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IJS

INTERMOUNTAIN JOURNAL OF SCIENCES

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Manuscripts are submitted to the Editor-in-Chief (EIC) for initial consideration for publication in the IJS. This review shall include, but not be limited to, appropriateness for publication in this journal, correct formatting, and inclusion of a letter of submittal by the author with information about the manuscript as stated in the "Guidelines for manuscripts submitted to the *Intermountain Journal of Sciences*" (Dusek 1995). This cover letter must also include a statement by the author that this paper has not been submitted for publication or published elsewhere. The EIC notes the date of receipt of the manuscript and assigns it a reference number, IJS-xxxx. The EIC forwards a letter of manuscript receipt and the reference number to the corresponding author. The corresponding author is the author who signed the submittal letter.

Three hard copies of the submitted manuscript, with copies of the "Guidelines and checklist for IJS referees" attached are forwarded to the appropriate Associate Editor. The Associate Editor retains one coy 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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For accepted manuscripts, each copy of the manuscript containing comments thereon and other comments are returned to the corresponding author. Revised manuscripts are to be returned to the EIC in hard copy, four copies if further review is required, or one hard copy plus the computer disk if only minor revision or formatting is necessary. The revised manuscript shall be returned to the EIC within 14 days of the notification. Review of the revised manuscript by the Associate Editor and reviewers shall be completed and returned to the EIC within 14 days. An accepted manuscript will then be forwarded to the Managing Editor (ME) for final processing.

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Each manuscript submitted by an Associate Editor shall be reviewed by the EIC and a minimum of two other reviewers with expertise in the subject being addressed. Each manuscript submitted by the EIC shall be forwarded with the necessary review materials to the Chairman of the Editorial Board of IJS, who will serve as the EIC for that manuscript.

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Only abstracts from the annual meetings of the sponsoring organizations will be published in IJS. Other submissions of abstracts shall be considered on a case-by-case basis by the Editorial Board. Sponsoring organizations shall collect abstracts, review them for subject accuracy, key or scan them onto a 3.5" diskette, and submit the diskette and hard copy of each abstract to the EIC on or before November 1. Each abstract shall be reviewed by the EIC to assure proper grammar, compliance with IJS "Guidelines for Abstracts Only" and for assignment to the appropriate discipline section. All abstracts will be published in the December issue only.

COMMENTARY

Submissions concerning management applications or viewpoints concerning current scientific or social issues of interest to the Intermountain region will be considered for publication in the "Commentary" Section. This section will feature concise, well-written manuscripts limited to 1,500 words. Commentaries will be limited to one per issue.

Submissions will be peer reviewed and page charges will be calculated at the same rate as for regular articles.

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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DRIFTING INVERTEBRATE COMPOSITION, DENSITIES, AND BIOMASS FROM FALL THROUGH WINTER IN THREE WYOMING TAIL WATERS

Jason L. Hebdon, Wyoming Cooperative Fish and Wildlife Research Unit, USGS, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166
Wayne A. Hubert, Wyoming Cooperative Fish and Wildlife Research Unit, USGS, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166

ABSTRACT

We studied three regulated rivers downstream from reservoirs (tailwaters) in Wyoming from October 1997 through February 1998 to assess the temporal variation in composition, density, and biomass of drifting invertebrates. Macroinvertebrates were numerically dominated by Diptera (primarily Chironomidae) and Ephemeroptera in the North Platte and Big Horn rivers with Trichoptera, Oligochaeta, and Arachnida (Hydracarina) also common. In the Shoshone River, the predominant macroinvertebrate taxon was Oligochaeta followed by Diptera and Ephemeroptera. Densities of drifting macroinvertebrates were lowest in November and highest in January in the North Platte and Big Horn rivers. However, densities of drifting macroinvertebrates were lowest in October and highest in November in the Shoshone River. The composition of drifting invertebrates changed from exclusively macroinvertebrates in October and November to predominantly zooplankton in December through February in all three rivers. However, drifting macroinvertebrates were relatively abundant throughout the winter in all three tailwaters compared to other river systems.

Key words: aquatic invertebrates, drifting, macroinvertebrates, river regulation, tailwaters, winter

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INTRODUCTION

Dams have been constructed on many rivers to store water and regulate downstream flows thereby altering the physical conditions of the downstream river, particularly within reaches immediately downstream from reservoirs (tailwater). A notable change is the release of cool, nutrient rich water from the hypolimnion during summer (Allan 1995). As a consequence of the altered thermal regime, endemic fishes and invertebrates can be extirpated. Managers have frequently introduced trout into tailwaters to create highly valued, coldwater sport fisheries (Pfitzer 1967). In such systems, drifting macroinvertebrates are a primary food of trout (Filbert and Hawkins 1995, Simpkins and Hubert 2000, Hebdon and Hubert 2001).

Invertebrates in lotic systems are transported downstream in the water column in substantial numbers (Allan 1995). Their downstream transport has been related to a variety of biotic and abiotic factors including catastrophic events, i.e., floods, anchor ice or high water temperatures, and behavior, i.e., diel activity, avoidance of predators, or accidental dislodging. However, most research on drifting invertebrates has been conducted on unregulated streams with natural flow regimes. Few studies have been conducted on drifting invertebrates in tailwaters supporting trout, and temporal trends in drifting invertebrates and their potential effects on trout fisheries in tailwaters are poorly understood (Armitage 1977). Perry and Perry (1986) and Poff and Ward (1991) assessed the effects of shortterm variation in discharge on the magnitude of drifting invertebrates during different seasons in Montana and Colorado tailwaters. Seasonal variation in density of drifting invertebrates has been described in a Utah tailwater (Filbert and Hawkins 1995). In the only previous study of fall through winter trends known to us, Simpkins and Hubert (2000) found that densities of drifting macroinvertebrates in a Wyoming tailwater declined by almost 90 percent from September to December, but by February they recovered and surpassed September levels. How widespread such temporal patterns may be among tailwaters supporting trout in the western United States is unknown. Because long sections of tailwaters remain free of surface ice, trout continue to feed during winter (Filbert and Hawkins 1995, Simpkins and Hubert 2000, Hebdon and Hubert 2001). Understanding the dynamics of drifting invertebrates during winter could be important to managing these fisheries.

