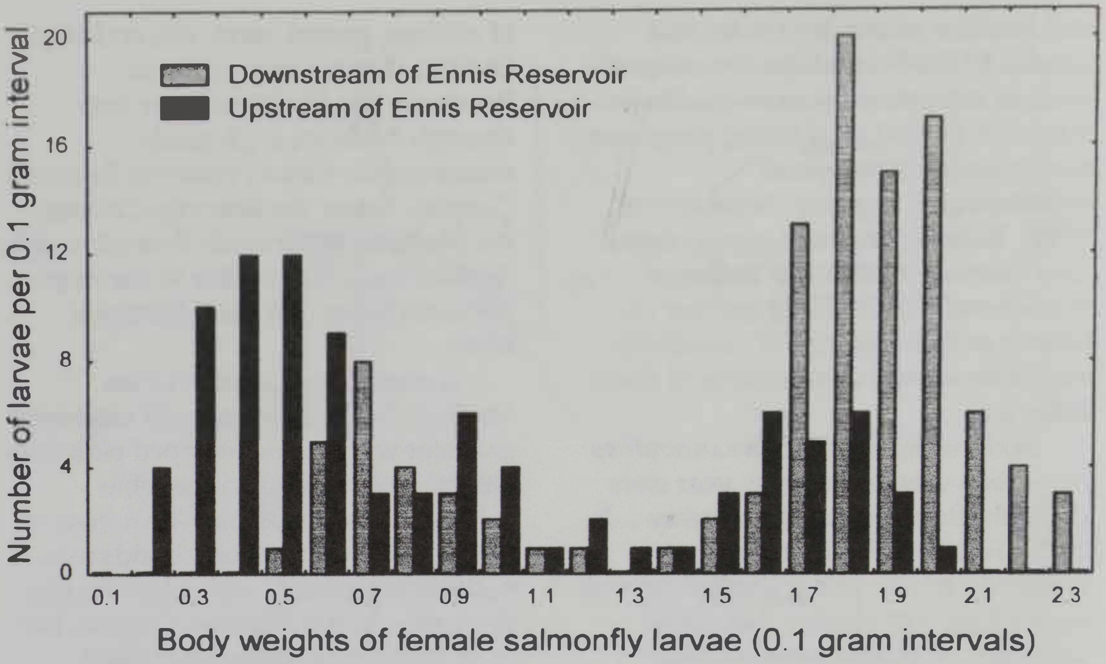

Figure 2. *Weight frequency distribution of female larval salmonflies in the upstream and downstream sites of the Madison River, 1995 (*n = *109 larvae downstream,* n = *92 larvae upstream).*

analysis (two-tailed, equal variances). Pre-emergent larvae were determined to be those from the largest weight group in our histogram analysis (Fig. 2).

Exuviae Collections

Transects, each 15 m long and 1 m wide, were sampled at 24 sites along the banks of the Madison River in June of 1994 and June and July of 1995 (Fig. 1). We sampled 15 sites downstream and nine sites upstream of Ennis Reservoir (Fig. 1). One-meter wide transects were chosen because very few salmonfly exuviae were observed further than 1 m from the water's edge. We selected transects that were free of obstructions and contained recently shed exuviae. Sites consisted of rocks or small cliffs, grassy areas, or willow areas. Sampling involved walking in the river along each transect and recording the number and sex of exuviae. Exuviae were then crushed and dropped into the river to avoid being recounted. To estimate the number of adult salmonflies produced per m^2 of river, we assumed that half of the last instar larvae cohorts crawled to each side of the river. Determination of exuviae gender was facilitated by dimorphic genitalia and size. Females have distinctly pointed epiprocts whereas males have rounded epiprocts; females also tend to be larger.

Wing Counts

Wings of recently emerged salmonflies were counted at seven sites in 1994 and one site, Eight-Mile Hole, in 1995, to estimate bird predation. The total number of wings at each site was divided by four, which is the number of wings on an adult salmonfly. This estimated the number of salmonflies eaten by predators that selectively remove salmonfly wings.

Substrate Sampling and River Measurements

We conducted Wolman 100-pebble count substrate sampling (Wolman 1954) during late summer at three exuviae collection sites in the upstream section and seven sites in the downstream section in 1994 and 1995. From two to four transects were made at each site except the Norris Bridge site where only one transect was made because of the combination of high water velocity and depth D_{50}'s (median particle size) were estimated for each transect. Particles were categorized as 'embedded' or 'not embedded' and percent embeddedness was estimated at each transect. An estimate of river width was made at each exuviae collection site using a compass and tape measure (Hauer and Lamberti 1998) because many sections of the Madison River in the Beartrap Canyon were difficult to cross, even at low water.

Statistical Analyses

We used STATISTICA for Windows (Statsoft, Inc. 1995) for all statistical analyses. Student's *t*-test (two-tailed, equal variances) was used to compare larval weights and exuviae abundance. Correlation coefficients (Pearson R-values) and *P*-values were used to compare substrate size and percent stream embeddedness (arc sin transformed) with number of exuviae.

RESULTS

Larval Weights

Both female and male pre-emergent larvae were significantly heavier in the downstream section than in the upstream section of the river. Mean pre-emergent female larval weight was 1.83 g (± 0.20 SD, minimum = 1.35 g, maximum = 2.30 g, $n = 83$) in the lower section and 1.63 g (± 0.19 SD, minimum = 1.25, maximum = 2.05 g, $n = 45$) in the upper section, whereas mean male pre-emergent larval weight was 0.99 g (± 0.11 SD, $n = 78$) in the lower section and 0.83 g (± 0.9 SD, $n = 26$) in the upper section. Pre-emergent female salmonfly larvae in the lower section of the river were 1.85 X heavier than males. Larval sex ratio was 0.57 females: 0.43 males.

It appears that salmonfly larvae developed in two years downstream of Ennis Reservoir, but may have required an additional year upstream as judged by the weight-frequency distributions of female larvae (Fig. 2). Two distinct peaks corresponding to separate age classes were evident for larvae from the downstream reach, but the size distribution upstream was not as clear. A minor peak at 0.9-1.0 g may have indicated a separate year class, but may alternatively have been the result of sampling error, as numbers of individuals in these size classes were low. We also would expect this peak to be distinct and equidistant between the other two peaks to be considered a separate age class, but it overlaps broadly with the one-year old size class. Therefore, it remains unclear if two or three age classes of larvae were present in the upstream section.

Most of the female larvae (77.1 %) downstream of Ennis Reservoir were ≥1.4 g and large enough to emerge as adults and there was an absence of ≤0.5 g larvae. This can be seen as a right shift in the weight frequency distribution histogram (Fig 2). Upstream of Ennis Reservoir, the largest proportion (43.5 %) of female larvae were ≤0.7 g while only 27.2 percent were large enough (≥1.4 g) to emerge as adults (Fig 2).

Exuviae Abundances

Estimated number of adult salmonflies produced per m^2 in the upper Madison River was 2.58 (±2.21 SD) in 1994 and 8.25 (± 5.83 SD) in 1995. Estimated numbers of adult salmonflies produced per m^2 of river in the lower Madison River were 0.43 (± 0.32 SD) in 1994 and 1.37 (± 1.28 SD) in 1995. Numbers of exuviae decreased rapidly downstream of the Beartrap Canyon (sites 5, 6, 7, and 8 in Fig. 1) and Norris Bridge (site 9). No exuviae were found in 1994 and 1995 at the Cobblestone Fishing Access (site 13) and only one exuviae was found at Black's Ford (site 10) in 1995, none were found in 1994. Grey Cliff Fishing Access (site 12) produced only two exuviae in 1994 and 22 exuviae in 1995. In contrast, in the

Beartrap Canyon, the mean number of exuviae was 53.4 per transect in 1994 and 147.6 per transect in 1995. Mean numbers of exuviae in the upstream portion per transect (sites 1,2,3, and 4) were 120.9 in 1994 and 452.9 in 1995. McAtee Bridge (site 1) produced the most exuviae per transect at 620.0 in 1995.

Emergence times of adult salmonflies in the Madison River varied among sites and between years, with downstream emergence starting prior to upstream emergence. Emergence occurred 1-10 June 1994 in the lower Beartrap Canyon and 28 June to 11 July 1994 at Varney Bridge. In 1995 emergence occurred from 16-27 June in the lower Beartrap Canyon and 17-21 July at Varney Bridge. Male salmonflies typically emerged one or two days before females and male peak emergence usually occurred before female peak emergence.

Predation

Red-winged blackbirds (*Agelaius phoeniceus*) were the only species of bird observed that immediately removed wings of recently emerged salmonflies. Other bird species were not observed removing salmonfly wings. We did observe other bird species capturing adult salmonflies but were unable to get an estimate of predation rates. We counted 118 discarded salmonfly wings, representing 30 salmonflies during a 2-day collection period (29, 30 June, 1995) at the Eight-mile Hole study site. We collected 208 exuviae; therefore, at this study site an estimated minimum of 14.4 percent of adult salmonflies was captured by predators. Estimated predation ranged between zero and 15 percent at the other sites.

Substrate composition

Much of the substrate throughout the river, excluding the Beartrap Canyon section, was composed of cobbles, with six of nine sites having mean D_{50}'s in the 96 mm size class. Substrate sizes were not significantly different between the upstream and downstream sections of the river. In contrast, the percent of the substrate embedded with sand and silt was significantly higher in the lower section of the river (mean = 22.4 % embedded in the downstream section; mean = 6.3 % embedded in the upstream section; $P = 0.00$). Salmonfly exuviae abundance was significantly negatively correlated with percent substrate embeddedness (arc sin transformed $R = -0.70$, $P = 0.02$ for 1994 and $R = -0.63$, $P = 0.04$ for 1995, $n = 11$) but not significantly correlated with substrate size ($R = 0.45$, $P = 0.17$ for 1994 and $R = 0.46$, $P = 0.16$ for 1995, $n = 11$).

Crayfish Abundance

Crayfish were more abundant in the lower Madison River than in the upper Madison River. We caught 6.6 times as many crayfish per salmonfly larvae in the lower Madison River than in the upper Madison River in 1995. 200 crayfish were caught in the lower Madison River with 203 salmonfly larvae, whereas only 36 crayfish were caught with 241 salmonfly larvae in the upper Madison River.

DISCUSSION

If our density estimates are correct, then differences in salmonfly densities between the upper and lower Madison River are greater than we have demonstrated. If the upper Madison River salmonflies develop in 3 years, then we have sampled 1/3 of the population by using exuviae counts. Likewise, we have measured 1/2 of the population in the lower Madison River. Also, our estimates of predation probably under-represented the true mortality because we were unable to estimate the number of adult salmonflies captured by predators that did not remove the wings or that captured molting larvae.

Madison Dam (Ennis Reservoir) and Hebgen Dam (Hebgen Reservoir) on the Madison River (Fig. 1) have altered thermal regimes and patterns of discharge and run-off in downstream reaches. Elimination of 'flush flows' and the resulting changes to downstream ecosystems has been well documented in the Colorado River (Bureau of Reclamation 1995) and other river systems (Stanford and Ward 1984). The geology of the Beartrap Canyon section of the Madison River provides inputs of fine sediments to the lower Madison River. Without flood events, sedimentation is likely to increase in the lower Madison River with greater loss of salmonfly habitat.

Our observation of an accelerated 2 year life cycle in the downstream portion of the river support Fraley's (1978) findings on the effects of water temperature on macroinvertebrates in the Madison River. Effects of water temperature on periphyton, macroinvertebrate, and fish assemblages in the Madison River have been well documented (Dodds 1991, McMichael and Kaya 1991, Jourdonnais *et al.* 1992, Marcus 1980, Gillespie 1969, Brown and Kemp 1942, and Montana Fish, Wildlife, and Parks 1999). Daily water temperatures upstream and downstream of Ennis Reservoir are available from the U. S. Geological Survey and the Montana Department of Fish, Wildlife, and Parks.

Higher average water temperatures may have also allowed for the greater relative abundance of eurythermal crayfish in the lower Madison River, although sedimentation could also be important. Crayfish can compete with salmonflies for limited substrate habitat; however, crayfish were observed digging retreats under embedded cobbles in the lower Madison River. Salmonflies have never been observed digging retreats. Freilich (1991) reported that salmonflies avoid sand bottomed pools. Therefore, we suggest that as sediment levels increase, intra and inter-specific, pre-emptive competition may also increase. This study was conducted during a dry spring (1994) and a wet spring (1995); therefore, continued exuviae counts could help illustrate the relationship between abundance and discharge.

CONCLUSION

Salmonfly abundance, distribution, and life history differs, both spatially and temporally, between the upper portion and the lower portion of the Madison River. These differences can be attributed to both human and natural causes. Salmonflies are good bio-indicators of water quality, including sedimentation impacts and this study was designed to facilitate future monitoring of salmonflies.

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BIOLOGY OF THE FLATHEAD CHUB IN THE LOWER YELLOWSTONE RIVER, MONTANA

ABSTRACT

The flathead chub (Platygobio gracilis) (Cyprinidae), *which has declined in much of the Missouri River drainage, was investigated in 1997 by sampling with stationary nets at a mainstem irrigation diversion dam on the lower Yellowstone River, Montana. Total lengths of 1,327 chubs sampled ranged from 32 mm to 304 mm. Mean length of 71 known females (181 mm TL) was significantly greater than mean length of 145 known males (138 mm TL, P<0.05). Ages of 281 fish of both sexes ranged from one to seven years. Maximum ages of males and females were 5 and 7 years, respectively. Mean number of eggs per female (mean length, 186 mm TL; mean weight, 68.5 g) was 6,981; eggs were typically of two or more sizes per fish, indicating non-synchronous development. One large female had 36,150 eggs, of which 28,200 were fully developed. The presence of numerous chubs of diverse sizes and ages at the free-flowing, turbid lower Yellowstone River contrasts with declines in abundance at other more altered locations in the Missouri River basin.*

Key Words: Missouri River, fishes, *Cyprinidae*, fish ecology.

INTRODUCTION

The flathead chub *(Platygobio gracilis) (Cyprinidae)* is a small minnow inhabiting the interior plains region of the United States and Canada (Olund and Cross 1961). It is widespread in the United States throughout the Missouri and Lower Mississippi rivers and also is found in parts of the South Canadian River in Oklahoma and the Rio Grande in New Mexico. Its range in Canada extends from southern Saskatchewan and Alberta northward to the Mackenzie River drainage (Kucas 1978). The latitudinal distribution of the flathead chub is one of the most extensive of any North American freshwater fish.

Flathead chubs are found typically in turbid, alkaline waters with moderate to strong currents and naturally-fluctuating hydrographs (Olund and Cross 1961). Impoundments and channel alterations along much of the Missouri River have altered the hydrograph and decreased turbidity. These changes have reduced the amount of suitable habitat for the flathead chub and many other native fishes (Pflieger and Grace 1987, Hesse 1994). The species remains abundant, however, in the lower Yellowstone River and portions of the upper Missouri River (Hesse 1994) where suitable habitat remains.

We collected flathead chubs as part of a fish entrainment study at a major irrigation diversion canal on the Lower Yellowstone River that permitted investigation of aspects of this species' age, growth, fecundity, and food habits. Such information has been fragmentary and inadequate. Most reports on flathead chubs have focused on

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distribution and general habitat requirements (Cross and Moss 1987, Bramblett and Fausch 1991); only a few studies have addressed its biology (Martyn and Schmulbach 1978, Gould 1985, Hesse 1994). Our objective was to characterize the life history of this species in the Lower Yellowstone River.

STUDY SITE

The study was conducted at the Intake Diversion Dam and Canal, 25 km downriver from Glendive, Montana, on the lower Yellowstone River. The Intake Diversion Project was authorized in 1904 and under the Reclamation Act of 1902 to provide irrigation water for agriculture in the lower Yellowstone valley in eastern Montana and western North Dakota. It was constructed over the period 1905-1909. The project irrigates 22,312 ha of cropland that produces alfalfa, other hay crops, silage, and sugar beets (U.S. Bureau of Reclamation 1983).

Water is briefly retained at the Intake site by a low head dam across the main channel, and impounded water flows by gravity through 11 orifices into the canal. The canal is operated from May through September (U. S. Bureau of Reclamation 1983).

METHODS

Fish sampling

Three of the eleven canal orifices were sampled in 1997. Stationary nets of multifilament nylon (1.27-cm bar mesh) with bags narrowing to a cod end (0.64-cm bar mesh) were suspended over the orifices (on the canal side) and captured fish as they entered the canal. Nets were fished intermittently, day and night; chubs were sampled from 22 May through 29 August. The nets were typically set for one hour and checked immediately thereafter for fish. Numerous species in addition to flathead chubs were captured. We assumed that chubs sampled in the nets as they entered the canal were representative of the population in the river.

A total of 1,327 chubs was caught and measured for total length (TL) during the entire sampling season; 424 of these fish were also weighed. Age was determined for 281 fish, which included 27 males, 48 females, and 206 individuals of unknown sex. Sex was determined by visual examination of gonads for 145 males and 71 females, stomachs sampled for food items from 178 fish, and fecundity estimated for 53 female fish. Male fish were classified as mature based on the presence of large developed testes, usually with flowing milt; females were classed as mature based on the presence of large eggs loosely attached to the skein.

Age and growth

Scales for age determination were taken from immediately above the lateral line and posterior to the dorsal fin. Impressions of the scales were made on plastic slides (Clutter and Whitesel 1956). Scales were interpreted for age by counting annuli with the aid of a Biosonics Optical Pattern Recognition System (OPRS). We were not able to independently validate annuli because no other information on age of individual fish was available.

Fecundity

We separated egg samples from ovarian tissue and obtained an aggregate egg weight for each fish. Total weights of large, mature eggs and small, undeveloped eggs were recorded separately. Numbers of eggs of each size were estimated based on total weights of large and small eggs and the weights of random subsamples of 100 eggs of each size. The diameter of 25 eggs of each size from each female were measured with an ocular micrometer We attempted to assess maturation stage of different sizes of eggs from stained histological cross-sections of six samples of large and small eggs.