Our goal was to determine the dynamics of drifting invertebrates from fall through winter in Wyoming tailwaters. We assessed temporal variation in composition, density, and biomass of drifting macroinvertebrates and zooplankton from October through February in three selected tailwaters in Wyoming to determine if temporal trends were similar among them.

STUDY SITES

We selected for study three of the five tailwaters in Wyoming that support economically important trout fisheries: (1) the North Platte River downstream from Gray Reef Dam, (2) the Bighorn River downstream from Boysen Dam, and (3) the Shoshone River downstream from Buffalo Bill Dam. The North Platte River downstream from Kortes Dam was omitted because there is only a short segment of river (~2 km) between the dam and Pathfinder Reservoir. The Green River downstream from Fontenelle Dam was not studied because it is difficult to access during winter.

One study site was on the North Platte River, 15 km downstream from Gray Reef Dam. Mean October discharge (1904-1998) has been 18 m^3/s and it generally remains constant or declines slightly during winter. This site has a mean wetted width of about 60 m during fall and winter. The tailwater supports naturalized populations of rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*), and receives annual stocking of rainbow trout.

The second study site was on the Bighorn River, 22 km downstream from Boysen Dam. Mean October discharge (1951-1998) has been 34 m^3/s and often fluctuates between 30 and 34m^3/s during winter. The river is 50 m wide at this site during winter flows. The river has a naturalized population of brown trout and rainbow trout are stocked annually to maintain the fishery although a small amount of natural recruitment by rainbow trout has been observed over a short portion of the tailwater (Wiley 1995).

A third study site was on the Shoshone River, 13 km downstream from Buffalo Bill Dam. Mean discharge during October (1943-1998) has been 19 m^3/s and it generally declines to 14-15 m^3/s during winter. The wetted width at this site is about 30 m at winter flows. This tailwater supports populations of naturalized brown trout, stocked cutthroat trout (*Oncorhynchus clarki*), and rainbow trout that escape from Buffalo Bill Reservoir. This site was unique in that warm springs approximately 8 km upstream from the study site added concentrations of hydrogen sulfide lethal to salmonids and many invertebrate taxa and warmed the water 4-5 °C. Hydrogen sulfide dissipated so it was no longer detectable 3-4 km upstream from the study site (Dare et al. 2001), but water temperatures warmer than ambient persisted at the study site (Hebdon 1999).

METHODS

Water temperatures were recorded at 30-minute intervals from October 1997 through February 1998 using two thermographs (Optic Stowaways, Onset Computer Corporation, Pocassett, Massachussetts) approximately 2 km upstream and downstream of each study site. Thermographs were placed in water at least 0.5 m deep with velocities greater than 15 cm/s. Daily estimates of discharge were obtained from gages between the upstream reservoirs and the study reaches (Water Resources Data System, Department of Civil and Architectural Engineering, University of Wyoming, Laramie).

We sampled during the day, 3-4 hours after sunrise. Diel variation in the density of drifting macroinvertebrates is common with greater densities during the night (Allan 1995), but whether such temporal trends occur during fall and winter in tailwaters is not known. Since our purpose was to assess temporal variation from fall through winter, we limited our sampling to a short duration during the day to reduce variability at individual sites and enhance the statistical power of comparisons among monthly sampling periods.

Field sampling occurred monthly, October 1997 through February 1998, at a single site in all three tailwaters. Twenty samples of drifting invertebrates were collected each month from each tailwater. Sampling occurred diagonally across a 50-m reach at points where the water was 0.6-0.9 m deep with velocities of 30-60 cm/s. A 363-micron-mesh net (45 x 30 x 90 cm) was placed midway between the surface and the bottom. Sampling began at the downstream boundary of the reach and progressed across and upstream to avoid collecting invertebrates dislodged by observers. Sample duration (3-5 minutes) was adjusted so that approximately 15 m^3 of water was filtered for each sample.

Samples were separated into macroinvertebrate and zooplankton components by sieving through a 2-mm mesh screen. All macroinvertebrates retained by the seive were identified to family and enumerated. Because of high densities of zooplankton in many samples, the apparatus described by Wrona et al. (1982) was used to subsample. The zooplankton portion was placed into a 1-L graduated Imhof settling cone fitted with an aquarium airstone sealed in the bottom and connected to a compressed air supply. The total volume of the sample was increased to 1-L by adding water. The sample was mixed for 2-5 minutes by bubbling air and three subsamples were removed in known volumes of 10, 25 or 50 ml depending on the density of zooplankton in the cone. Zooplankton in subsamples were identified as Cladocera or Copepoda and enumerated. The mean and standard error (SE) of the number of zooplankton per subsample were calculated with adjustment to the SE to account for the finite population: corrected $SE = SE * (1-f)^{0.5}$ where f = number of subsamples/total number of subsamples possible. If the coefficient of variation (CV) was less than 20 percent, no additional subsamples were obtained. If the CV exceeded 20 percent, additional subsamples were drawn until the CV was reduced to less than 20 percent. The proportions of each taxon in the subsamples were multiplied by the estimate to give an estimate of the number of individuals in each taxon.

Estimates of the biomass of macroinvertebrates and zooplankton were made by multiplying the estimated number of individuals in a taxon by the mean weight of individuals in the taxon after drying. Individuals of each taxon from each river were pooled within each month and dried for 24 hr at 60 °C to estimate mean biomass/individual for each taxon.

Sample distributions of densities and biomass were consistently skewed so a Kruskall-Wallis test was used to determine if differences in density and biomass of drifting invertebrates occurred among months. Analysis was conducted using Minitab 12.21 (Minitab, Inc.) and Sigmastat 1.0 for Windows (Jandel Scientific). Significance was determined at $\alpha = 0.05$ for all tests.

RESULTS

Water temperatures during the study were colder in the North Platte and Bighorn rivers than in the Shoshone River. Mean daily water temperature between 1 October 1997 and 28 February 1998 (151 days) was 0.0-3.9 °C with a mean <4 °C recorded 89 days in the North Platte River, 0.1-14.6 °C with a mean <4 °C recorded 86 days in the Bighorn River, and 3.8-12.6 °C with a mean <4 °C on only 2 days in the Shoshone River.

Discharge patterns varied among the three tailwaters during the study. A planned flushing flow resulted in a 50 m^3/s discharge in the North Platte River between 6 and 10 October 1997 (prior to our first sampling), but during sampling the discharge was 16-17 m^3/s. Discharge in the Bighorn River was 65 m^3/s during most of October, but it was reduced to winter levels from 24 to 28 October 1997. For the study period, excluding October, flows were 26-34 m^3/s in the Bighorn River. Flows on the Shoshone River were reduced to winter levels from 7 to10 October 1997, and during the study period they were 13-15 m^3/s.

The major taxonomic groups of drifting macroinvertebrates among samples from all three rivers were Diptera, Ephemeroptera, Oligochaeta,Trichoptera, Arachnida (Hydracarina). Diptera were composed primarily of Chironomidae and Simulidae, but Stratiomyidae were also observed. Ephemeroptera were primarily Baetidae, Ephemerellidae, and Trichorythidae.

Trichoptera were Hydropsychidae, Limniphillidae, Hydroptillidae, and Helicopshchidae with Hydropshchidae being most common. Other macroinvertebrate taxa collected sporadically included Coleoptera, Hemiptera, Hymenoptera, Odonata, and Plecoptera. When zooplankton were collected, Cladocera and Copepoda were present in relatively equal proportions.

Taxonomic composition of the invertebrates was similar among samples from the North Platte and Bighorn rivers, but differed from the Shoshone River due to the high abundance of Oligochaeta and low abundance of zooplankton in the Shoshone River (Table 1). Diptera and Ephemeroptera comprised 70-92 percent of the macroinvertebrates in samples from the North Platte and Bighorn rivers over the 5 months. Whereas, Diptera and Ephemeroptera comprised 33-78 percent and Oligochaeta comprised 17-61 percent of the macroinvertebrates in the Shoshone River. Zooplankton was absent from all samples taken in October and November, but occurred in high densities in December through February in all three rivers. In December through February, zooplankton comprised 96-99 percent of the invertebrates in samples from the North Platte and Bighorn rivers, but made up a somewhat lower percentage (60-87%) of the invertebrates in samples from the Shoshone River.

Significant differences in densities of drifting macroinvertebrates occurred from October to February among most taxa that were assessed in all three rivers (Table 1). The sampling months with minimum and maximum densities of various taxa of macroinvertebrates and zooplankton differed among the three rivers with no consistent temporal trends among tailwaters. However, Diptera and Ephemeroptera tended to increase in densities through the fall and to be most abundant in January and February.

The biomass of drifting invertebrates also varied significantly from October to February among most taxa that were assessed in all three rivers (Table 2). Biomass of drifting macroinvertebrates was dominated by Diptera and Ephemeroptera in all three rivers. Together, these two taxa comprised 66-95 percent of the biomass of macroinvertebrates in samples from the three rivers over the 5 months. However, Oligochaeta comprised up to 25 percent of the biomass of macroinvertebrates in the Shoshone River. Zooplankton comprised 53-99 percent of the biomass of drifting invertebrates in the North Platte and Bighorn rivers, but only 3-10 percent in the Shoshone River from December to February.

Table 1. Mean densities (number/100 m^3) of drifting invertebrates in monthly samples during the fall and winter of 1997-1998 from three regulated rivers in Wyoming. Standard deviations in parentheses. *P*-values are for Kruskal-Wallis tests assessing differences among months.

	Month					
Taxa	October	November	December	January	February	*P*
			North Platte			
Diptera	146 (71)	75 (55)	78 (33)	462 (247)	265 (141)	<0.001
Ephemeroptera	197 (91)	53 (47)	118 (51)	346 (353)	204 (91)	<0.001
Trichoptera	16 (19)	4 (9)	32 (29)	156 (117)	21 (24)	<0.001
Oligochaeta	29 (21)	8 (13)	14 (20)	29 (43)	8 (17)	0.109
Arachnida	5 (7)	2 (5)	4 (8)	34 (54)	15 (21)	0.012
Other macroinvertebrates	5 (15)	2 (2)	<1 (4)	25 (<1)	18 (7)	0.003
Zooplankton	0	0	6,470 (1,388)	127,043 (24,264)	77,458 (36,251)	<0.001
			Big Horn			
Diptera	252 (175)	20 (25)	13 (16)	119 (232)	144 (172)	<0.001
Ephemeroptera	468 (242)	43 (45)	142 (74)	474 (439)	288 (141)	<0.001
Trichoptera	8 (17)	7 (9)	11 (15)	70 (239)	8 (19)	0.121
Oligochaeta	44 (7)	8 (14)	20 (22)	84 (237)	25 (51)	0.046
Arachnida	7 (11)	3 (6)	3 (6)	59 (241)	5 (18)	0.486
Other macroinvertebrates	14 (45)	1 (4)	0	41 (52)	0	<0.001
Zooplankton	0	0	121,479 (43,151)	43,427 (13,784)	21,913 (5,428)	<0.001
			Shoshone			
Diptera	33 (24)	363 (150)	259 (289)	323 (414)	422 (270)	<0.001
Ephemeroptera	53 (44)	137 (69)	193 (189)	225 (173)	248 (149)	<0.001
Trichoptera	14 (18)	7 (15)	32 (47)	29 (38)	7 (14)	<0.001
Oligochaeta	159 (188)	737 (409)	253 (182)	121 (125)	389 (224)	<0.001
Arachnida	0	0	1 (4)	<1 (2)	4 (14)	0.544
Other macroinvertebrates	0	0	0	0	0	
Zooplankton	0	0	5,042 (2,666)	1,069 (434)	3,798 (1,228)	<0.001

DISCUSSION

Our results and those of previous studies indicated that Diptera and Ephemeroptera tend to be the primary taxa of drifting macroinvertebrates from fall through winter in tailwaters of the western United States. This was the case in the Bighorn and North Platte rivers and it has also been observed in tailwaters in Wyoming, Montana, Colorado, and Utah (Kroger 1974, Perry and Perry 1986, Poff and Ward 1991, Filbert and Hawkins 1995). However, the predominant macroinvertebrate taxa in samples from the Shoshone River was Oligochaeta, followed by Diptera and Ephemeroptera. This unique situation may have resulted from the input of toxic levels of hydrogen sulfide 8 km upstream from the study site. Dare et al. 2001 found that hydrogen sulfide concentrations lethal to salmonids extended downstream to with 3-4 km of our sampling site. The relatively high abundance of Oligochaeta and Diptera may have occurred because our sampling site was within the zone of recovery associated with impacts from a point source of hydrogen sulfide (Hynes 1960).