Food habits

Stomach contents were removed, examined under a dissecting microscope, and individual organisms identified when practicable. Contents were then filtered, patted dry, and weighed with an analytical balance. Mean weight of contents was expressed as a percent of body weight.

Statistical analyses

Linear regression methods were used to characterize length-weight relationships, and t-tests were used to compare slopes of regression lines and lengths of fish by sex (Steele and Torrie 1980). P<0.05 was required for statistical significance.

RESULTS

Fish lengths and weights

The 1,327 flathead chubs sampled ranged from 32 mm to 304 mm TL (mean, 147 mm TL). Lengths of fish were unimodally distributed with most fish 110-190 mm TL (Fig. 1). For fish of known sex (145 males, 71 females) from which length and weight were measured, mean length of females (181 mm TL) was significantly greater than of males (138 mm TL, t-test; P<0.05). No significant difference was found in the slopes of length-weight relations for males and females (*t*-test, *P*>0.05), so known males and females were combined with 208 fish of unknown sex to create one combined length-weight relation (Fig. 2).

Age and growth

Ages of 281 fish, which had total lengths of 86-266 mm, ranged from one to seven years. The youngest mature males were age-1, and the youngest mature females were age-2. The overall proportion of fish of each age that was mature was not accurately determined because of small sample sizes of fish of known sex and age. None of 27 males were older than age-5, although seven females out of the 48 fish of known sex were ages 6 or 7.

Mean lengths of fish at the time of sampling were 108 mm TL at age-1+ (i.e., with one annulus plus any post-

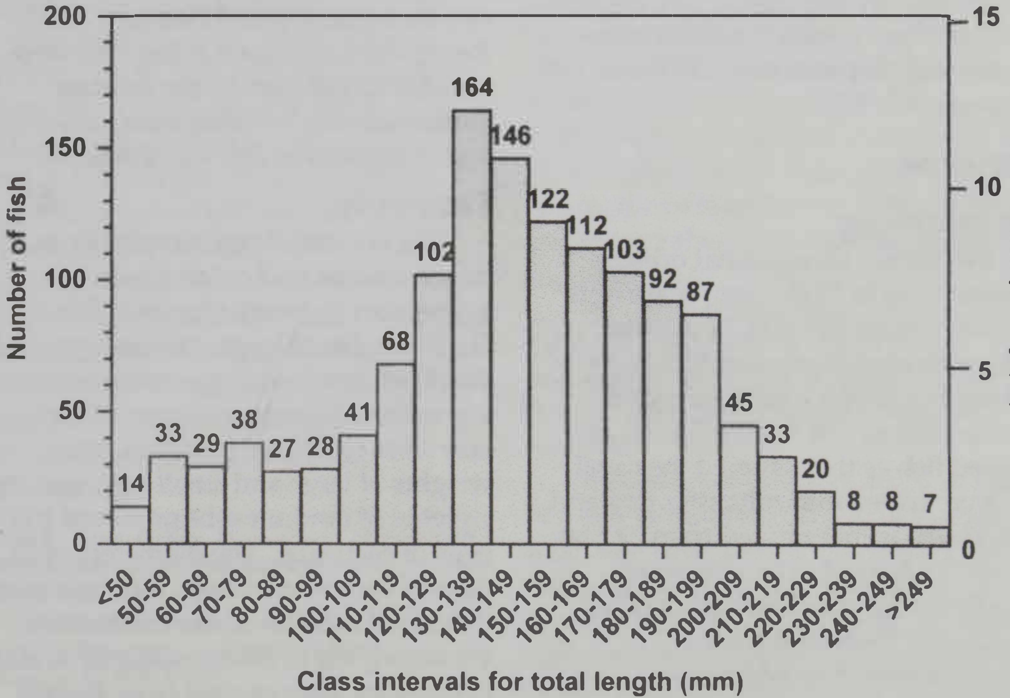

Figure 1. *Length-frequency distribution of flathead chubs (n = 1,327) sampled 22 May - 29 August, 1997, at the Intake Diversion Canal.*

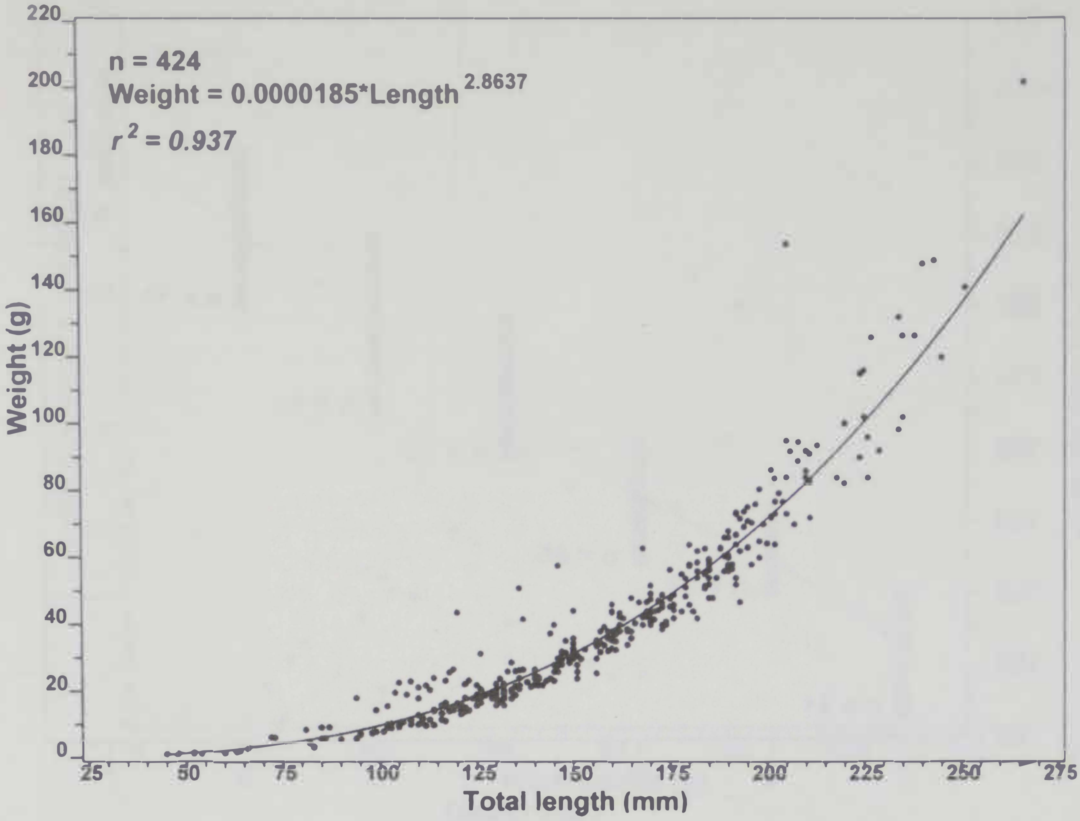

Figure 2. *Combined male and female length-weight relation for flathead chubs, Intake Diversion Canal.*

annulus growth), 129 mm at age-2+, 147 mm at age-3+, 164 mm at age-4+, 196 mm at age-5+, 221 mm at-age 6+, and 246 mm at age-7+. Considerable overlap existed in length for a given age. Length increments did not decrease with age (Fig. 3).

Fecundity

We observed no countable developed eggs in 11 of 53 (21%) female fish dissected to determine fecundity. Two of these 11 females were small (107 and 127 mm TL), and the other nine females ranged from 146 to 218 mm TL. Because these nine females were caught late in the sampling season (29 July-21 August), absence of developed eggs indicated that each had already spawned.

We observed that eggs in many specimens occurred in two distinct size classes (large and small) based on diameter; some specimens seemingly had a range of egg sizes. Thirty-four of 42 (81%) females with developed eggs contained two different sizes of eggs falling into two size categories that slightly overlapped in diameter. Twenty-nine samples with both large and small eggs contained predominantly (>50%) large eggs. Lengths of these fish ranged from 133 to 251 mm TL (mean, 187 mm). Five samples (14%) contained predominantly (>50% by number) small eggs. Lengths of these fish ranged from 122 mm to 211 mm TL (mean, 179 mm). Eight of 42 fish contained only one size class of eggs; seven had only small eggs and one had only large eggs.

The total number of eggs per fish peaked in late June. Mean weight of all eggs combined was 5.4 grams, or 7.8 percent of mean body weight. The largest number of eggs in an individual fish was 36,150 of which 28,200 were

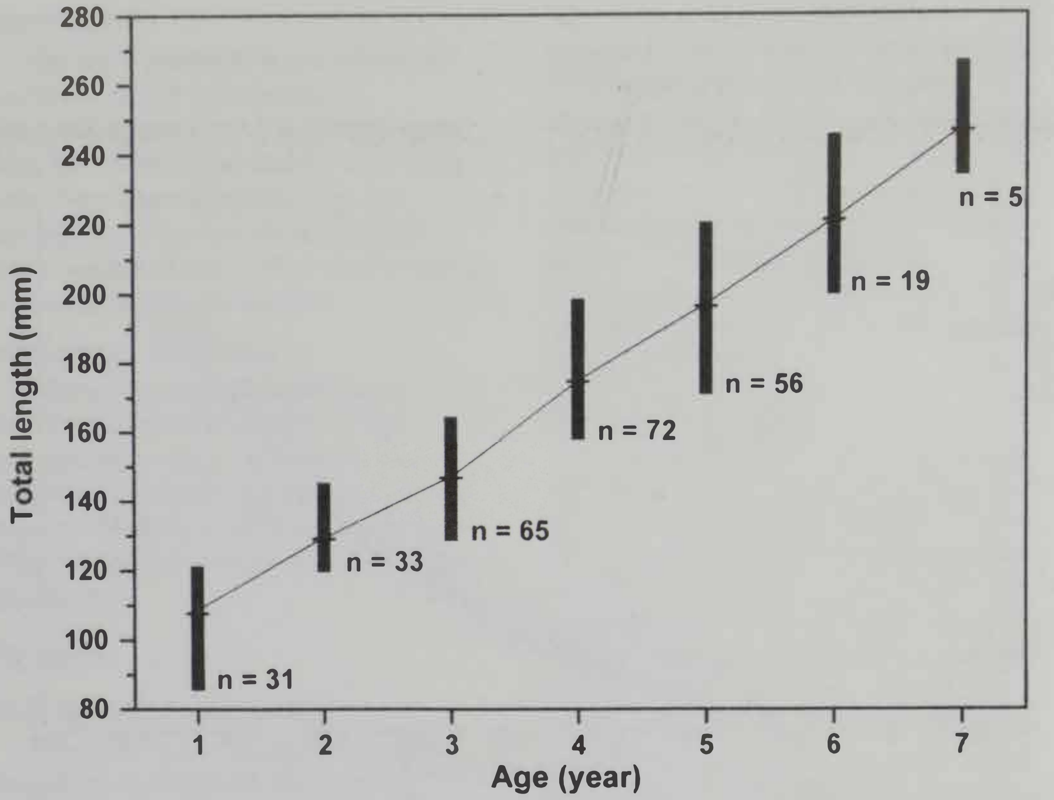

Figure 3. *Mean lengths and range of lengths by age, flathead chubs, Intake Diversion Canal.*

large eggs. Egg numbers were highest in a few fish aged 4 and 5. Mean total number of eggs per specimen (mean length 186 mm TL, mean weight 68.5 g) was 6,981, of which about 58 percent were large eggs. Large eggs were typically greater than 1 mm in diameter (mean, 1.11 mm) and small eggs typically less than 0.8 mm in diameter (mean, 0.41 mm). Large and small eggs occurred over a large range of fish lengths and ages. The relation between fish weight and estimated fecundity was positive but not close (Fig. 4); it was obscured by the apparent spawning activity during the sampling period.

Histological analysis of cross sections indicated that the different sizes of eggs (both large and small) were at intergrading stages of development. There was no evidence that the eggs were in the process of being reabsorbed.

Food habits

Only three of 178 stomachs examined contained identifiable organisms. Sixty-seven stomachs were empty. Identifiable organisms were insects in the orders Coleoptera, Hymenoptera, Orthoptera, and Trichoptera. Contents of all other stomachs were masticated beyond recognition, a mixture of organic debris and invertebrate parts. Stomach contents constituted an average of 0.26 percent of the total fish weight. Larger fish of both sexes tended to have greater weight of stomach contents. There was no evidence of a consistent seasonal pattern to stomach fullness.

DISCUSSION

The ages at first maturity of fish in our study (age-1 for males, age-2 for females) were similar to those reported from a small Missouri River tributary in Iowa (Martyn and Schmulbach 1978) where maturation occurred mostly at age-2. Lengths of mature fish in their

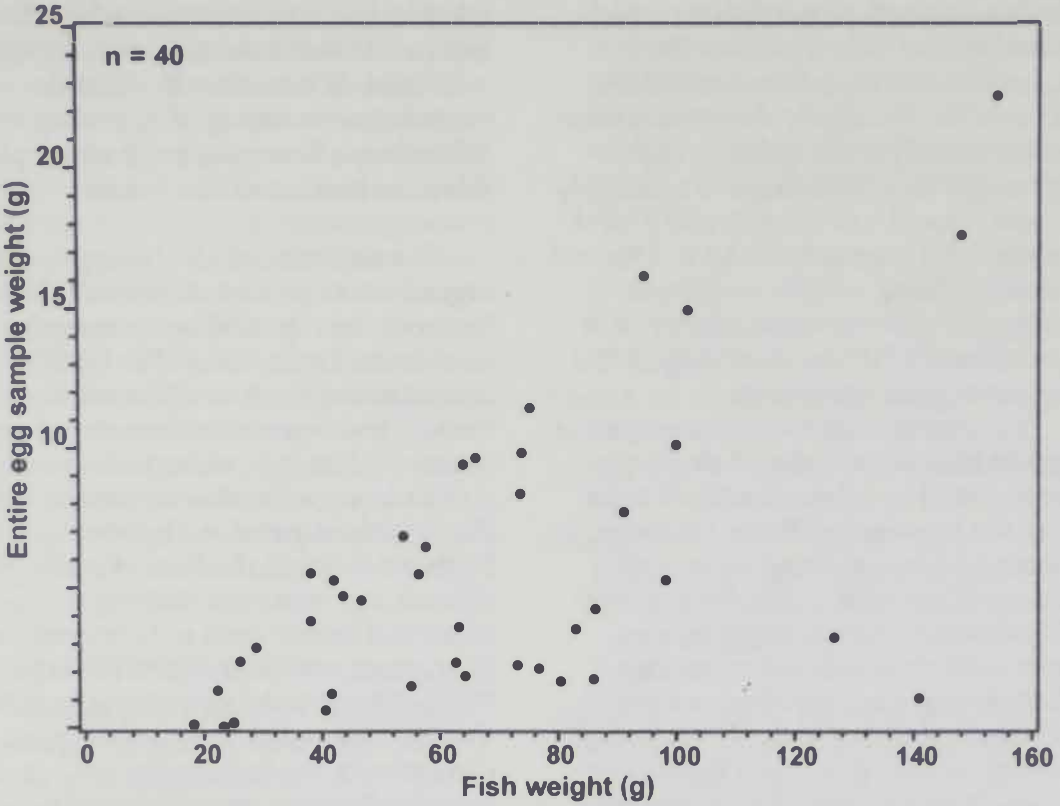

Figure 4. *Relation between flathead chub weight and weight of eggs, Intake Diversion Canal.*

study exceeded 127 mm TL, whereas in our study, the smallest mature female was 107 mm TL. Gould (1985) reported that flathead chubs from the Musselshell River, Montana, fell into three size groups although he was unsuccessful in determining the age of specimens using scales, opercula, or vertebrae. He concluded that maturation occurred at age-3 based on sizes of mature fish.

Sexual size dimorphism was evident in flathead chubs. Females lived longer, grew larger, and matured at an older age than males. Most freshwater fishes show a larger-female dimorphism to some extent, thereby permitting higher fecundity in large females (Bell 1980). The rarer larger-male pattern is more characteristic of clearer waters where courtship pairing has strong visual cues, and would be expected to be absent in fishes inhabiting more turbid waters. However, no information is available on the spawning behavior of flathead chubs (Gould 1985).

Our ability to age flathead chubs with scales contrasted with Gould (1985), whose efforts were unsuccessful. We experienced difficulty in using scales to age flathead chub in this study but detected annuli only within a small anterior portion of the scale. Scales from two other areas of the body (above the lateral line posterior to the head, and immediately posterior to pectoral fins) were also evaluated for use in age determination. These scales proved typically smaller and the circuli even more closely packed than those from our preferred location (above the lateral line and posterior to the dorsal fin).

Fecundities of fish in this study (mean, 6,981 eggs) were much higher than reported by Gould (1985, <1,000 mature eggs/fish) and Martyn and Schmulbach (1978, mean = 4,974 eggs). Much of this difference is attributable to larger fish in our samples. The largest fish reported by Martyn and Schmulbach (1978) was 172 mm TL and the largest by Gould (1985) was 160 mm

TL. Mean length of our fish for which fecundity was estimated was 186 mm TL, and 15 fish were between 200 and 255 mm TL. Fecundity differences were not necessarily attributable to higher egg weight as a percentage of total body weight. Gould's (1985) fish had gonad weights that ranged from 2.3 to 5.9 percent of body weight, our 40 fish averaged 7.8 percent, and Martyn and Schmulbach's (1978) fish averaged 10.3 percent at peak spawning.

The presence of two or more sizes of eggs in individual flathead chubs was not reported by other authors. Chubs from the Musselshell River, Montana, contained a range of egg sizes at all seasons (Gould 1985), but the presence of both small and large eggs in an individual chub was not mentioned. Multiple egg sizes are often associated with fractional and multiple spawning, which is common in many freshwater fishes. It may increase fitness through repeated use of the available body cavity for holding eggs. (Matthews 1998).