Drifting macroinvertebrates were relatively abundant throughout the fall and winter in all three Wyoming tailwaters. Densities of macroinvertebrates in the three

Table 2. Mean biomass (mg/100 m^3) of drifting invertebrates in monthly samples during the fall and winter of 1997-1998 from three regulated rivers in Wyoming. Standard deviations in parentheses. *P*-values are for Kruskal-Wallis tests assessing differences among months.

	Month					
Taxa	**October**	**November**	**December**	**January**	**February**	***P***
North Platte						
Diptera	13 (8)	10 (8)	13 (7)	82 (42)	42 (22)	<0.001
Ephemeroptera	7 (4)	3 (4)	14 (15)	58 (34)	29 (40)	<0.001
Trichoptera	1 (1)	<1 (1)	<1 (1)	19 (19)	<1(<1)	<0.001
Oligochaeta	3 (2)	3 (5)	1 (3)	4 (6)	1 (2)	0.378
Arachnida	1 (1)	<1 (1)	<1 (<1)	3 (5)	<1 (<1)	0.014
Other macroinvertebrates	0	0	0	4 (3)	14 (14)	0.867
Zooplankton	0	0	31 (31)	607 (610)	369 (330)	<0.001
Big Horn						
Diptera	21 (15)	2 (3)	1 (2)	23 (37)	61 (67)	<0.001
Ephemeroptera	8 (9)	1 (1)	4 (2)	13 (12)	10 (6)	
<0.001						
Trichoptera	<1 (1)	<1 (<1)	<1 (<1)	1 (2)	<1 (<1)	0.255
Oligochaeta	2 (2)	<1 (1)	<1 (<1)	7 (20)	17 (35)	0.195
Arachnida	<1 (<1)	<1 (<1)	<1 (<1)	2 (7)	<1 (1)	0.486
Other macroinvertebrates	4 (17)	0	0	1 (2)	0	<0.001
Zooplankton	0	0	919 (327)	329 (104)	166 (41)	<0.001
Shoshone						
Diptera	4 (4)	26 (11)	20 (23)	23 (28)	45 (29)	<0.001
Ephemeroptera	4 (5)	8 (7)	6 (6)	11 (9)	19 (12)	<0.001
Trichoptera	3 (5)	2 (4)	5 (8)	3 (4)	1 (2)	0.103
Oligochaeta	1 (1)	6 (3)	3 (2)	1 (1)	4 (2)	<0.001
Arachnida	0	0	<1 (1)	<1 (1)	2 (5)	0.544
Zooplankton	0	0	14 (7)	3 (1)	10 (3)	<0.001

Wyoming tailwaters during fall and winter were similar to what has been observed among other tailwaters in the western United States. We observed that mean densities of drifting macroinvertebrates had ranges of 263-800/100 m^3 in October, 189-777/100 m^3 in December and 469-1073/100 m^3 in February among the three Wyoming tailwaters. Mean densities of macroinvertebrates in the Green River, Utah, downstream from Flaming Gorge Reservoir were estimated to be to be 525/100 m^3 in October 1987 and 271/100 m^3 in February 1988 (Filbert and Hawkins 1995). Similarly, densities of drifting insects in the Colorado River, Colorado, downstream from Grandby Reservoir were observed to be 540-630/100 m^3 in November 1985 at stable flows (Poff and Ward 1991).

Densities of macroinvertebrates among tailwaters in the western United States appear high relative to other lotic systems during fall and winter. Culp et al. (1994) defined low densities of drifting invertebrates to be less than 50/100 m^3 and high densities to be greater than 500/100 m^3. Given these standards, the Wyoming tailwaters had moderate to high densities of macroinvertebrates drifting in the daytime during fall and winter. Macroinvertebrate densities during winter in Wyoming tailwaters were similar to tropical streams in Costa Rica (Pringle and Ramirez 1998) and generally exceeded large rivers in Europe

(Cellott 1989). Densities of drifting macroinvertebrates in the three Wyoming tailwaters during fall and winter appeared to be substantially greater than what has been observed in Appalachian Mountain streams (O'Hop and Wallace 1983, Cada et al. 1987) and regulated and unregulated streams in Great Britain (Armitage 1977).

Similar monthly samples of drifting macroinvertebrates were collected from October 1995 through February 1996 in the same reach of the Bighorn River that we studied (Simpkins and Hubert 2000). Densities of drifting insects in our study were similar to those in 1995-1996 during October, December, and January, but substantially lower in November and February. Water temperatures were similar during both fall through winter periods, with the exception that water temperatures cooled more rapidly in October 1995 that in October 1997 (Hebdon 1999, Simpkins and Hubert 2000).

Zooplankton originating from upstream reservoirs dominated the drifting invertebrates during winter (December-February) in the three Wyoming tailwaters, but the extent to which drifting zooplankton occur in other tailwaters of the western United States during winter is unknown. Simpkins and Hubert (2000) first described the winter pattern of high densities of drifting zooplankton in the Bighorn River downstream from Boysen Reservoir. We observed similar occurrence of zooplankton in the North Platte and Shoshone rivers. In all three tailwaters, drifting zooplankton were found after the upstream reservoirs became ice covered. However, densities of zooplankton were substantially lower in the Shoshone River than in the North Platte and Bighorn rivers. We believe that this is likely due to lethal levels of hydrogen sulfide between Buffalo Bill Reservoir and the study site (Dare et al. 2001).

Our results combined with those of Hebdon and Hubert (2001) suggest that drifting macroinvertebrates are sufficiently abundant through the fall and winter in the Bighorn and North Platte rivers to provide adequate food resources for trout. Hebdon and Hubert (2001) studied the stomach contents and body conditions of subadult trout in these two tailwaters at the same time that our study of drifting invertebrates was conducted. They found that fish fed throughout the winter and maintained greater than average body conditions. These observations indicate that starvation was not a cause of overwinter mortality of subadult trout in these two tailwaters. However, we found that the density of drifting macroinvertebrates were lower in the Shoshone River compared to the Bighorn and North Platte rivers. Also, Hebdon and Hubert (2001) observed fewer food items in stomachs and declining body conditions during the winter in the Shoshone River. It is likely that the combination of lower densities of drifting macroinvertebrates and higher metabolic rates associated with warmer water temperatures may affect overwinter survival of subadult trout in the Shoshone River. The presence of warm springs in the Shoshone River appear to make it unique among Wyoming tailwaters and the dynamics of trout in the system appear to differ from other tailwaters as a result.

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EXTRACTION OF WHIRLING DISEASE MYXOSPORES FROM SEDIMENTS USING THE PLANKTON CENTRIFUGE AND SODIUM HEXAMETAPHOSPHATE

Jay C. Lemmon. Ecology Department, Montana State University, Bozeman. MT 59717
Billie L. Kerans, Ecology Department, Montana State University, Bozeman, MT 59717

ABSTRACT

Myxobolus cerebralis, the causative agent of whirling disease in salmonids, has two transmission stages: the myxospore (released by salmonids) and the triactinomyxon (released by an aquatic tubificid worm, *Tubifex tubifex).* Myxospores are released into sediments after fish infected with *M. cerebralis* die and their carcasses decompose. The purpose of this study was to determine if it was possible to extract and enumerate *M. cerebralis* myxospores that were experimentally added to autoclaved sand and benthic sediments using a plankton centrifuge alone or in conjunction with sodium hexametaphosphate. The plankton centrifuge is commonly used to extract myxospores from salmonid skeletal elements and the technique involves filtration and sedimentation of myxospores. Sodium hexametaphosphate is a non-sudsing detergent that decreases soil aggregation making filtration more efficient. When the plankton centrifuge technique was used alone, we were only able to extract an average of 8 percent of myxospores, inoculated into sediments. However, we were able to extract between 50-70 percent of *M. cerebralis* myxospores when sodium hexametaphosphate and the plankton centrifuge were used together. This technique could further enhance understanding of the ecology of the parasite and its association with *T tubifex.*

Key Words: extraction, *Myxobolus cerebralis*, myxospores, plankton centrifuge, sodium hexametaphosphate, *Tubifex tubifex*, whirling disease.

INTRODUCTION

Whirling disease, the common name of a disorder of some salmonids, e.g., trout, salmon, is caused by the microscopic parasite *Myxobolus cerebralis* (Hedrick et al. 1998). The parasite has recently been implicated as the cause of severe declines in some wild rainbow trout (*Oncorhynchus mykiss*) populations in the Intermountain West (Nehring and Walker 1996, Vincent 1996). The life cycle of *M. cerebralis* alternates between fish and the tubificid, *Tubifex tubifex* (Markiw and Wolf 1983, Wolf and Markiw 1984). *Tubifex tubifex* expels the triactinomyxon form, which becomes suspended in the water column (El-Matbouli and Hoffmann 1998). Sporoplasms are injected into the fish's tissue, e.g., epithelium and gills, when triactinomyxons come in contact with salmonids (Hedrick et al. 1998). After contact the sporoplasms migrate toward the cartilage in vertebrae, gill arches, and cranium where infection develops (El-Matbouli et al. 1995). As fish die and decompose, myxospores (10-µm dia.; Hedrick et al. 1998) are released into benthic sediments where they are ingested by *T. tubifex* and the cycle begins again.

Abundances of *M. cerebralis* myxospores in benthic sediments are unknown and no technique has been developed to detect and enumerate them. However, the plankton centrifuge is routinely used to extract myxospores from skeletal elements of salmonids (O'Grodnick 1975). The technique involves filtering macerated skeletal elements and sedimenting myxospores in the plankton centrifuge. Our goal was to use the plankton centrifuge technique to extract myxospores from sediments. However, we suspected that small soil particles (silt and clay) would promote soil aggregation and make filtration and visualization of myxospores difficult; thus, the plankton centrifuge technique might be inefficient if used alone (Buffle and Leppard 1995b). Consequently, we also tested the plankton centrifuge with aqueous sodium hexametaphosphate ($[NaPO_3]_{6aq}$), a non-sudsing detergent, that induces de-aggregation of natural soil aggregates (Bakken 1985, Buffle and Leppard 1995a, Day et al. 1995). Our objective was to ascertain the efficiency of the plankton centrifuge, alone and with $[NaPO_3]_{6aq}$, to extract *M. cerebralis* myxospores that were experimentally added to sediments.