The reasons for the non-synchronous egg development in flathead chubs are not clear. The chub is developing eggs of several stages at the same time, of which two or more sizes probably will be spawned in a single season. Although spawning of this species is poorly known, the non-synchronous egg development in the flathead chub may be adaptive in river habitats where peak discharge and optimal spawning condition vary yearly by a month or more. We have observed other species in the Yellowstone River, including paddlefish (*Polyodon spathula*) and shovelnose sturgeon (*Scaphirhynchus platorynchus*) to spawn over periods exceeding a month, depending on river discharge. The collection of spawned-out females from 29 July to 21 August is consistent with previous studies (Olund and Cross 1961, Martyn and Schmulbach 1978) indicating spawning between late June and early September, depending on location. For definitive conclusions and reliable data on maturation schedules, individual chubs should be monitored over time. It is unclear if a relation exists between timing of spawning and Yellowstone River discharge although this identifies a need for future investigation.

The difficulty of identifying specific organisms in the diet of flathead chubs has not been reported by investigators elsewhere. Davis and Miller (1967) characterized them as a "fortuitous feeder" and a generalist based on anatomical and physiological comparisons with other minnows, but did not investigate food habits. Flathead chubs in the Peace River, Alberta, fed mainly on drifting terrestrial insects such as Hymenoptera, Hemiptera, and Trichoptera (Bishop 1975). Olund and Cross (1961) reported that the flathead chub was chiefly carnivorous, feeding mostly on terrestrial insects and occasionally vegetation. Their sample sizes were <10 fish per location at seven sites throughout the Great Plains (Canada to New Mexico), however, and many stomachs contained no food (their Table 1). Inasmuch as other non-minnow species sampled at the Intake Canal contained identifiable organisms, the advanced state of digestion of the stomach contents in our study was probably aided by the hooked pharyngeal teeth of the chubs (Olund and Cross 1961). Other methods such as visual observation must be used to adequately determine food habits of these fish.

The presence of chubs of all sizes and ages in the turbid, unimpounded Yellowstone River contrasts sharply with declines or disappearance of this species at other Missouri River locations (Pflieger and Grace 1987, Hesse 1994). Pflieger and Grace (1987) reported that flathead chubs have suffered a large decline in the lower Missouri River since the 1940s coincident with declines in turbidity, a result of upriver impoundment. They suggested that declines in chub abundance may have resulted from increased predation from sight-feeding predators and increased competition from other minnows favored by clearer waters. The turbid, unimpounded discharge of the lower Yellowstone River may be a significant factor in the high chub abundance and year-class diversity observed in our study. As plausible as such speculation may be, the actual cause(s) of declines elsewhere may be difficult to determine in the large-river habitats of flathead chubs. In view of the disappearance of these fish from other altered and impounded locations in the Missouri River drainage, maintenance of a natural hydrograph and turbidity should be considered vital to the conservation of this species.

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BISON FORAGE UTILIZATION IN THE UPPER MADISON DRAINAGE, YELLOWSTONE NATIONAL PARK

ABSTRACT

*We monitored bison (*Bison bison*) use of forage on winter ranges in the Madison, Gibbon, and Firehole drainages of Yellowstone National Park (YNP) to determine how bison used wintering areas in these drainages and to determine if use patterns had detectable impacts on standing biomass. Bison were observed in wintering areas in the three drainages during all seasons of the year. Probability of bison occupying individual sites on a given day within the area during summer, autumn, winter, and spring, 1996-1997 ranged from 0-40 percent, 0-29 percent, 0-91 percent, and 0-67 percent, respectively. Sites identified as historic high use areas had high frequency of use (78 and 91%) during the 1996-1997 winter. Two sites identified as historic medium winter use had lower frequency of use (56%), and sites identified as historic low use areas had no observed use during the 1996-1997 winter. Exclosure cages placed at the six sites allowed us to estimate forage removal during summer 1996 through summer 1997. Over all sites and sampling periods, plots exposed to grazing had 23 percent less biomass (dry weight) than plots protected from grazing. Bison use at individual sites was weakly correlated ($r=0.28$, $P=0.05$) with estimated forage utilization and more strongly correlated with estimated grams of forage removed ($r = 0.55$, $P <0.01$). Despite high variability in vegetation biomass within sites, we did identify one site, Terrace Springs, as heavily impacted by bison foraging during summer. A reduction of >50 percent in bison numbers in the Madison, Gibbon, and Firehole drainages between summer 1996 and summer 1997 did not reduce foraging pressure on the Terrace Springs site.*

Key words: **bison, *Bison bison*, forage utilization, Yellowstone National Park.**

INTRODUCTION

Management of ungulates in YNP has been contentious since the Park was founded (Tyers 1981). Current controversies involve arguments over the impacts of ungulates on vegetation (Houston 1982, Kay 1990 1998, Kay and Wagner 1994, Coughenour 1991, Coughenour et al. 1994, Singer et al. 1994, 1998, Wagner et al. 1995, Boyce 1998, Wambolt 1998) and the potential for bison, and to a lesser extent, elk (*Cervus elaphus nelsoni*), to transmit brucellosis to domestic livestock when they leave the Park (Cheville et al. 1998). Arguments over cause and effect have polarized natural resource groups that generally agree on the need for conservation. Some range and wildlife managers advocate allowing ungulate populations in YNP to change with minimal human interference (Houston 1982, Dobson and Meagher 1996, Boyce 1998). Other biologists view ungulates in YNP as prime candidates for human-sponsored population regulation (Kay and Wagner 1994, Wagner et al. 1995, Kay 1998). If ungulates are controlled by human actions, careful consideration

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should be given to determining what densities are appropriate. Wright (1998) noted that visitors to national parks expect to see large numbers of animals. In parks such as YNP, visitor satisfaction is closely linked to seeing numerous large mammals such as bison. If moderate reduction in large herbivores fails to remedy impacts on plant communities and/or problems associated with egress of animals from YNP, management efforts would be wasted. If large mammals were reduced to very low densities or if fencing were introduced to protect plant species or inconspicuous vertebrates, vocal criticism by visitors who value seeing large free-roaming animals can be expected, and management costs would markedly increase.

We describe how bison used one area of the Park, and we attempted to determine if bison herbivory had detectable impacts on forage biomass at specific sites within this area. Our study sites were located in the Madison, Gibbon, and Firehole drainages, an area in which large scale movement outside YNP is a recent phenomenon (Meagher 1998). Our study encompassed one growing season in which bison numbers were close to record highs, a severe winter in which bison numbers were reduced by starvation and control actions outside YNP by nearly 40 percent, and one relatively wet growing season post-population reduction.

Studies of ungulate foraging on seasonal ranges associated with YNP's northern winter range suggested that herbaceous plants are heavily grazed in winter, but subsequent regrowth is not affected by this utilization except under drought conditions (Frank and McNaughton 1992, Singer and Harter 1996). Woody species on the northern winter range are evidently much more heavily impacted by ungulate herbivory (Kay 1990, Singer et al. 1994, Singer and Cates 1995, Wagner et al. 1995, Wambolt 1998). Impacts of ungulates on summer ranges associated with the northern winter range are difficult to detect (Frank 1990, Norland, pers. commun.). No data in these studies specifically addressed the impacts of bison forage utilization (including feeding and trampling). No data on impacts of forage utilization by any ungulates were available for the smaller winter ranges associated with the Madison, Gibbon, and Firehole Rivers, but Meagher (1998) noted increasing use of these areas over the past decade in non-winter months.

STUDY AREA

Study sites were located in the Madison, Gibbon, and Firehole drainages in the northwest corner of YNP (Fig. 1). Elevations in riparian corridors varied from 2,079-2,252 m. The corridors were characterized by gentle to moderate slopes supporting lodgepole pine (*Pinus contortus)* forests with a mixture of open meadows, shrub communities, forests, and geothermal features along the floodplains (Craighead et al. 1973). The climate is cold, continental with cool summers, cold winters, and high snow accumulation.

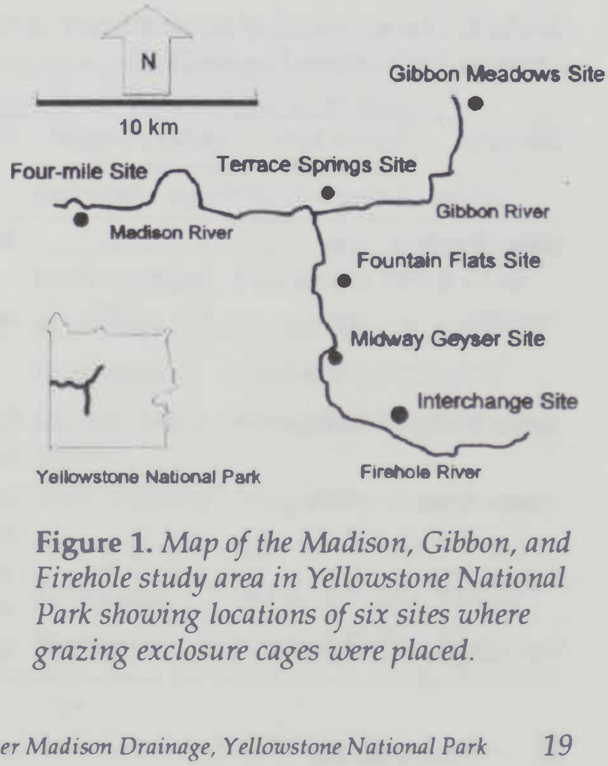

Figure 1. *Map of the Madison, Gibbon, and Firehole study area in Yellowstone National Park showing locations of six sites where grazing exclosure cages were placed.*

All sites where we placed exclosures were in open meadows or shrub lands, the physiographic types favored by bison in YNP (Meagher 1973, Reynolds et al. 1982, Norland et al. 1985, Ferrari 1998). Sampling was conducted at six sites (Fig. 1) selected to reflect low, medium, and high bison use during winters prior to the study (Bob Siebert, pers commun., Bob Garrott, pers commun.). Characteristics of each site are given in Table 1. The Gibbon Meadows site was located in a high snowfall area and was identified as a low winter-use area. The Four Mile site, also a low winter-use area, was primarily a movement corridor used lightly during early winter and spring. Both moderate winter-use sites, Terrace Springs and Midway Geyser, were thermally influenced. In both sites, riparian areas supported much more dense vegetation than the active (Terrace Springs) or fossil (Midway Geyser) thermal areas. The two sites with historic heavy winter-use, Fountain Flats and Interchange, were in meadows along the Firehole River but not closely associated with the river. Both had areas of standing water throughout the year.

METHODS

We used visual observations to provide an index of ungulate presence at sites and exclosure cages to measure ungulate effects on standing biomass. Ground counts of bison and elk within 100 m of the exclosure cages in each site were made weekly from May 1996 through August 1997. Results were expressed as proportions of counts with bison or elk near sites and as bison or elk-days per sampling period (mean animals per count during each period multiplied by the number of days between cage placement and clipping). We calculated an index of total ungulate use, animal unit-days, by adding mean bison sightings to mean elk sightings divided by 1.4. This conversion approximated the ratio of daily dry weight forage consumption by an average individual in a bison herd (6.7 kg) to an average individual in an elk herd (4.9 kg) (Westfall et al. 1993).

Exclosure cages were clustered in 2-9 ha areas in each site to facilitate relocation and to minimize visibility to Park visitors. Cage construction and clipping treatments were modified from procedures described by Brown (1954)

Table 1. *Characteristics of six sites where exclosure cages were placed in the Upper Madison drainage, Yellowstone National Park.*

Site name	Historic winter use level	Hectares sampled		Community type	Dominant plant species
		Forage	Animal use		
Gibbon Meadows	Low	2	9	Wet meadow	Bluegrasses (*Poa* spp.) Sedges (*Carex* spp.)
Four Mile	Low	9	25	Shrub grassland	Big sagebrush (*Artemisia tridentata*) bluebunch wheatgrass (*Agropyron spicatum*)
Terrace Springs	Medium	9	25	Dry to mesic riparian meadow	Kentucky bluegrass (*Poa pratense*) Mixed forbs
Midway Geyser	Medium	2	9	Dry to mesic riparian meadow	Western wheatgrass (*A. smithii*) /sedge/ rush (*Juncus* spp.)
Fountain Flats	High	9	25	Thermal springs/ wet meadow	Beaked spike-rush (*Eleocharis rostellata*)
Interchange	High	4	16	Wet meadow	Beaked spike-rush

and Frank and McNaughton (1992). One hundred exclosure cages, measuring 1.2 x 1.2 x 1.5 m^2, were constructed using cattle panels and steel fence posts. Twenty more cages, measuring 1.8 x 1.8 x 1.8 m^2, were available from a previous study. We estimated the number of cages needed per study site and the size of plots clipped within cages based on variances in biomass estimates given by Frank (1990). He identified grazing effects in subjectively chosen sites using 5-7 caged plots per site and a double-sampling method that employed plant intercepts by pins as a surrogate for actual measurement of plant biomass. We increased the number of plots per site to 10 or 20 for individual seasonal samples and based our biomass estimates on vegetation clipped in 0.33-m^2 circular plots. The mesh size on the fencing (15x15 cm) precluded bison muzzle entry into the exclosures. The 0.33-m^2 plot clipped within each cage left a minimum space of 27 cm from the edge of the clipped plot to the exclosure fencing. This distance minimized potential cage effects and prevented deer and elk from grazing in areas we clipped. Cage effects were not measured but were expected to be small for the relatively short time intervals of exclosure and for the habitat types that we were sampling (Frank 1990, Irby, unpublished data).

In June 1996 20 cages per study site were randomly placed using an XY coordinate system to form a grid that allowed us to move cages within a grid cell at least six times (Table 2) without intercepting areas covered by cages in previous time periods. At each site, 10 cages were randomly selected as season-long sample units and 10 other cages as partial-season sample units. Partial-season cages were moved at 6-12 week intervals during the growing season (May-October). Fixed cages were left in place through the growing season. This allowed us to identify when grazing occurred during the growing season (partial-season samples), provided a crude indication of the ability of regrowth to compensate for early grazing (late-summer samples), and provided an estimate of the net effects of restricting access to forage for the whole growing season (season-long samples). All cages were left in place from November 1996 to May 1997. When cages were moved, the

Table 2. *Sampling scheme used to estimate utilization of herbaceous vegetation during eight time intervals for six sites in the Madison, Gibbon, and Firehole River drainages, Yellowstone National Park, 1996-1997.*

Period when vegetation was clipped	Exclosure period	Sample type	Utilization period measured
5-10 July 1996	1 Jun - 10 Jul 1996	Green vegetation	Early summer 1996 (6-7 wks)
15 Sep - 20 Oct 1996	15 Jul - 15 Sep or 15 Oct 1996	All vegetation	Late summer 1996 (8-12 wks)
15-20 Oct 1996	20 May - 20 Oct 1996	All vegetation	Summer 1996 (20-21 wks)
10-15 May 1997	20 Oct 1996 - 10 May 1997	Residual (dead) vegetation	Winter 1996-1997 (29-30 wks)
10-15 May 1997	April - May 1997	Green vegetation	Spring 1997 (6-7 wks)
5-10 Jul 1997	15 May - 10 July 1997	Green vegetation	Early summer 1997 (6-7 wks)
25-30 Aug 1997	10 Jul - 30 Aug 1997	All vegetation	Late summer 1997 (6-7 wks)
25-30 Aug 1997	15 May - 30 Aug 1997	All vegetation	Summer 1997 (13-14 wks)

new location was 2-4 m north (a random direction chosen at the beginning of the study) of the old location.

Vegetation samples collected inside and outside cages consisted of all standing plant material within circular, 0.33-m^2 plots. Samples were clipped with garden shears to approximately 13 mm above ground level. Plots outside of cages were always clipped 1 m from the eastern exclosure wall. Clipped material was separated into live (photosynthetic) and dead (non-photosynthetic) biomass. Vegetation samples were stored in paper bags and transported to drying facilities in YNP or at Montana State University. Clipped samples were oven-dried at 60° C for 48 hrs and weighed using an Ohaus electronic scale with an accuracy of ± 0.1 g.

We used Wilcoxon's ranked sum tests to compare standing biomass inside and outside individual exclosure cages using the S-PLUS statistical package (MathSoft 1999). Corrections for continuity were used when ties occurred in comparisons. Comparisons were made for each site in each of eight designated seasons (Table 2). To better illustrate forage utilization, we converted dry weights to percent differences between protected and unprotected plots in graphic displays of data. This difference was expressed as "percent utilization" (inside biomass-outside biomass/ inside biomass X 100). Because we paired plots on a spatial basis rather than subjectively pairing plots with similar vegetation, as Frank (1990) did, negative values (i.e., more biomass in unprotected plots than in paired protected plots) were possible. We truncated mean percent differences to a range of 0 to 100 percent in graphs to eliminate negative means. We assessed the association between bison and/or elk presence and estimated forage utilization by calculating the correlation between bison-days, elk-days, and animal-use days (bison + elk) per hectare and two response variables (mean difference between vegetation protected by cages and vegetation exposed to ungulate grazing [expressed as grams per 0.33 m^2] and estimated percent forage removal at individual sites) (Steel and Torrie 1960).

RESULTS

Bison numbers in the study area during 1996 and 1997 were highly variable due to movement of animals through the area. The Madison, Firehole, and Gibbon drainages served as a corridor connecting bison habitat in the Hayden Valley with habitat outside the west boundary of YNP. During winter and spring 1997, ground censuses yielded counts of 504 (May 1997) to 1,102 (January 1997) bison in the Madison, Gibbon, and Firehole drainages (Ferrari 1998). Approximately 400 bison were removed by control actions along the west boundary during winter 1996-1997 (Gogan, unpubl. data), and up to 100 died of starvation within the study area (M. Ferrari and R. Garrott, pers commun.). Fewer bison were in the area during summer. We were unable to make total counts during the 1996 and 1997 summers, but our weekly counts along roads paralleling the 3 drainages averaged 42 bison/count (n = 22) during June - October 1996 and 12 bison/count (n = 16) during May-August 1997 (Dawes 1998).