METHODS AND MATERIALS

We tested myxospore extraction from autoclaved sand and benthic sediments. We used autoclaved sand because we expected optimal myxospore recoveries when the percentage of fine sediments (silt and clay) and their associated bacteria were low. We used benthic sediments to test myxospore extraction under natural conditions and to determine if we could detect wild *M. cerebralis* myxospores. The benthic sediments were collected from the East Fork of Rock Creek and the West Fork of the Madison River, Montana, where whirling disease is epizootic (Vincent 2000). Using particle fractionation and size analysis (Day 1965), we determined that the autoclaved sand was 99 percent sand (2000 to 50 µm in diameter), 1 percent silt (50 to 2 µm in diameter) and had no clay (< 2 µm in diameter). The benthic sediments were composed of more silt and clay than the autoclaved sand (West Fork of the Madison River, 85-87% sand, 11-12% silt and 2-3% clay; East Fork of Rock Creek, 61-73% sand, 25-31% silt and 2-8% clay). For all trials, *M. cerebralis* myxospores were removed from fish by grinding heads in a blender, filtering the myxospore solution through a 50-µm sieve, and sedimenting the filtrate (the solution passing through the sieve) that contained the myxospores in a plankton centrifuge (O'Grodnick 1975). The resulting pellet was resuspended in water and myxospores were enumerated by placing an aliquot of the solution on a 0.4-mm Neubauer hemacytometer (Markiw and Wolf 1974). The numbers of myxospores counted on the hemacytometer were then extrapolated to calculate the total number of myxospores in solution. Myxospores were counted in a similar manner after extraction from sediments. In the trials with autoclaved sand without $[NaPO_3]_{6aq}$ and for two trials of autoclaved sand with $[NaPO_3]_{6aq}$, we only counted myxospores on the hemacyctometer once at the beginning and once at the end of the trials. In all other trials, we enumerated myxospores on the hemacytometer three times at the beginning of a trial and three times at the end of the trial. The mean of three replicate hermacytometer counts was used to characterize total myxospore numbers. Our method of comparing myxospore numbers assumed that any biases in enumeration techniques were similar before and after extraction and that those myxospores unaccounted for were lost during extraction.

Autoclaved sand without $[NaPO_3]_{6aq}$

In the first trial about $4.3x10^5$ myxopores were placed in 100 ml of autoclaved sand and covered with water. The myxospore and sand solution was thoroughly mixed and then passed through a series of sieves (500 to 123 µm) while being flushed with water. The filtrate (solution passing through the sieves containing the myxospores) was placed in the plankton centrifuge. The resulting pellet was resuspended in water and passed through a 20-µm sieve. The number of myxospores in the filtrate was determined using the methods described above. Only one replicate hemacytometer count was used before and after the trial.

The second trial was similar to the first, except that about $3.6x10^4$ myxospores were added to 25 ml of sand and then water was added to bring the volume to 75 ml. The sieve series ran from 500 to 63 µm. The filtrate that passed through the 63-µm sieve was placed in the plankton centrifuge and the resulting pellet was resuspended in water, sieved (20 µm), and examined for myxospores as above. Testing was abandoned after two trials because of low extraction success.

Autoclaved sand with $[NaPO_3]_{6aq}$

A range of myxospore abundances ($1.4x10^4$-$2.2x10^5$) were added to 7 g of autoclaved sand and 35 ml of $[NaPO_3]_{6aq}$ in a 50-ml centrifuge tube. Aqueous $[NaPO_3]_6$ was prepared by using 6200 mg of $[NaPO_3]_6$/L. The myxospores, autoclaved sand, and $[NaPO_3]_{6aq}$ were agitated for three minutes by repeated inversion of the centrifuge tube. The sand was then allowed to settle out of solution (40 seconds; Gee and Bauder 1979, 1986). The supernatant with the silt, clay, and myxospores was removed with a macropipet and placed in a 1000-ml beaker. The remaining particles in the centrifuge tube were subsequently washed with 35 ml of $[NaPO_3]_{6aq}$. This washing process was repeated 25 times to maximize the removal of myxospores from the sediments. All of the combined supernatants (the 25 repetitions) were wet sieved through a 20-µm filter with deionized water. Myxospores were sedimented from the filtrate using a plankton centrifuge. The concentrated filtrate was diluted with deionized water and three replicate counts on the hemacytometer were made to determine the number of myxospores recovered. We regressed the mean number of myxospores recovered against the mean number of myxospores that were initially stocked into the sediments. We also examined the material collected by the filter to determine if myxospores were retained in the sediment.

Benthic sediments with $[NaPO_3]_{6aq}$

The procedures for benthic sediments were similar to those with the autoclaved sand, except myxospores were stained before the initial enumeration to distinguish them from wild myxospores (if present) in the benthic sediments. Only nonviable myxospores will stain so myxospores were killed by heating to 90°C for 10 minutes (Hoffman and Markiw 1977). Nonviable myxospores were stained for 10 minutes with 0.25 percent aqueous methylene blue (18 µl 0.25% aqueous methylene blue/37 µl myxospore solution). After staining, the solution was centrifuged at 4000 revolutions/minute for 20 minutes to remove residual stain in solution and the supernatant with the residual stain was discarded. The pellet was resuspended with deionized water and centrifuged again (4000 revolutions/minute for 20 minutes) for further removal of stain. The resulting pellet containing the myxospores was resuspended in water. We added between $7.5x10^3$ and $4.7x10^5$ myxospores to 7 g of benthic sediment. The extraction protocol and statistical analysis used in the autoclaved sand experiment with $[NaPO_3]_{6aq}$ were then followed.

RESULTS AND DISCUSSION

We extracted no myxospores from our first trial and only 5834 myxospores (16 %) from the second trial when the plankton centrifuge was used alone with sand. We were able to extract *M. cerebralis* myxospores from both sediment types when aqueous $[NaPO_3]_6$ was used with the plankton centrifuge. Mean percent myxospore recovery was higher in sand (70.9 ± 7.6 [1 SE], $n = 7$) than in benthic sediment (59.4 ± 15.3 [1 SE], $n = 9$). Slopes of the regressions of myxospore recovery in sand and benthic sediments were statistically significant (Fig. 1), suggesting that percent recovery was similar across myxospore doses within a sediment type. The regressions relating number of myxospores recovered to initial number of myxospores fit very well ($r^2 > 0.96$). Consequently, it would be possible to predict the number of myxospores in sediments based on the number recovered.