We observed bison and elk in open areas within the riparian corridor along the Madison, Firehole, and Gibbon Rivers in all seasons of the study. Bison were observed at one or more of the six sites where we placed exclosure cages on 32 of 59 counts (54%). Total numbers of bison sighted ranged from 0 to 168 individuals per count. We recorded the highest frequency of counts with one or more bison sighted in winter and spring 1997 (Fig. 2) and the lowest frequencies in late summer 1996 (17% of counts)

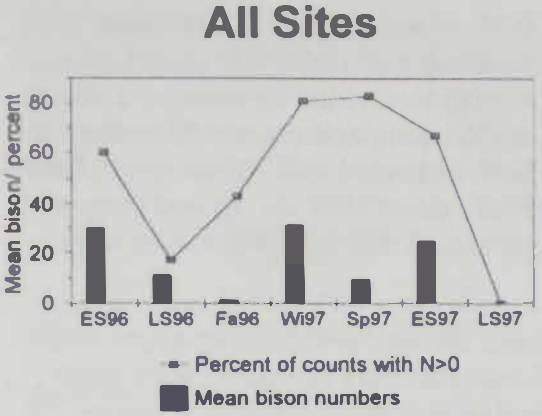

Figure 2. *Frequency of bison sightings at one or more of six sites and number of bison sighted per count in the Madison, Gibbon, and Firehole drainages, Yellowstone National Park, 1996-1997. Period designations (number of counts per period) are: ES96 (5) = 16 June - 19 July 1996; LS96 (12) = 20 July - 12 October 1996; Fa96 (7) = 13 October - 30 November 1996; Wi97 (16) = 1 December 1996 - 31 March 1997; Sp97 (6) = 1 April - 15 May 1997; ES97 (6) = 16 May - 5 July; LS97 (7) = 6 July - 31 August 1997.*

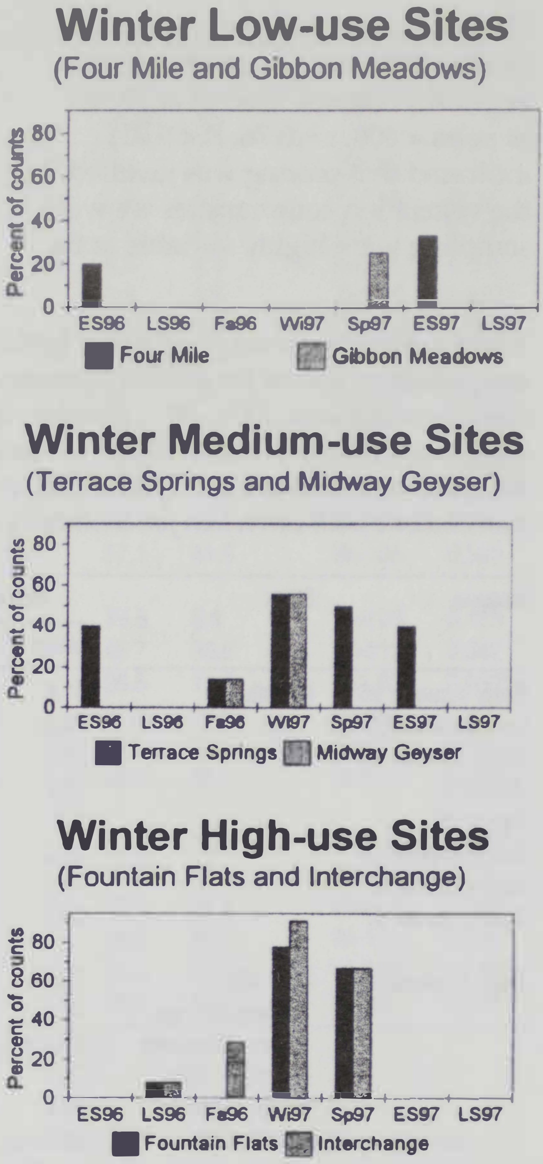

Figure 3. *Frequency of sightings of bison at individual sites in the Madison, Gibbon and Firehole drainages, Yellowstone National Park, 1996-1997. Seasonal designations are given in Figure 2.*

and 1997 (no bison observed). Mean numbers of bison per count were highest in early summer (1996 and 1997) and winter (Fig. 2). We observed elk at two of our sampling sites (7 elk total) during the summer and early autumn of 1996, four of the six sites during winter (a total of 77 elk counted), two sites during spring (6 elk total), and at one site during summer 1997 (8 elk total).

We only observed bison at the two sites with historic low levels of winter use by bison (Four Mile and Gibbon Meadows) during spring and early summer. Bison were observed <35 percent of counts at the two sites during these periods (Fig. 3). Bison were observed on both sites with historic moderate winter-use (Terrace Springs and Midway Geyser) in 56 percent of winter counts in 1997 (Fig. 3). Frequency of use of the Midway Geyser site was only high in winter. Bison frequently used Terrace Springs in spring and early summer as well as winter. Bison were recorded at historic high winter-use sites in 78 percent and 91 percent of winter counts for the Fountain Flats and Interchange sites, respectively. Frequency of use of these sites also was high in spring (Fig. 3).

Over all sites, graminoids made up 77 percent, forbs 23 percent, and shrub leaves <1 percent of vegetation biomass.

The correlation between vegetation biomass inside and outside cages in vegetation classes used in analyses (n pairs = 600, r = 0.76, $P < 0.01$) indicated that pairing was justified, but the vegetation communities we were sampling were highly variable at the 0.33-m^2 scale (Table 3). The mean coefficient of variability (standard deviation divided by mean) for site by season comparisons was 83 percent for both protected and unprotected plots. Mean dried biomass clipped from plots protected from grazing varied from

Table 3. *Mean dried weight of forage (g/0.33m^2) and standard deviations on means inside and outside exclosures for all sites by season and individual sites by season for the upper Madison study area, 1996-1997. Numbers of paired values used to calculate means are 10/site for summer samples and 20/site for winter/spring samples. Test statistics for a 1-tailed Wilcoxon=s rank-sum test (H_a: In > Out) are W (rank-sum statistic, no ties) and Z (rank-sum statistic with correction for continuity for tests including ties).*

Season	Sites	Inside		Outside		Test statistic	1-tailed P
		Mean	SD	Mean	SD		
Early summer 96	(All sites)	41.6	30.9	31.1	24.7	Z=1.99	0.024*
Late summer 96		30.2	29.5	28.1	30.5	Z=0.39	0.350
Total summer 96		29.1	22.7	21.2	18.5	Z=2.19	0.014*
Winter 97		18.7	31.1	9.7	15.6	Z=1.19	0.116
Spring 97		8.2	11.3	5.0	4.6	Z=1.71	0.044*
Early summer 97		35.2	29.5	28.8	28.4	Z=1.45	0.074*
Late summer 97		46.1	41.6	38.7	32.0	Z=0.79	0.215
Total summer 97		46.6	33.4	41.6	35.0	Z=1.13	0.130
Early summer 96	Four Mile	23.4	17.8	17.4	9.9	W=114	0.264
	Terrace Springs	47.4	30.2	21.2	12.0	W=130	0.032*
	Gibbon Meadows	37.9	18.6	28.4	10.0	W=117	0.196
	Fountain Flats	33.7	24.1	24.0	19.4	W=115	0.240
	Midway Geyser	45.5	53.4	42.1	44.2	Z=- 0.45	0.675
	Interchange	61.9	16.9	53.6	16.7	Z=1.10	0.136
Late summer 96	Four Mile	10.3	4.3	11.6	9.7	Z=0.19	0.425
	Terrace Springs	26.5	16.5	17.5	11.3	W=120	0.140
	Gibbon Meadows	29.4	13.6	29.6	10.4	W=103	0.456
	Fountain Flats	10.1	11.2	13.5	13.6	W=95	0.241
	Midway Geyser	50.5	53.1	43.9	57.6	Z=0.76	0.225
	Interchange	53.7	18.4	52.7	25.8	W=107	0.456
Total summer 96	Four Mile	17.9	12.6	11.2	4.9	W=119	0.158
	Terrace Springs	24.7	17.8	9.5	4.7	W=135	0.012*
	Gibbon Meadows	37.9	17.4	21.9	14.9	Z=2.16	0.016*
	Fountain Flats	12.2	6.8	19.1	14.7	W=94	0.218
	Midway Geyser	26.9	30.1	17.8	18.3	Z=1.10	0.136
	Interchange	54.9	18.4	47.9	19	Z=0.38	0.352
Winter 97	Four Mile	2.7	3.4	2.3	3.3	Z=-0.18	0.571
	Terrace Springs	1.9	3.5	1.5	3.6	Z=0.72	0.236
	Gibbon Meadows	16.2	14.2	15.8	12.5	Z=-0.23	0.580
	Fountain Flats	16.0	26.4	10.2	16.3	Z=0.30	0.380
	Midway Geyser	7.6	18.2	<0.1	0.2	Z=1.48	0.069*
	Interchange	68.1	39.5	28.4	21.5	Z=3.63	< 0.001*

Table 3. *(Cont.)*

Season	Sites	Inside		Outside		Test statistic	1-tailed P
		Mean	SD	Mean	SD		
Spring 97	Four Mile	12.0	7.4	5.4	2.7	Z=3.67	< 0.001*
	Terrace Springs	8.0	5.5	5.9	4.3	Z=1.15	0.125
	Gibbon Meadows	3.6	4.1	3.7	5.7	Z=0.77	0.220
	Fountain Flats	7.7	9.8	4.3	3.9	Z=0.26	0.398
	Midway Geyser	15.1	21.5	5.8	4.9	Z=1.85	0.032*
	Interchange	3.2	6.1	5.3	6.0	Z=-2.16	0.980
Early summer 97	Four Mile	28.3	20	24.7	14.2	Z=0.15	0.440
	Terrace Springs	37.1	25.6	14.4	9.9	Z=1.97	0.025*
	Gibbon Meadows	24.9	15.5	25.3	13.5	Z=0.01	0.500
	Fountain Flats	23.9	25.6	16.5	19.1	Z= 0.07	0.248
	Midway Geyser	41.0	30.8	35.5	37.1	W=116	0.218
	Interchange	56.5	44.2	57.1	41.5	W=105	0.500
Late summer 97	Four Mile	22.5	14.8	19.5	6.8	W=106	0.485
	Terrace Springs	48.1	27.1	45.7	36.8	W=111	0.342
	Gibbon Meadows	34.0	10.9	26.5	11.4	Z=1.63	0.052*
	Fountain Flats	26.2	21.9	27.9	28.6	W=102	0.426
	Midway Geyser	46.4	44.5	34.5	32.5	Z=0.57	0.285
	Interchange	99.5	58.6	78.4	28.2	W=114	0.264
Total summer 97	Four Mile	30.1	20.0	22.0	13.1	Z=0.83	0.202
	Terrace Springs	56.8	42.9	33.7	25.8	W=119	0.158
	Gibbon Meadows	45.3	22.1	42.9	21.4	W=110	0.370
	Fountain Flats	32.9	19.1	26.6	23.7	W=118	0.176
	Midway Geyser	30.8	23.8	32.3	38.8	W=116	0.218
	Interchange	83.7	35.2	92.6	31.1	W=92	0.176

* Biomass inside cages greater than biomass outside cages ($\underline{P} < 0.10$).

zero, i.e., no vegetation >13 mm in height, to 228 g/0.33 m^2 . Over all paired comparisons ($n = 600$), the mean difference between dried weights of herbaceous vegetation in plots protected from grazing (mean = 28.3 g, SD = 31.7) versus paired plots exposed to grazing (mean = 21.9 g, SD = 26.7) was 6.4 g, a 23 percent difference (Wilcoxon=s rank-sum continuity-corrected $Z = 3.39$, $P < 0.001$).

When all sites were combined, biomass in protected plots was greater ($P < 0.10$) than biomass in plots exposed to grazing (Table 3) in early summer 1996, total summer 1996, spring 1997, and early summer 1997. Combining sites, however, is inappropriate because exclosure cages were clustered at sites with very different vegetation production and utilization patterns. When individual sites were tested by season, we found significantly greater biomass in plots protected from grazing at the Four Mile (spring 1997), Terrace Springs (early summer 1996, total summer 1996, and early summer 1997), Gibbon Meadows (total summer 1996 and late summer 1997), Midway Geyser (winter and spring 1997), and Interchange (winter 1997) sites (Table 3).

Correlations between estimated ungulate days of use and the difference in biomass between protected plots and plots exposed to grazing (g/ 0.33m^2) over all sites and seasons were significant for bison-days (n pairs = 48, $r = 0.55$, $P < 0.001$) and animal-use days (n pairs = 48, $r = 0.53$, $P < 0.001$) but not for elk-days (n pairs = 48, $r = 0.09$, $P =$

0.56). When we correlated animal days of use per hectare with estimates of mean percent utilization for individual sites by sampling period, we identified weak, positive relationships for bison (r = 0.28, $P = 0.05$) and animal-use (r = 0.28, $P = 0.05$) days but no significant relationship for elk-days (r = 0.08, $P = 0.61$).

When we compared estimated percent utilization of forage with bison and elk days for individual sites in specific seasons (Fig. 4, 5, and 6), high estimated bison-days per hectare were only associated with high utilization at the Interchange site (Fig. 6) during winter. Moderate values for bison-days were associated with significant utilization at the Terrace Springs (Fig. 5) site during early and total summer 1996 and early summer 1997 and at the Midway Geyser site in winter 1997. At other sites, significant utilization was associated with low bison counts, or high bison counts were associated with non-significant utilization values. Estimates of elk-days were low at all sites in all seasons.

DISCUSSION

Because of controversy surrounding investigations of ungulate impacts in Yellowstone (Cheville et al. 1998), we elected to minimize potential bias in sampling by strict spatial randomization within sites. Our goal

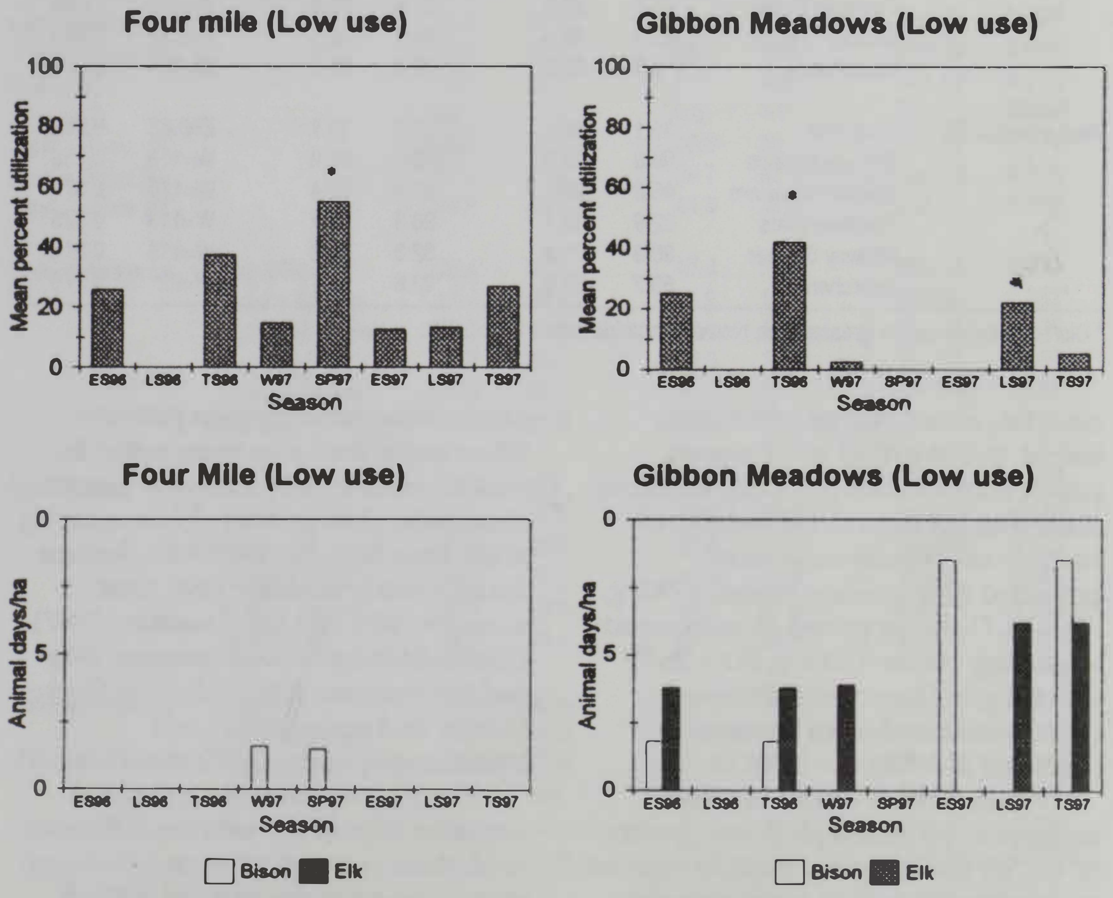

Figure 4. *Mean estimated forage utilization (%) at two historic low winter-use sites (Four-Mile and Terrace Springs) and estimated bison-days and elk-days per hectare in each site by season in the Madison, Gibbon, and Firehole drainages, Yellowstone National Park, 1996-1997. Asterisks in utilization graphs indicate significantly greater biomass in exclosure cages than in plots outside cages (1-tailed Wilcoxon's paired tests,* $P < 0.10$*).*

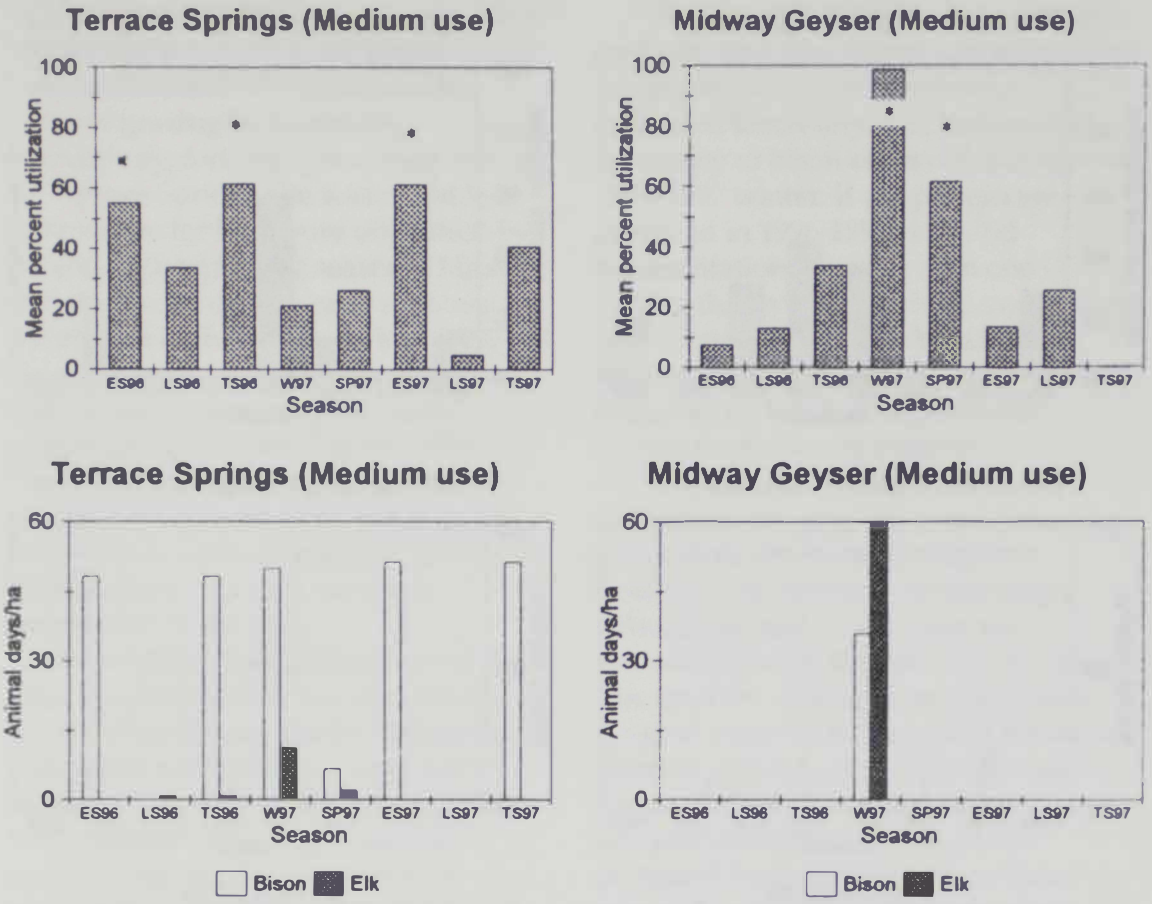

Figure 5. *Mean estimated forage utilization (%) at two historic medium winter-use sites (Terrace Springs and Midway Geyser) and estimated bison-days and elk-days per hectare in each site by season in the Madison, Gibbon, and Firehole drainages, Yellowstone National Park, 1996-1997. Asterisks in utilization graphs indicate significantly greater biomass in exclosure cages than in plots outside cages (1-tailed Wilcoxon=s paired tests,* P *< 0.10).*

was not to demonstrate the possibility of ungulate impacts on herbivorous vegetation, as was that of Frank and McNaughton (1992, 1993), but to determine if measurable impacts occurred on wintering areas in the Madison, Firehole, and Gibbon drainages. We discovered that use of sites by ungulates and forage availability varied tremendously at the scale we were measuring, and thus, under-sampled study sites. We were only able to detect utilization >40 percent in most sites. We estimated that 327 pairs of 0.33-m^2 plots per site would be needed to detect a 20 percent difference and 1,355 pairs to detect a 10 percent difference in means (based on power analysis modules in Borenstein and Cohen 1988) for the average site in the upper Madison study area using a completely randomized pairing system and parametric statistics (1-tailed t-test with P <0.05 and power = 0.80). This sampling intensity was well beyond the capabilities we had.

Despite their limitations, our data did shed light on foraging patterns in the study area.

Suitable bison habitat in the Madison, Firehole, and Gibbon drainages is limited to patches and linear swaths of open meadows in riparian corridors (Ferrari 1998). Bison used all sites where we placed exclosure cages during periods when vegetation was growing so the area cannot be considered only as a winter range. The

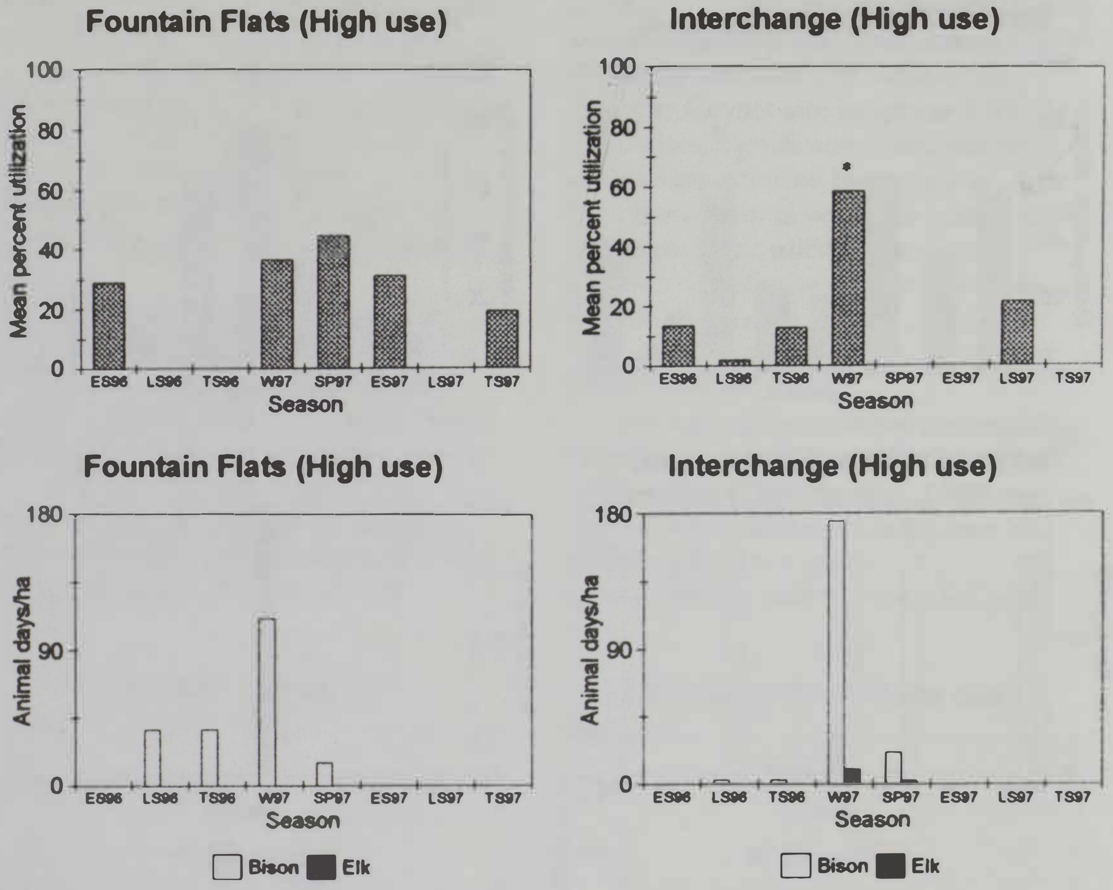

Figure 6. *Mean estimated forage utilization (%) at two historic high winter-use sites (Fountain Flats and Interchange) and estimated bison-days and elk-days per hectare in each site by season in the Madison, Gibbon, and Firehole drainages, Yellowstone National Park, 1996-1997. Asterisks in utilization graphs indicate significantly greater biomass in exclosure cages than in plots outside cages (1-tailed Wilcoxon=s paired tests, $\underline{P} < 0.10$).*

extent and seasonality of use varied widely among sites.

Estimated utilization of forage at the Four Mile site, a low winter-use site located in a migration corridor connecting wintering areas outside YNP with areas inside YNP, was highest in spring 1997 (55%). This was a period when bison that survived the harsh 1997 winter were moving back into the Park through this site and could easily have been missed in our weekly counts. We did not record any other significant seasonal utilization at this site and rarely saw buffalo or elk on the site.

Utilization in the other low winter-use site, Gibbon Meadows, was only statistically different from zero for the total summer 1996 and late summer 1997 sampling periods. Bison rarely were observed in this site, but it had the most consistent use by elk of any site we measured. It is likely, however, that the estimated percent utilization in summer 1996 (42%) and late summer 1997 (22%) were artifacts of vegetation variability rather than a response to 4 to 6 elk-days of use.

Estimated utilization at Terrace Springs, a medium winter-use site, was not significant during winter but was during early summer 1996 (55%), total summer 1996 (62%), and early summer 1997 (61%). Bison numbers observed at this site were 5-10 times greater than at low winter-use sites, and use during early summer was as high as use during winter. Although Frank and

McNaughton (1993) demonstrated that herbaceous forage in some plant communities in YNP responded to summer grazing by increasing productivity, forb and grass regrowth at the Terrace Springs site was not able to compensate for herbivore utilization by the end of the growing season. This site attracted bison during early summer under both high (1996) and low (1997) bison populations, and it had the highest canopy coverage of exotic grasses of the six sites (Dawes 1998). The high relative abundance of exotic species is consistent with, but does not prove, bison-induced changes in the species composition of the plant community at this site.

Bison and elk were observed at the other medium winter-use site, Midway Geyser, only during winter. Estimated utilization, however, was significant during winter (99%) and spring (62%) 1997. Significant spring utilization could be due to sampling error or consumption of regrowth protected by snow during late winter.

Estimated utilization at the Interchange site, a historic high winter-use area, was significant (58%) only in winter 1997. Estimated use per hectare by bison in winter 1997 was 3 times greater than at Midway Geyser. Higher use by bison and lower utilization of forage at the Interchange site compared to the Midway Geyser site in winter were consistent with differences in site productivity. The Interchange site had 10 times more forage available in winter than the Midway Geyser site. Bison numbers on the Interchange site declined in spring, and bison were seldom seen on the site during summer.

The other historic high winter-use site, Fountain Flats, did not have significant utilization in any season. Based on the number of bison we observed on this site, our failure to detect significant winter utilization was probably due to the extreme variability in forage productivity within the site.

The sites identified as historic high, medium, and low winter-use areas were ranked in that order in terms of estimated bison-days per hectare and frequency of bison observed during the 1996-1997 winter. If the pattern we observed in 1996-1997 is a valid representation for more than one winter, the probability that a site in high winter-use range in the Madison-Firehole-Gibbon complex will be occupied by bison on a given day during winter is >80 percent.

Our index of winter forage utilization, the previous year's standing vegetation, produced ambiguous evidence supporting a relationship between animal-days of use and estimated forage utilization in winter. The extreme variability in vegetation cover at some sites, especially Fountain Flats, is probably the best explanation for our failure to demonstrate unequivocal differences in plots protected from grazing versus those exposed to grazing. However, when ungulates remove snow from a site to reach forage, they promote melting and refreezing which protects the site from further foraging (Turner et al. 1994). Moving snow from one site to access forage may also create a crust at the site where it is moved thereby making foraging at the stacking site very difficult (P. Farnes, pers. commun.). Moving snow to reach forage, a common practice by bison in YNP (Meagher 1973), would thereby increase variability in utilization at the microsite level at sites used heavily by bison.

Mean standing dead biomass inside exclosure cages in May 1997 was <50 percent of mean standing biomass at the same sites recorded in exclosures in October 1996 at four of the six sites, indicating a major loss in biomass not related to grazing. The decline in forage protected by exclosures was probably due to some combination of herbivory by small mammals, mechanical removal of standing plant material due to snow weight, and fungal/bacterial action on standing dead vegetation in thermally warmed soil covered by an insulating snow cover.

The mean percent difference between caged and uncaged plots for winter forage utilization we calculated for the four sites used most heavily by bison in winter (Terrace Springs, Midway Geyser, Fountain Flats, and Interchange), 54 percent, was similar to the average winter forage removal by ungulates, ~55 percent, reported for the northern range of YNP during 1986-1990 by Singer and Harter (1996). Given the extent of bison egress from Yellowstone and the high mortality within Yellowstone during the 1996-1997 winter, we expected higher utilization if forage were limiting in the Gibbon, Firehole, and Madison drainages. Snow depth at two of the three most heavily used sites (Fountain Flats and Terrace Springs) never reached chest height (~60 cm) on female bison, a depth that is believed to preclude most bison use (Telfer and Kelsall 1984), during the 1996-1997 winter and was >60 cm only during January 1997 at the Interchange site so snow depth should not have been a major factor limiting bison access to forage. Assuming snow crusting did not limit availability and small mammal herbivory, microbial activity, or mechanical processes did not mask utilization, bison that exited Yellowstone via the Madison River were not responding to absolute shortages of forage in the study area.

Reducing the number of bison in YNP did reduce the number of bison sighted at our sample sites during summer 1997. The reduction did not reduce apparent utilization during the early growing season in 1997 at the only site where we could unambiguously detect significant impacts on standing biomass due to bison during the 1996 growing season, Terrace Springs. This suggests that moderate reductions in bison numbers are unlikely to limit overgrazing at specific sites favored by bison in YNP.

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SPECIES-AREA RELATIONS OF SONG BIRDS IN THE BLACK HILLS, SOUTH DAKOTA

ABSTRACT

We investigated the effects of stand size resulting from current logging practices on occurrence and species richness of song birds in the Black Hills. Richness of forest interior and forest interior/edge song birds was not related to stand area (P ≥ 0.40) in stands of ponderosa pine (Pinus ponderosa) *in the Black Hills. Brown creepers* (Certhia americana) *occurred only in stands of unmanaged forest >18 ha, but large diameter trees appeared to be more strongly associated with brown creepers than stand area. Ovenbirds* (Seiurus aurocapillus) *occurred in all size categories of stands but more frequently in stands 25-35 ha. Western tanagers* (Piranga ludoviciana) *did not occur in stands less 10 ha but do not appear to depend on dense late-seral forest in the Black Hills. These sizes of forest stands are within the normal range of stand sizes in the Black Hills National Forest. We offer an explanation why logging in the Black Hills might not fragment the forest for song birds.*

Key words: song birds, fragmentation, species-area relations, logging.

INTRODUCTION

The Black Hills National Forest (BHNF) is an intensively managed forest dominated by ponderosa pine (*Pinus ponderosa*) in western South Dakota. Approximately 70 percent of the BHNF is managed primarily for timber production and harvest (Black Hills National Forest 1996). Logging in the BHNF alters the density and age (or average diameter-at-breast height, DBH) of forested stands, but only under special management objectives are forest stands converted to openings. Silvicultural techniques for logging in the BHNF include seed-tree and three-step shelterwood. Logged stands must have 370 to 741 established seedlings/ha within five years after logging is completed (National Forest Management Act 1976). Thus, the context of forest fragmentation from logging in the BHNF differs from that described for eastern deciduous forests (e.g., Whitcomb *et al*. 1981, Ambuel and Temple 1983, Freemark and Merriam 1986, Faaborg *et al*. 1993). Nonetheless, some scientists maintain that logging and roads fragment the BHNF (Crompton 1994, Shinneman 1996) and are pushing the forest ecosystem farther from its range of natural variation (Shinneman and Baker 1997). In addition, fragmentation caused by logging has been a central theme in administrative appeals of timber sales in the BHNF by public organizations concerned with environmental protection. If logging activities fragment the forest in the Black Hills, it is important to understand the context and

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nature of the effects. The species-area relation for song birds is one aspect of forest fragmentation. In this paper, we investigate the species-area relations for song birds in the BHNF.

STUDY AREA AND METHODS

Forested stands, in the BHNF, are land units of relatively homogeneous forest vegetation 4-32 ha in size, but occasionally are larger. We described vegetation in stands is described in a hierarchal system using dominant vegetation types, DBH, and overstory canopy cover. Hereafter, we will refer to stand vegetation descriptions as forest vegetation structural stages. The boundaries of stands are delineated from topographic features such as ridges, drainages, and roads, and by changes in forest vegetation structural stage. Figure 1 depicts typical stands and boundaries in the BHNF.

We selected 40 stands of ponderosa pine; 20 stands were commercially logged within the previous 10 years (managed stands), and 20 stands had no timber management activity for >40 years (unmanaged stands). Because nearly all of the Black Hills have had some human intervention since nonnative settlement, we used this criterion to identify stands of dense mature timber as unmanaged stands. These stands represent the forest structure that is considered fragmented by logging in the BHNF. We digitized the area of each stand from aerial photographs. Stand area ranged from 4 to 50 ha. Managed stands averaged 16 m^2/ha basal area, 23.4 cm DBH, and 43 percent overstory canopy cover; unmanaged stands averaged 28 m^2/ha basal area, 22.2 cm DBH, and 68 percent overstory canopy cover (Dykstra *et al.* 1999). Lower average DBH in unmanaged stands resulted from the small trees beneath the primary forest canopy.

In each stand, we located two to five sites for variable-radius bird counts (Reynolds *et al.* 1980). Generally, more sites for bird counts were located in larger stands than smaller stands. Sites for bird counts were >100 m from the stand boundary except in three small stands where size and configuration necessitated placing sites 50-70 m from the stand boundary. Bird counts began 1/2 hour before sunrise and were completed by 1100 hrs (Mills *et al.* 2000). We identified and recorded all birds seen or heard near the site while approaching the site (Hutto *et al.* 1986) and for eight minutes following arrival at each site. We conducted bird counts for two consecutive days, which constituted one count-session at each site. During 1993, we completed two count-sessions (beginning dates of 21 May and 9 June), and during 1994, we completed three count-sessions (beginning dates of 23 May, 7 June, and 20 June). We did not count birds during periods of moderate to heavy rain, when winds exceeded 10 km/h or if temperatures were <7 C or >24 C (Manuwal and Carey 1991).