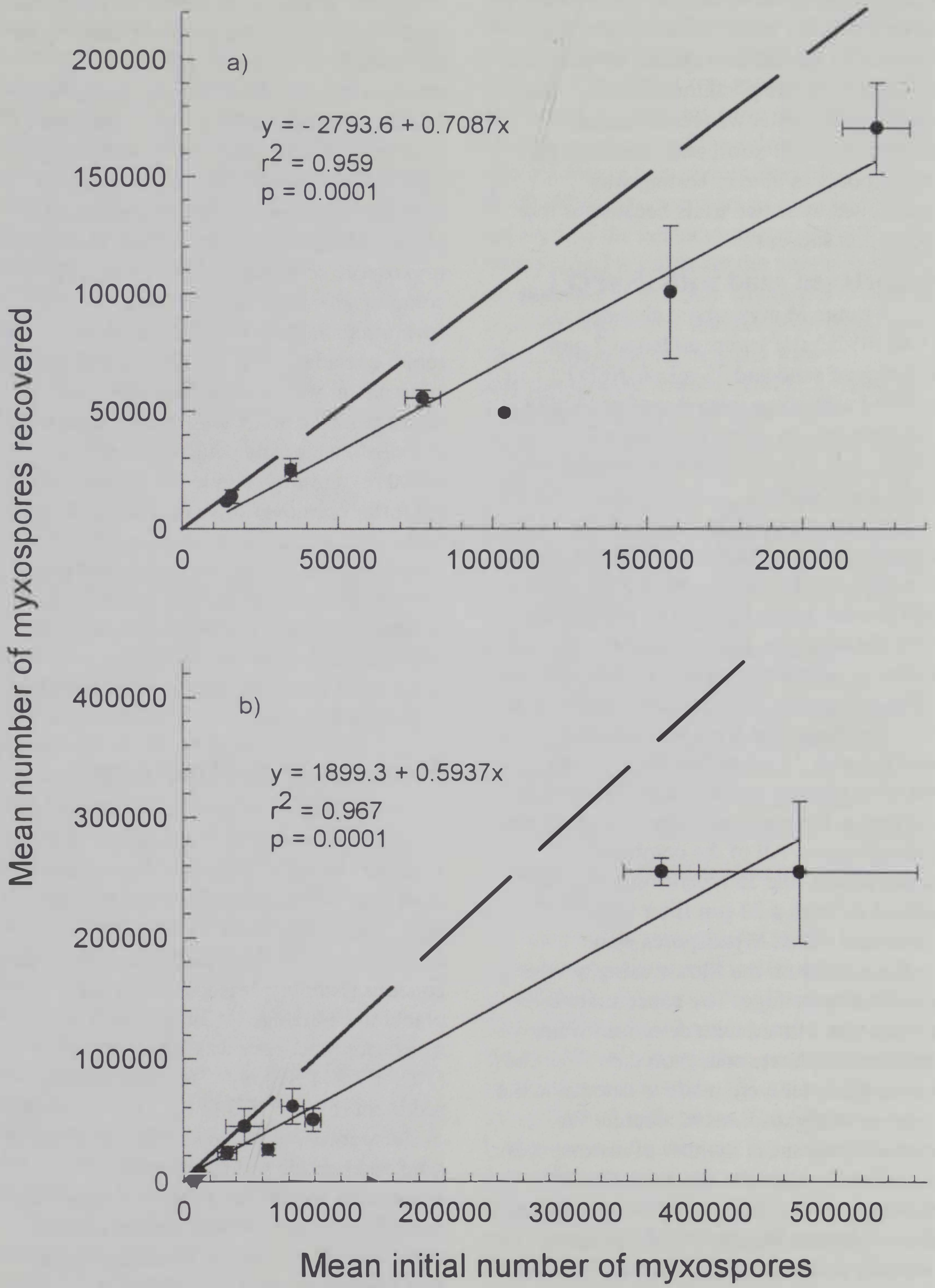

Figure 1. Number of *M. cerebralis* myxospores recovered from a) autoclaved sand and b) benthic sediments plotted against the number of myxospores initially stocked into the sediments. Trials in these experiments used a plankton centrifuge and aqueous sodium hexametaphosphate . Solid circles indicate means and error bars are ± 1 SE. Solid lines indicate the fitted regressions. Dashed lines indicate 100 percent recovery.

When aqueous $[NaPO_3]_6$ was used, the lower myxospore recovery in benthic sediments in comparison to autoclaved sand probably was the result of the higher amount of silt, clay, and organic matter present in the natural sediments. Moreover, the low myxospore recovery in sand when the planktonic centrifuge was used without aqueous $[NaPO_3]_6$ suggested that only a small percentage of silt can negatively affect myxospore extraction. Small soil particles, or organic material, increase aggregation and may reduce myxospore recovery. As small silt and clay particles increase in abundance, the size of the interstitial spaces decreases, thereby reducing fluid movement and extraction efficiency (Buffle and Leppard 1995b). Natural organic matter promotes bacterial growth, which also causes the soil to aggregate (Buffle and Leppard 1995b). Myxospores may be trapped within the aggregates and get deposited on the 20-µm sieve, resulting in reduction of flow and drastic underestimation of myxospore densities. We found only one occurrence of a myxospore in sediments collected on the 20-µm sieve from the autoclaved sand. However, we suspect more myxospores to be present in this residual material in both sediment types because our search was limited by poor visibility.

Myxospores recovered from benthic sediments were all stained. This suggests that wild *M. cerebralis* myxospores were either not present or below our detection limit. Because *M. cerebralis* occurs in these streams, myxospores should be present. However, their distribution may be patchy and our benthic samples may have been collected in patches where myxospore abundances were low. Moreover, temporal variability in myxospore abundance is unknown; therefore, we may have collected sediments when myxospore abundances were below our detection limits. Perhaps if we increased the quantity of sediments processed we would increase the probability of detecting wild myxospores.

CONCLUSIONS

This protocol using $[NaPO_3]_{6aq}$ effectively recovered myxospores in both sediment types. The procedure could be useful in laboratory assessments with *T. tubifex*. For example, reduction in myxospore numbers over the period of time it takes for *T. tubifex* to produce triactinomyxons could be monitored. Moreover, with some modification (specifically, analysis of increased volumes of sediment), this technique could provide researchers with insight on myxospore loads in the wild and add to our understanding of the ecology of the parasite.