Our analyses included birds ≤30 m from the bird count site that were perched in trees, on the ground, or in shrubs within the ponderosa pine forest. We selected 30 m as the furthest distance because observers begin to overlook birds at distances >30 m in forests (Emlen 1971, Verner and Ritter 1988). We assigned habitat affiliations of wide ranging, forest interior, interior/edge, or edge to birds based on Whitcomb *et al.* (1981), Blake (1991), and our understanding of species habitat requirements. Widely ranging species such as turkey vultures (*Cathartes aura*), hawks (Family *Accipitridae*), Merriam's turkeys (*Meleagris gallopavo merriami*), etc., were not included in these analyses. Species richness represents the sum of singing passerine and *Picidae* (e.g., Lescourret and Genard 1994) species occurring at sites or in stands, depending on the analysis. For example, analyses comparing species richness

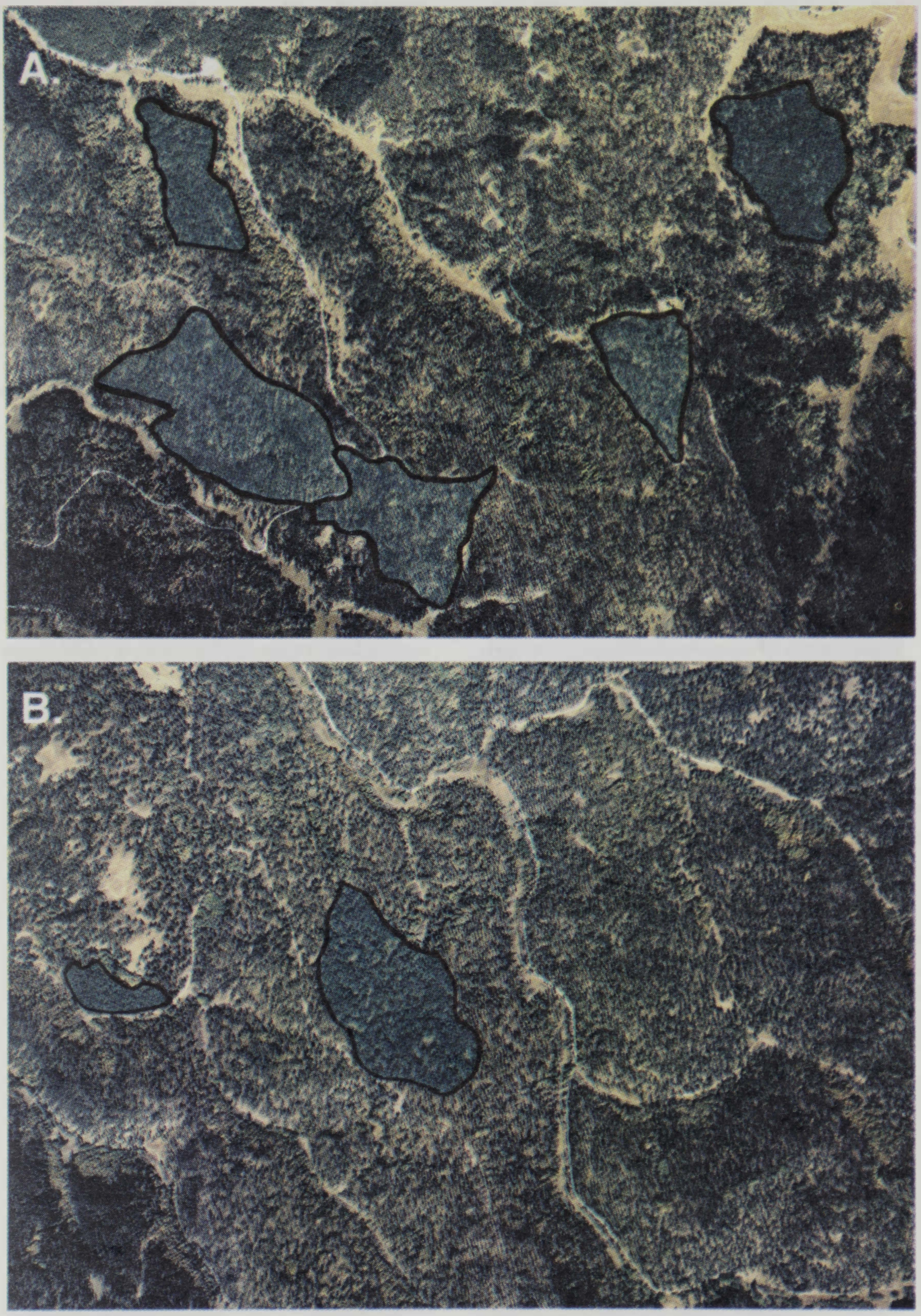


Figure 1. *Aerial photographs (1:24000) depicting typical stands included in this study. A). Unmanaged ponderosa pine stands (upper right of photo) surrounded by lower density pine forest, meadows, and roads, and several managed stands (lower portion of photo) surrounded by roads and meadows. B). Two unmanaged stands surrounded by less dense forest meadows, and roads.*

between years included the number of species occurring in each stand for each year. We used a paired *t*-test to compare species richness in stands between years. This test was not significant ($P = 0.78$); thus, species richness for subsequent analyses represents the sum of species occurring at sites or stands applicable to the analysis for both years.

We plotted species richness for successive count-sessions at sites in each stand to formulate species accumulation curves (Freemark and Merriam 1986, Blake and Karr 1987). These species accumulation curves were examined for evidence of asymptotes; an indication that the number of counts in the stand was adequate to estimate species richness. We tested the hypothesis "that occurrence of bird species was not related to the size of stands" using the following methods. We conducted linear regressions of species richness on stand area for 1) unmanaged stands, 2) managed stands, and 3) all stands (combined). For managed and unmanaged stands we conducted the regression analyses using: 1) all song birds (and *Picidae*) excluding wide ranging species, and 2) song birds and *Picidae* associated with forest interior or interior/edge conditions. Because placing more bird count sites in larger stands could result in detecting more species in those stands (Hutto *et al.* 1986), we also conducted linear regression analyses of species richness per count on stand area. We assessed the appropriateness of linear models by testing the residuals using the Shapiro-Wilk's test (Shapiro and Wilk 1965).

To estimate the pure effects that stand area has on occurrence of individual bird species, we compared the model chi square value of a logistic regression that predicted occurrence of species from vegetation characteristics with the model chi square of a logistic regression that predicted occurrence of species from vegetation characteristics and stand area (Lescourret and Genard 1994). The difference between the model chi square values tests the hypothesis "that the coefficient attributable to stand area is 0." We used both site-level and stand-level data to complete the logistic regression analyses. Site-level data are best for analyzing the effects of habitat characteristics on bird occurrence, but stand-level data better estimate effects of stand area on bird occurrence (Askins *et al.* 1987). To simplify vegetation characteristics for consideration in the logistic regression, we used principal components analysis (PCA) to develop a reduced number of variables that captured the vegetative features. Vegetation features data and sampling protocol are summarized in Dykstra *et al.* (1999). We completed the logistic regressions for a species only if that species occurred at more than five sites or in more than five stands for respective analyses because we felt there was little chance of obtaining meaningful results at lower rates of occurrence. We then used step-wise forward multiple regression including the PCA factor scores and stand area to determine if vegetation coupled with stand area showed a relation to species richness.

We calculated the average species observation frequency at sites within stands for six stand-size categories. Stand-size categories were selected as a post-hoc compromise between number of stands in each category and the range of area included in each category. The size-intervals and sample sizes (n) included 4-9 ha ($n = 4$), 10-14 ha ($n = 6$), 15-19 ha ($n = 10$), 20-24 ha ($n = 8$), 25-34 ha ($n = 5$), and 35-50 ha ($n = 7$). The average frequency of observation in stand size categories was plotted and these graphs were examined for a threshold in stand size, below which the species was absent or less common. This was a qualitative examination because all statistical evaluation of frequencies among uncommon species were not significant because of low and variable occurrences.

Scientific names for birds follow the AOU (1983) checklist with supplements. We set statistical significance for all tests at $\alpha = 0.05$, marginal significance was determined at $\alpha = 0.10$. For $\alpha = 0.05$, this study had 92 percent chance of detecting $r \geq 0.5$ when all stands ($n = 40$) were considered and a 64 percent chance of detecting $r \geq 0.5$ when managed or unmanaged stands ($n = 20$) were considered separately. We considered $r \geq 0.5$ large enough to be biologically significant.

RESULTS

Cumulative species richness of count-sessions in stands indicated some small stands with only two sites did not demonstrate an asymptote (unpublished data, Rocky Mountain Research Station, Rapid City, SD), suggesting that we might have underestimated richness in these small stands. Most larger stands demonstrated an asymptote in species richness after counting three to four sites and several stands >20 ha showed an asymptote in species richness after counting only two sites. All stands >25 ha, except one, clearly exhibited an asymptote in species richness for the count efforts we completed. We included the small stands with only two sites in our analyses because any bias that might occur was not evident. If we underestimated species richness in small stands, the effect would have been to overestimate the strength of species-area relations (see below).

Linear regressions of bird species richness on stand area were not significant for analyses including all stands ($P = 0.18$, Fig. 2), unmanaged stands ($P = 0.23$), and managed stands ($P = 0.34$). Regressions of species richness of forest interior and interior/ edge birds (combined) on stand area were also nonsignificant for all stands ($P = 0.40$), unmanaged stands ($P = 0.42$), and managed stands ($P = 0.65$). Residuals from these analyses were normally distributed ($P \geq 0.11$), indicating linear models were appropriate for these data. Linear regressions of species per count on stand area indicated a negative slope that indicateded species richness in large stands did not result from more counts (e.g., Hutto *et al*. 1986). These analyses did not change the interpretation of our results so are not presented here.

Eight principal components with eigenvalues greater than one accounted for 72 percent of the variation in the vegetation measurements. Including stand area in logistic regressions with PCA factor scores improved the logistic models at sites for red-naped sapsuckers (*Syphrapicus nuchalis*, $P = 0.04$), dark-eyed juncos (*Junco hymenalis*, $P = 0.03$), and chipping sparrows (*Spizella passerina*, $P = 0.07$). The associations of stand area and occurrence of these birds at sites were negative. Including area with stand-level PCA factor scores in logistic regressions improved logistic models for occurrence of yellow-bellied sapsuckers (*S. varius*, $P = 0.07$), white-breasted nuthatches (*Sitta carolinensis*, $P = 0.04$), and brown creepers (*Certhia americana*, $P < 0.01$). Of these species, only the occurrence of brown creepers in stands was positively associated with stand area. Nonetheless, adding stand area decreased the ability of the model to correctly classify stands with brown creepers from 80 percent, when only vegetation factors were considered, to 40 percent when stand area was added (the improvement in the logistic model was from improved classification of stands without brown creepers). To further evaluate the importance of stand area in predicting the occurrence of brown creepers in stands, we conducted a logistic regression with stand area as the only independent variable. This logistic regression was marginally significant ($P = 0.09$) with stand area positively associated with occurrence of brown

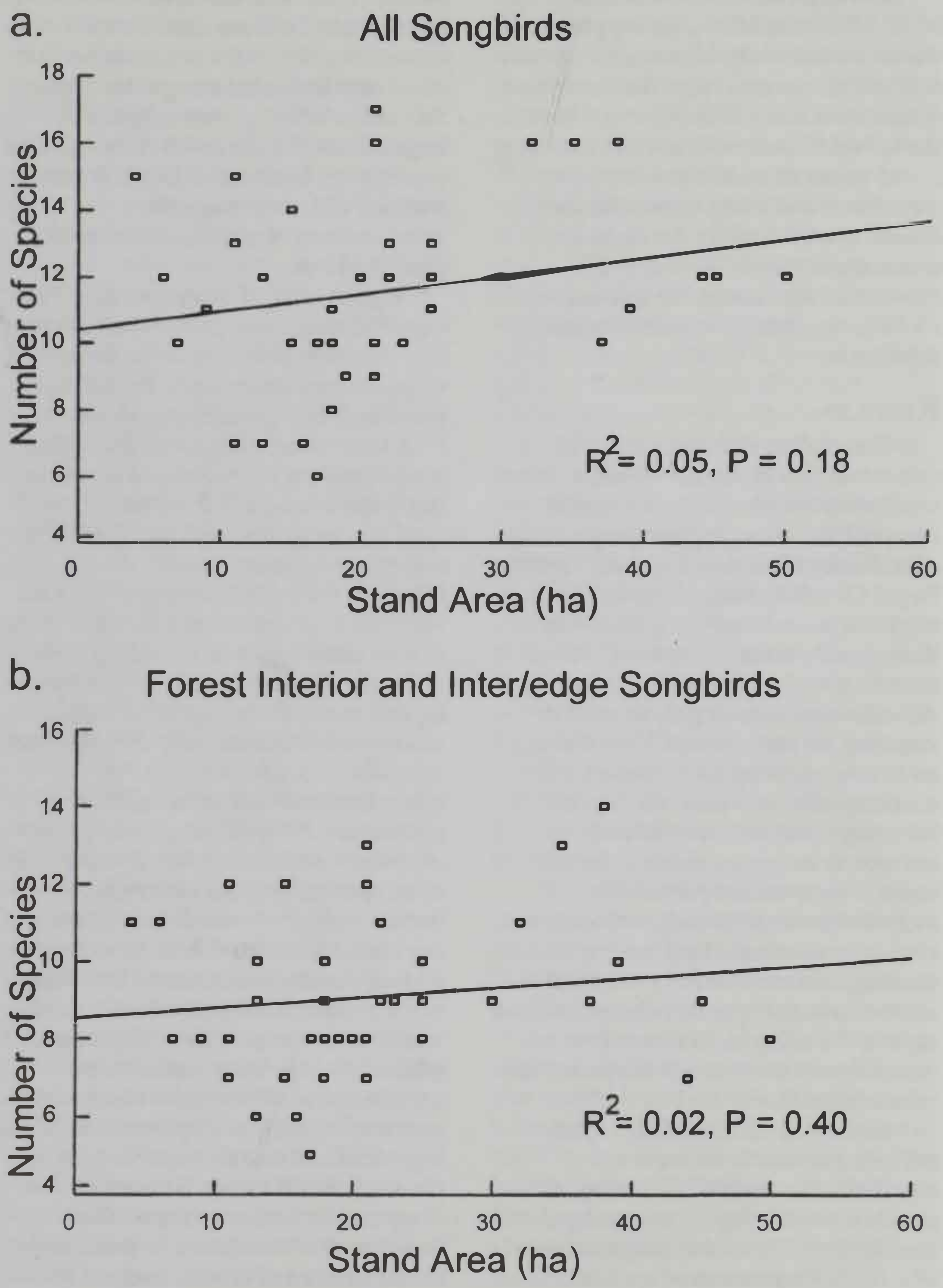


Figure 2. *Linear regressions of species richness with stand area for: a) all song birds, and b) song birds with habitat affiliations that are primarily forest interior or interior/edge.*

creepers. However, this model failed to correctly predict the occurrence of any stands with brown creepers. Thus, adding stand area to the logistic model for brown creepers predicted stands that did not have brown creepers (which was most of the stands).

Brown creepers were not observed in stands <18 ha (Fig. 3) but occurred only in unmanaged stands. Stands with brown creepers had greater ($P < 0.01$, *t*-test) densities of large diameter (>38 cm DBH) ponderosa pine trees than stands without brown creepers. Within stands >18 ha, those that had brown creepers also had more ($P < 0.01$, *t*-test) large ponderosa pine trees than stands >18 ha without brown creepers.

Western tanagers did not occur in stands < 10 ha. Ovenbirds, which are forest interior birds in some portions of their range, occurred in all stand size categories but were more common in stands 25-34 ha.

PCA factor one accounted for a significant, but small, amount of the variation in species richness among stands for all species ($R^2 = 0.15$, $P = 0.01$) and richness of forest interior/edge species ($R^2 = 0.12, P = 0.03$). Stand area was not included in the regression model for forest interior/edge species richness ($P = 0.65$) or for richness of all species ($P = 0.19$) after the entrance of PCA factor one.

DISCUSSION

Our analyses found little evidence that stand size in the BHNF precludes occurrence of some bird species . There was a small chance we could have underestimated species richness in small stands (e.g., Freemark and Merriam 1986, Blake and Karr 1987) and overestimated species richness in large stands by placing more bird count sites in them (e.g., Hutto *et al.* 1986). However, if this were true, the effect would have been to bias our conclusion toward significant positive species-area relations. Our analyses did not support this conclusion; large stands did not yield more bird species than small stands in either managed or unmanaged stands. Nor did large stands have more forest interior and interior/edge species than small stands. Species-area relations among song birds in conifer forests of the western United States and Europe tend to be weak (Rosenberg and Raphael 1987, Lehmkuhl *et al.* 1991, Lescourret and Genard 1994). In areas where forests surround logged stands that maintain some suitability for forest birds, species-area relations among birds may not occur (Estades and Temple 1999).

Although our study did not include stands that were extremely large, it did include the range of stand sizes for which species-area relations have been shown to occur elsewhere (Galli *et al.* 1976, Villard *et al.* 1993, Hinsley *et al.* 1996). These also represent the range of stand sizes for which opponents contend that logging fragments the forest in the Black Hills. Post-European settlement has greatly impacted forest vegetation in the Black Hills although most human impacts have resulted in greater tree densities than occurred historically (Parrish *et al.* 1996). Additionally, stands on the order of thousands of ha that are not broken by roads, natural meadows, or deciduous vegetation do not exist in the BHNF.

Evidence that brown creepers are sensitive to stand area was weak. They may require habitat blocks >18 ha, but brown creepers also require large snags or large trees with loose bark (Gilbert and Allwine 1991, Hansen *et al.* 1995). We observed brown creepers only in unmanaged stands of ponderosa pine with high densities of large diameter trees. Stands with brown creepers also had higher densities of large diameter ponderosa pine than stands of the same size categories. The weak logistic model in our study using stand area to predict occurrence of brown creepers and the strong differences in some habitat

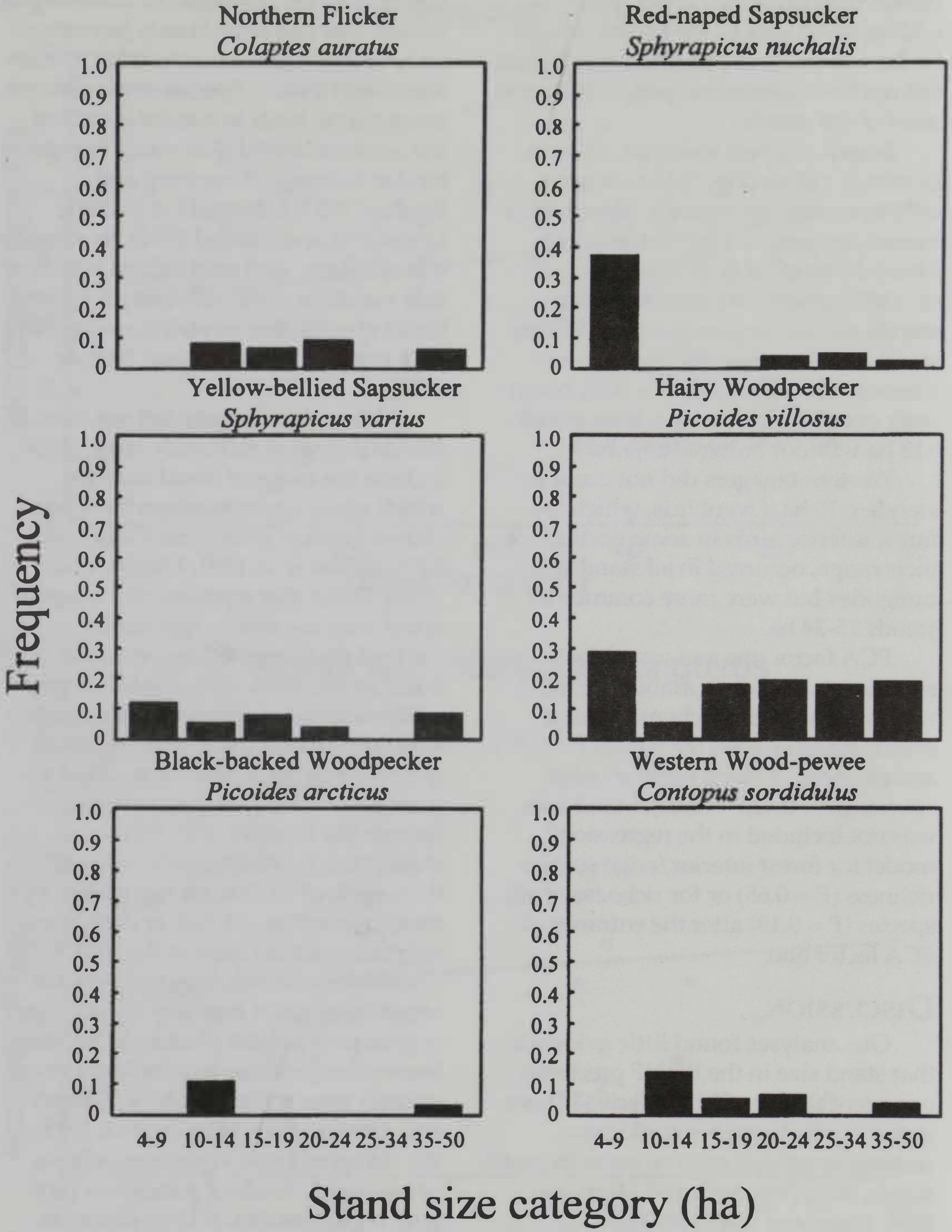
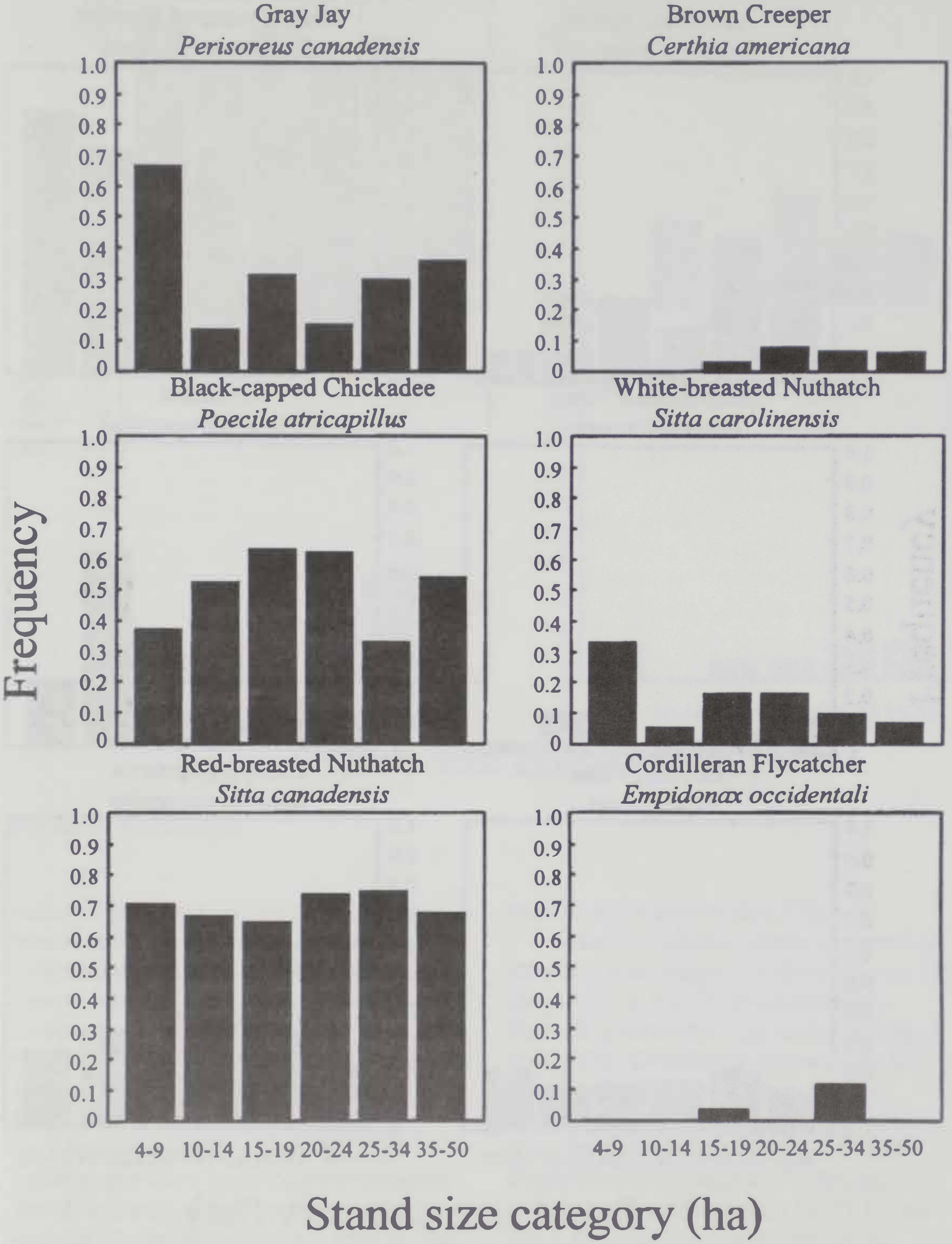


Figure 3. *Average frequency of birds at sites for six stand-size categories in the Black Hills, SD in 1993 and 1994.*



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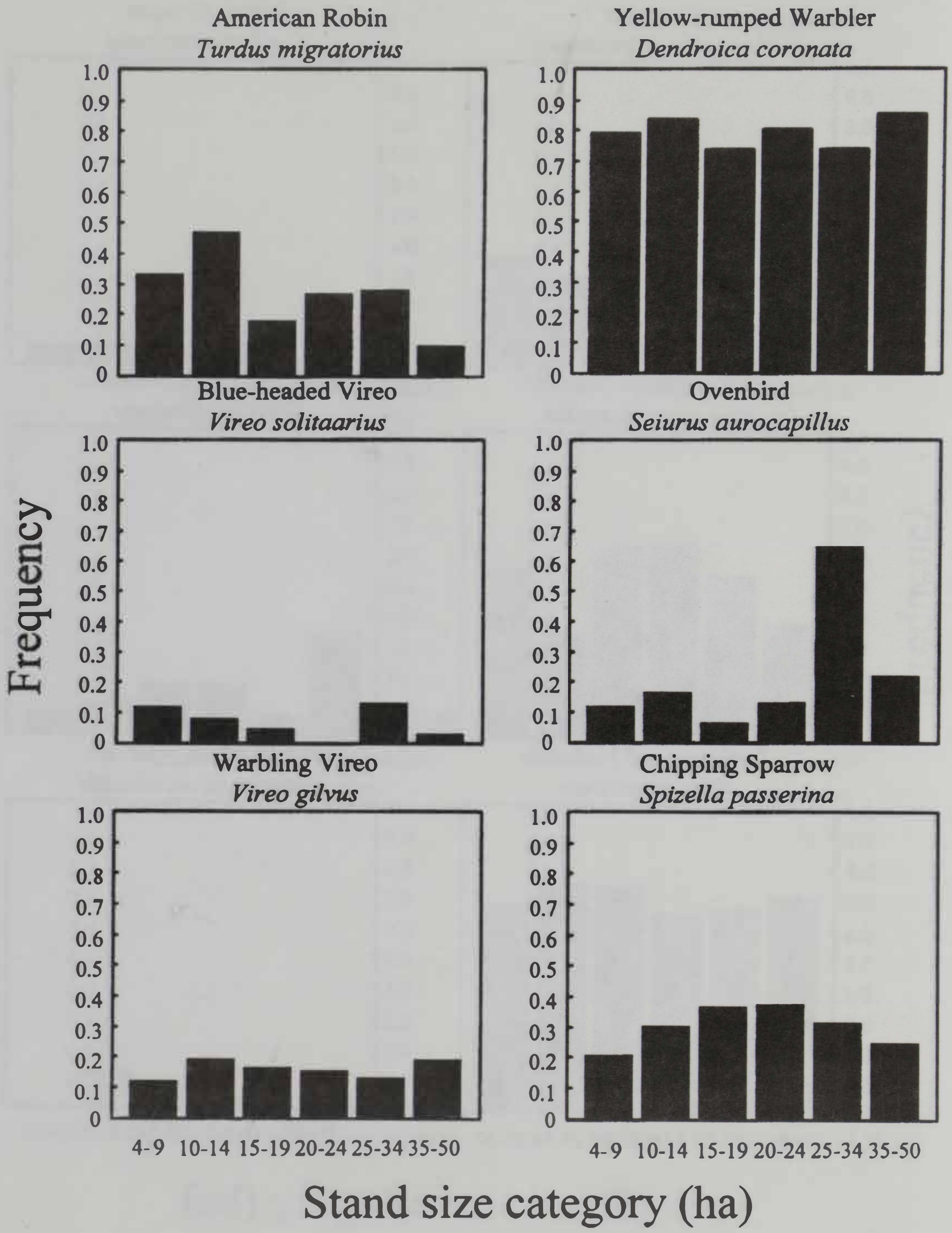

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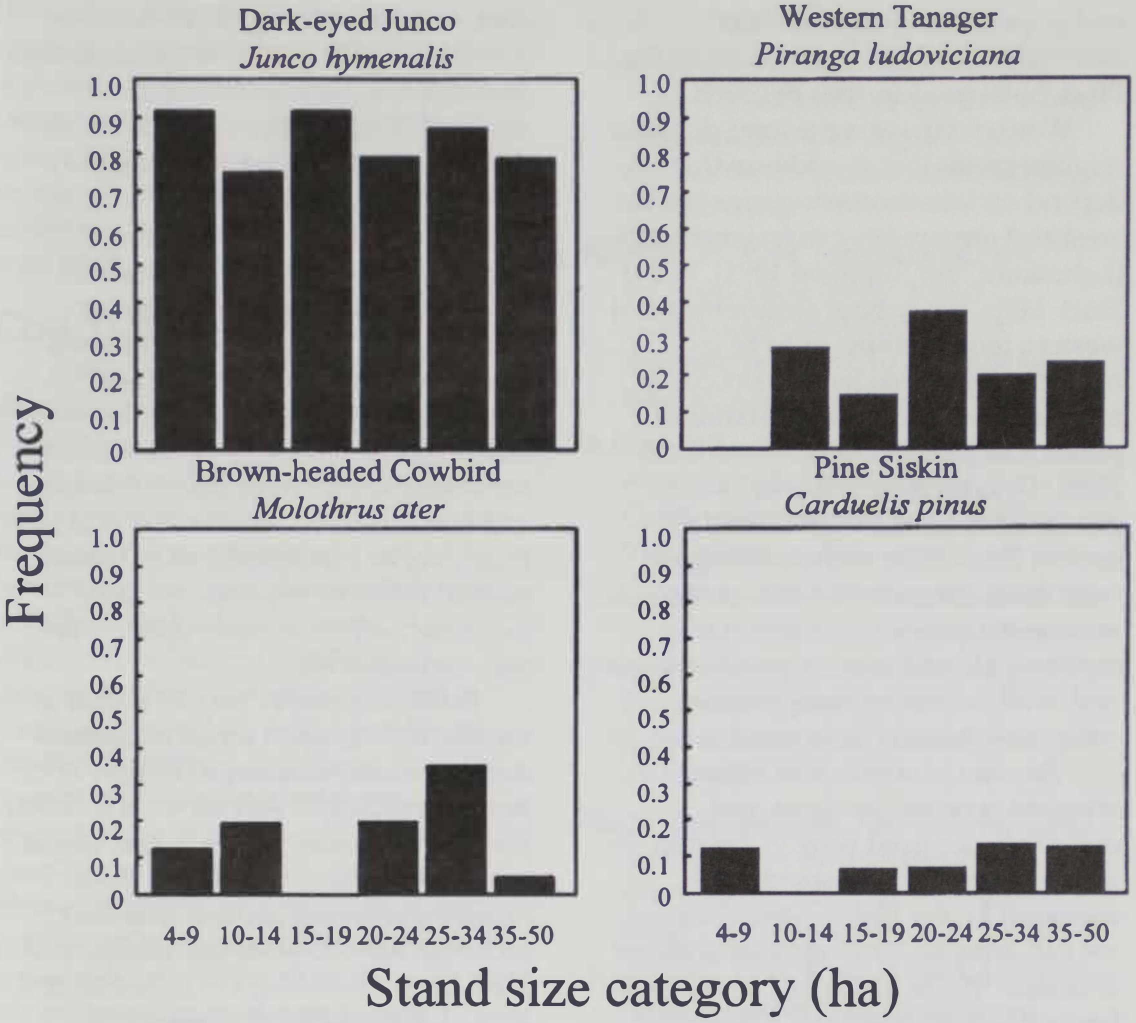

Figure 3. *(Continued)*

features suggest that large trees were more important than stand area in determining suitable habitat for brown creepers in the Black Hills. Brown creepers are dependent on late-seral forests but are not considered sensitive to fragmentation (Lehmkuhl and Ruggiero 1991). In Wyoming, (Keller and Anderson 1992) concluded that small stand sizes from logging reduced the abundance of brown creepers, but did not eliminate them from forests. The minimum stand size for brown creepers in Alaska was estimated at 1.7 ha (Hansen *et al.* 1996). Logging in the BHNF has a negative effect on brown creepers (Dykstra *et al.* 1999, Mills *et al.* in press), but that effect is more likely due to the alteration of forest structure than to alteration of stand size.

Even though ovenbirds occurred in all stand size categories, their increased frequency in stands 25-34 ha might indicate greater mating success (Villard *et al.* 1993). Ovenbirds require interior forest conditions in eastern forests (Whitcomb *et al.* 1981) and are aspen (*Populus tremuloides*) obligates in the Rocky Mountain region (Holthausen 1984, Finch and Reynolds 1987). In the Black Hills, we found ovenbirds in ponderosa pine if deciduous trees were present in the understory or in small patches. Unmanaged stands of ponderosa pine had more deciduous understory and greater abundance of ovenbirds than managed stands (Dykstra *et al.* 1999). Nesting, pairing, and population productivity of ovenbirds in relation to habitats of the Black Hills need further research.

Western tanagers are long-distance migrants with low abundance that depend on late-succession forest in the west and are sensitive to fragmentation (Lehmkuhl and Ruggiero 1991). In the Black Hills, the habitat requirements of western tanagers appear to be less restrictive. Western tanagers occur in managed and unmanaged stands of ponderosa pine in the northern Black Hills (Dykstra *et al.* 1999) but were absent from stands < 10 ha. In the central Black Hills western tanagers were most common in multi-storied stands, but also were common in sapling-pole and mature ponderosa pine and in all overstory canopy cover categories (Mills *et al. in press*).

The size of stands that brown creepers, western tanagers, and ovenbirds occurred were in the mid- to upper-range of forest stand sizes managed by the BHNF. Managing for the full array of forest structural stages in stands >25 ha, including stands with larger diameter trees and >70 percent overstory canopy cover, would ensure that habitat requirements for these species occur across the forest. Rosenberg and Raphael (1986) recommended managing old-growth forests in stands >20 ha in California.

We offer explanations why logging, as currently practiced in the BHNF, might not affect song birds as in eastern deciduous forests. Despite the fact that 70 percent of the BHNF is managed for timber production (Black Hills National Forest 1996), the managed forest does not result in abrupt edges between forested and nonforested stands. Predominant logging methods affect the vegetation structure of the forest, but do not eliminate the forest. National Forests are required to re-establish or regenerate the forest after logging (National Forest Management Act 1976). Although most of the BHNF has been logged in the past, 81 percent (SE ±1%) of the area surrounding the stands we studied were forested. Fragmentation effects are minimal until <60 percent of the forest remains (Franklin and Forman 1987, Andrén 1994). When surrounding habitat continues to support forest vegetation, species-area relations of song birds might become negative (Estades and Temple 1999). In forests where >60 percent of forest cover remains, bird species richness increases after logging because generalist birds are added to the community (Franklin and Forman 1987, Lehmkuhl *et al.* 1991). Proximity or connectedness to forest, even of different vegetation types, increases bird abundance (Lescourret and Genard 1994).

Before nonnative people settled in the Black Hills, open forest conditions dominated the landscape (Wright 1978, Brown and Sieg 1996, Parrish *et al.* 1996). Fewer, more widely spaced, and larger ponderosa pine trees resulted from recurring creeping ground fires that occurred 100-600 years ago (Fisher *et al.* 1987, Brown and Sieg 1996, Parrish *et al.* 1996). Large stands of dense forest common in the Black Hills today resulted from fire suppression (Covington and Moore 1994) and probably occurred historically only at higher elevations of the northwestern Black Hills (Parrish *et al.* 1996). Present vegetation patterns in the Black Hills might have developed only during the last few thousand years (FAUNMAP Working Group 1996) because of variation in climate and vegetation over the past 20,000 years (Graham 1990, Weedon and Wolken 1990, Pielou 1991). Ponderosa pine did not occur in the southern Black Hills ca. 26,000 years ago (Mead *et al.* 1990). This variation in climate and vegetation may not have provided adequate time for birds to develop small exclusive niches (e.g., Orians and Wilson 1964, Slobodkin and Sanders 1969, Gilbert and Allwine 1991). Thus, historical forest conditions in the

Black Hills, were probably more conducive to generalist birds that are not sensitive to stand area. The effects of forest fragmentation on song birds on naturally patchy western landscapes are seemingly different than those observed in eastern deciduous forests (Tewksbury *et al.* 1998).

CONCLUSIONS

Although our results are not dramatic, they are important because of the biological, economic, and political consequences if we had demonstrated that logging fragmented the BHNF for song birds. Our data should not be construed to suggest that logging does not affect the bird community in the Black Hills. Changes that logging induces to the forest alters species composition and abundance of birds in the BHNF (Mills *et al.* in press, Dykstra *et al.* 1999). We did not address reproductive success, survival, or densities of song birds in this study. However, effects of logging on these population parameters of song birds in western forests differ from those shown for midwestern or eastern forests (Franklin and Forman 1987, Lehmkuhl *et al.* 1991, Tewksbury *et al.* 1998). Within the context of species richness area relations for song birds, our findings do not support an argument that logging fragments the BHNF to an extent that adversely affects species richness of song birds.

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EFFECTS OF UNGULATE BROWSING ON ASPEN REGENERATION IN NORTHWESTERN WYOMING

ABSTRACT

*Although clear-cutting has been demonstrated to be an effective means to regenerate aspen (*Populus tremuloides *Michx.), stand replacement may be retarded under conditions of intense browsing of regeneration, such as that experienced near elk (*Cervus elaphus*) feedgrounds in northwestern Wyoming. We studied the effects of ungulate browsing on regenerating aspen following clear-cutting on the National Elk Refuge. Nine deteriorating, aspen-dominated stands were clearcut in the spring of 1988, and regeneration characteristics were subsequently measured periodically through 1996. Big game exclosures were placed in three stands immediately following treatment. Post-treatment sucker densities were relatively low but theoretically sufficient for stand replacement. The percentage of "suckers" that obtained heights >2 m was significantly greater inside the exclosures after 9 years than outside the exclosures. Average heights of browsed and unbrowsed suckers were markedly taller within the exclosures. Our findings suggest that repeated annual browsing substantially increased sucker mortality, and limited the height achieved by aspen stems. Small-scale clear-cutting to regenerate aspen may not be effective in areas of winter ungulate densities similar to those adjacent to elk feedgrounds.*

Key words: aspen, *Populus tremuloides*, browsing, clear-cutting, exclosures, National Elk Refuge, regeneration

INTRODUCTION

Ecologists and resource managers have been concerned over the declining condition of aspen (*Populus tremuloides* Michx.) stands throughout northwestern Wyoming and elsewhere in the western United States, particularly on big game winter ranges. Although the relative importance of various factors involved is unclear, fire suppression, ungulate browsing, and natural succession all directly contribute to the lack of successful regeneration observed in western aspen (Krebill 1972, Schier 1975, Basile 1979, Gruell 1980, Kay 1985, Mueggler 1989, and Romme *et al.* 1995).

Aspen reproduces almost exclusively through vegetative propagation, and is therefore clonal in nature (Barnes 1966). Adventitious shoots (suckers) arise from shallow lateral roots that grow in a complex interconnecting network among the individual ramets comprising an aspen clone. Suckering is normally suppressed by a process called apical

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dominance, whereby auxin produced in the leaves and buds of mature aspen stems is transported to the roots and inhibits sucker growth (Farmer 1962, Schier et al. 1985). Death of overstory trees eliminates this regulatory control, thus permitting rapid sucker growth.

Management strategies, such as clear-cutting and prescribed burning, are effective because they mimic natural disturbances that kill the overstory trees and stimulate suckering (Schier *et al.* 1985). However, questions remain regarding sucker survival and growth following treatment under conditions of intense browsing pressure, particularly where ungulates are concentrated on winter ranges and near elk feedgrounds (Krebill 1972). In this paper we examine the influence of browsing on aspen regeneration and growth following clear-cutting under conditions of heavy ungulate use. Our objectives were to quantify regeneration after treatment and to determine whether subsequent browsing by ungulates would prevent new suckers from growing beyond the reach of browsers.

STUDY AREA

Our study was conducted on the National Elk Refuge, located in Park County, northwestern Wyoming (43°30'N, 110°45'W). The refuge is located at the southern end of Jackson Hole, and is bordered to the east by the Gros Ventre Range and to the west by the Grand Teton National Park. The refuge encompasses over 10,000 ha with elevations ranging from 1900 to over 2200 m above sea level. Annual air temperature averages 3° C, and annual precipitation averages about 39 cm (Dept. of Commerce 1982). The refuge had 753 ha of aspen-dominated woodlands found in 143, mostly even-aged stands. Common understory associates included snowberry (*Symphoricarpos oreophilus*), serviceberry (*Amelanchier alnifolia*), willow (*Salix* spp.), *Calamagrostis rubescens*, *Poa* spp., *Lupinus argenteus*, *Helianthella uniflora*, *Epilobium augustifolium*, and *Geranium* spp.

The primary responsibility of the refuge is to provide winter habitat and food for approximately 7500 Rocky Mountain elk (*Cervus elaphus canadensis*) annually. The number of elk supplementally fed on the refuge during 1988 - 1996 ranged from 7753 to 10004 elk (Smith and Anderson 1998). Another 150-300 elk wintered on the refuge but did not attend feedgrounds. Other browsers that wintered on the refuge included about 75 mule deer (*Odocoileus hemionus*), 20 moose (*Alces alces*), and 110-260 bison (*Bison bison*).

METHODS

Nine aspen stands were selected for treatment from among 110 stands on the northern 6000 ha of the NER. Treated stands were 1.1-5.9 ha in size. Treated stands tended to be heavily browsed, lacked sufficient regeneration for stand replacement, and were experiencing significant mortality of overstory trees. Because the area of interest was under concentrated winter (15-20 moose and 150-300 elk), spring (7700-10,000 elk and 110-260 bison for 2-4 weeks), and summer (150-300 elk, 20-30 mule deer) ungulate use, treated stands were selected in clusters rather than in isolation to reduce the likelihood of ungulates congregating in any one stand (D. Bartos, N. DeByle, and W. Mueggler pers. comm.). Treated stands were located on generally north-facing slopes with similar soil types.

Each stand was clearcut during April-early May 1988. All aspen stems >5 cm dbh and all conifers, regardless of size, were cut. Afterward, rectangular (7x7 m) game exclosures were placed within three treated stands to measure the effects of ungulate browsing on aspen regeneration. Vegetation measurements were collected in each of the three stands with exclosures during late summer-early fall 1988 through 1996. Similar measurements were collected in the remaining stands during summer - early fall of 1988 and 1989, and every other year thereafter through 1995. A permanent transect was placed lengthwise through the middle of each stand. Five to 15 plots, depending on stand size, were permanently placed equidistantly along the length of transect. On each 1.6 m^2-plot, the number of aspen stems were counted and the level of browsing assessed. We measured the height of each stem and counted the number of years its terminal leader was browsed.

Data collected from each plot were pooled, and either a mean or proportion was estimated for each stand. We examined the effects of browsing by comparing vegetation measurements collected on plots within each exclosure to those outside the exclosure in a paired design. Statistical tests were conducted using SPSS 7.5 (SPSS Inc., Chicago, IL). Sucker density was tested for browsing effects, year effects, and treatment-year interaction using multivariate analysis of variance (MANOVA) with a repeated measures design (Norusis 1990). We tested for year effects on sucker density using MANOVA for data collected on plots outside of the exclosures from all nine stands. Year effects on browsing-related attributes and sucker height could only be examined descriptively because of missing data. Browsing-related effects were tested using a paired-samples t test, after calculating an average across years. Tests were considered significant at $P \leq 0.05$.

RESULTS

Mean sucker densities within the exclosures ranged from over 60,000/ha in 1988 to a minimum of about 16,000/ha in 1994 (*n* = 3). Sucker densities outside exclosures ranged from 17,200/ha in 1990 to 12,133/ha in 1996 (Fig. 1).

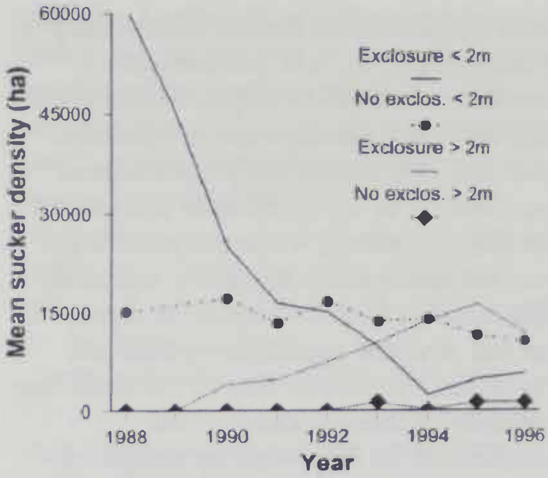

Figure 1. *Density of aspen suckers by treatment, 1988-1996.*

Sucker density was twice as great in the exclosures across all years, averaging over 28,000/ha (Table 1). We discerned no clear trends in average sucker density from all clearcut sites from 1989 to 1995, ignoring counts within the exclosures ($F_{year} = 0.5$, df = 4, 28, $P = 0.719$). Clearcut sites averaged 9136 suckers/ha, ranging from 7178 in 1989 to 10333/ha in 1991 (*n* = 9). With the exception of one treated stand, all stems recorded outside exclosures were <2 m tall over the course of the study.

After 1990, the density of aspen suckers >2 m tall was significantly greater inside exclosures than outside

Table 1. *Effects of year and protection of aspen from herbivory within exclosures on density (stems/ha) of aspen measured in 2 size classes on the National Elk Refuge, 1988-1996.*

	Mean Density (SE)		Test
Variable	Exclosure	No Exclosure	Result[2]
< 2 m tall	20,659 (3965)	13,074 (1824)	A
> 2 m tall[1]	9943 (1426)	590 (590)	B, C
Total	28,393 (4748)	13,533 (1771)	A

[1] estimated from 1990-1996

[2] A denotes a significant (P <0.05) treatment-year interaction

B denotes a significant treatment effect

C denotes a significant year effect

and the difference increased annually (Table 1, Fig. 1). The proportion of suckers >2 m tall averaged 51percent in the exclosures compared to 4 percent outside. We found the proportion of suckers >2 m tall continued to increase in the exclosures, while the proportion outside exclosures remained relatively stable (Fig. 2). The density of aspen <2 m tall was not significantly different between treatments due to the declining density of these suckers in the exclosures as they were recruited into the >2 m tall size class (Table 1, Fig. 3).

Both unbrowsed suckers and previously-browsed suckers were markedly taller within the exclosures than outside (Table 2). The average number of terminal leaders browsed was five times greater outside the exclosures, which showed an increasing trend over time (Fig. 3). No observable trends occurred within the exclosures for this variable. Thirteen percent of the suckers inspected within the exclosures showed evidence of browsing, as compared with 57 percent of suckers outside exclosures. The percentage of aspen suckers that were browsed was constant over time, in and out of the exclosures. Average height of suckers <2 m tall showed an increasing and asymptotic trend over time within exclosures. We observed no increase in average sucker height outside of the exclosures over time.

DISCUSSION

Sucker densities outside the exclosures remained stable from 1988 to 1995, averaging 7000-10,000/ha nine years post-treatment. Since no pre-treatment data were collected, we have no basis for comparison to judge the effectiveness of clear-cutting in stimulating suckering on these sites.

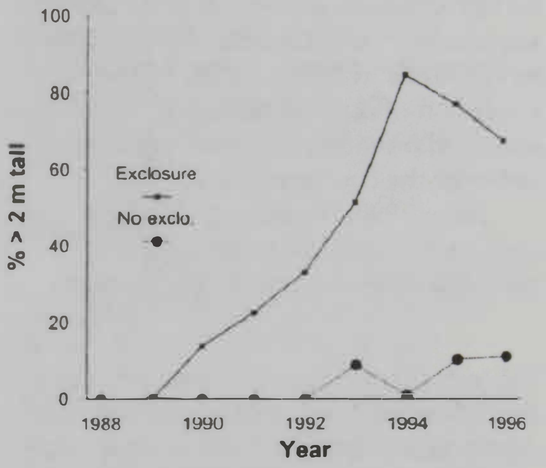

Figure 2. *Percent of aspen suckers > 2 m tall, 1988-1996.*

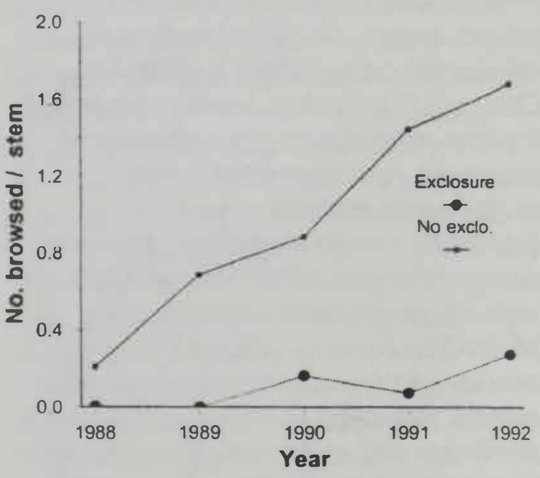

Figure 3. *Average number of terminal leaders browsed per aspen stem, 1988-1992.*

Table 2. *Browsing effects on regenerating aspen (<2 m tall) on the National Elk Refuge averaged from 1988 to 1996. Measurements obtained inside and outside exclosures were compared with paired Student's* t *tests.*

	Mean (n = 9 years)			
Variable	Exclosure	No exclosure	Differ. (SE_d)	P
Browsed sucker height (cm)	133	79	+54 (17)	0.086
Unbrowsed sucker height (cm)	120	42	+78 (9)	0.014
No. of terminal leaders browsed	0.3	1.5	-1.2 (0.2)	0.034

Crouch (1983) reported sucker densities approaching 76,000/ha one year following clear-cutting, as compared with 2500 on uncut control stands in southwest Colorado. Schier and Smith (1979) reported first year sucker densities averaging about 129,000/ha, in comparison with 8500/ha on the controls on a clearcut in Utah. In the same study, twelfth-year densities averaged over 14,000/ha, and were 4000/ha more than that recorded in our ninth year. Bartos and Mueggler (1982) reported sucker densities exceeding 45,000/ha two years post-clear-cutting in northern Utah, while uncut control sites averaged < 5000/ha.

Based on the results of these studies, we conclude that sucker generation substantially increased on our clearcut sites. The relatively low production of suckers may be related to the declining condition of the stands prior to treatment, or to site characteristics (Schier 1975). Regardless, initial sucker densities post-treatment should have been sufficient for stand replacement (Bartos et al. 1991). In contrast, sucker densities estimated in our exclosures followed trends typically observed in western aspen, i.e., a first year irruption, followed by a sharp decline in abundance in subsequent years (Bartos *et al*. 1991). We are uncertain if the difference in first year sucker densities between treatments was related solely to browsing-related effects.

The beneficial effects of clear-cutting in regenerating aspen stands are best demonstrated by the number of suckers that grow beyond 2 m tall. We considered 2 m the effective height beyond which young aspen stems will likely escape further browsing of terminal buds (Kay 1985). We found that sucker densities > 2 m tall were significantly greater in the exclosures across all 9 years, and more importantly, that the proportion of suckers recorded in this size class also was far greater inside exclosures than outside. During the ninth year post-treatment, <5 percent of the suckers outside of the exclosures were > 2 m tall, and these stems were restricted to a single stand. In contrast 68 percent of the suckers recorded in the three exclosures were >2 m tall during the ninth year. Browsing apparently inhibited aspen growth and recruitment on these sites. This conclusion is corroborated by our observation that the proportion of suckers browsed was four times greater outside exclosures than inside (also indicating that our exclosures, as physical barriers to ungulates, were less than completely effective).

As expected, we observed an increasing trend in the frequency of terminal leader browsing over time outside of the exclosures, and average sucker heights were considerably taller in the exclosures than outside. We also observed that suckers, which had never been browsed, were considerably shorter outside of exclosures than inside. This suggested that repeated annual browsing substantially increased mortality, stimulated further suckering, and in effect, created younger sucker age classes. This also would explain the lack of declining trend in sucker densities outside of the exclosures. If true, continued browsing may expedite the decline of these treated stands as food reserves in the clonal root systems are exhausted (Schier *et al*. 1985). In fact, clear-cutting may have actually hastened the demise of these stands.

It is clear from our data that browsing-related effects prevented young suckers from growing beyond the reach of further browsing and reduced the rate of recruitment for overstory replacement. Increasing the size of clearcuts may help mitigate this problem in areas of high ungulate use. Mueggler and Bartos (1977) concluded that, "Without control of ungulate use, clear-cutting or burning less than about

5 hectares of mature aspen might be futile." Our results support their conclusions. Persistent ungulate browsing on the refuge may necessitate treating much larger areas of mature aspen in the future, or reducing elk numbers to facilitate maintenance of multi-aged aspen stands on the landscape.

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