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BREEDING SEASON FOOD HABITS OF BURROWING OWLS IN SOUTH-CENTRAL MONTANA

Denver W. Holt, Owl Research Institute, P.O. Box 39, Charlo, MT 59824
William D. Horton, Owl Research Institute, P.O. Box 39, Charlo, MT 59824
Eric C.Atkinson, Marmot's Edge Conservation, 4580 East Baseline, Bozeman, MT 59714

ABSTRACT

We studied the diet of the burrowing owl (*Speotyto cunicularia*) during the breeding season in south-central Montana from 1990 to 1992 One thousand. eight hundred, ninety-six pellets, and various prey remains yielded 2497 prey items or these, 72.2 percent were small mammals with prairie voles (*Microtus ochrogaster)* most dominant. Mice (*Peromyscus spp.*) were the second most numerous prey eaten. Insects were difficult to quantify from pellets and likely were under-represented in the sample. few amphibians and birds were eaten. Prey ranged in size from < 1 -g insects, to 104-g northern pocket gophers *(Thomomys, talpoides*) with most vertebrate prey weighing about 35 g.

Keywords: breeding season, burrowing owl, diet, Montana, *Speotyto cunicularia*

INTRODUCTION

The burrowing owl (*Speotyto cunicularia*) is widely distributed in dry prairie grasslands, steppes, deserts, and some agricultural areas throughout North America (Haug et al. 1993, Holt et al. 1999). Its breeding season diet has been well documented in the prairies of the United States and Canada, e.g., North Dakota (Konrad and Gilmer 1984), Oregon (Gleason and Craig 1979), South Dakota (McCracken et al. 1985), Wyoming (Thompson and Anderson 1988), and Saskatchewan (Haug 1985). Prior to our study we found no comparable data for Montana although a recent study conducted over a single breeding season in 1998 (Restani et al. in press) provided some comparative information.

Throughout much of its range in North America, burrowing owl populations appear to be in decline although specific reasons remain unknown (Haug et al. 1993, Holt et al. 1999). Collectively, a number of factors that may have contributed to this decline have been offered (Grant 1965, Coulombe 1971, Thomsen 1971, Zarn 1974, Wedgwood 1978, Collins 1979, James et al. 1997, Schmutz 1991, Haug et al. 1993). These include: conversion of native habitat to agriculture and human habitation; extermination of fossorial mammals that provide prey and nest sites; pesticides, mining; and some sport shooting among other factors. Similar declines have also been noted for many other species of grassland birds (Robbins et al. 1986).

In 1984 Montana Fish Wildlife and Parks (MFWP) identified the burrowing owl as a species of special concern (Montana Fish Wildlife and Parks 1984). In 1990 and continuing through 1992, we examined the diet of burrowing owls in south-central Montana during the breeding season. Our objective was to collect baseline data on the burrowing owl diet from Montana for comparison with result from other studies in the northern prairies. In 1998 MFWP, USDI Bureau of Land Management (BLM), Owl Research Institute (ORI), Marmot's Edge Conservation (MEC), and others initiated the state's first surveys to ascertain the status of burrowing owls in Montana.

STUDY AREA

We surveyed Hailstone and Halfbreed National Wildlife Refuges and surrounding sites, Stillwater County, south-central Montana, for burrowing owls during May-October 1990, 1991 and 1992. The National Wildlife Refuges were characterized as short-grass prairie, dominated by native grasses with a few shrubs and alkaline ponds. Study sites outside the refuges contained a mixture of native and introduced grasses. Intensity of cattle grazing varied among years. All sites had a mixture of black-tailed prairie dog *(Cynomys ludovicianus),* Richardson's ground squirrel *(Spermophilus richardsonii),* and American badger *(Taxidea taxus)* burrows scattered throughout. Ambient temperatures ranged from 7.7 to 37.3 EC, (0 = 9.3 EC) and precipitation averaged 5.9 cm per month (NOAA 1990, 1991, 1992). Soils were characterized as loams (USDA 1980), and elevation ranged from 1207 to 1258 m.

METHODS

Burrowing owl pellets and prey remains were collected at nest burrows and roost sites twice/week. Pellets were teased apart by hand to separate, quantify, and identify prey.

Prey remains and carcasses also were identified and quantified using various methods described below.Mammals were identified to species using skulls, mandibles, and dental characteristics (Hoffmann and Pattie 1968). Voles were identified to species based upon dental characteristics where practical. Otherwise, we noted voles under the unidentified *Microtus* category. Two species of mice *(Peromyscus* spp.), which are almost identical in size, pelage, dental, and cranial characteristics (Hoffmann and Pattie 1968, Burt and Grossenheider 1976, Foresman 2001), occur in the study area. Because these traits are only detectable on recently captured animals, well-preserved specimens, or skulls, we did not differentiate these to species among prey items.

Birds were identified to species by comparing feathers, feet, skulls, and mandibles at the Philip L. Wright Vertebrate Museum, University of Montana, Missoula. Those not identified were placed in an unidentified category. While some pellets were composed entirely of feathers, we could not quantify the number of birds eaten. Rather, most birds were found a carcasses at nests or roost sites. Identification of amphibians to species followed Thompson (1982) and Stebbins (1986).

We identified insects to family (Borror and White 1970, White 1983). Insects were not quantified or identified since we did not collect insect remains in 1990 although we counted the number of pellets that contained predominately insect remains. In 1991 and 1992 we attempted to count the number of insects among pellets and remains of exoskeletons found at nest burrows and roost sites. We used heads, thoraxes, abdomens, legs, and wings to count insect prey

We made every attempt not to duplicate the counting of prey by matching or pairing body parts of vertebrate or insect prey. We used a conservative approach in tallying the total numbers. We estimated prey body mass by using < 1 g for insects and the mid-point of the range for mammals. We used the mid-point (see Burt and Grossenheider 1976) because of inconsistencies in mean body mass of prey reported in the literature, and because age differences among prey species are not always delineated (see Holt et al. 1991, Blem et al.1993). Furthermore, depending on the size of the owl and the prey, not all prey body parts are eaten, i.e., head, legs and wings of birds (see Holt 1994, Holt and Petersen 2000). Because of difficulty in assigning specific pellets to individual pairs of owls, we combined the prey for a general overview.

RESULTS

Seasonal Diet within Years

In 1990 411 pellets and various prey remains yielded 963 vertebrate prey items from six breeding pairs and one individual owl. Small mammals accounted for 98.7 percent of that prey. Collectively, voles accounted for 85.6 percent ($n = 825$) of the prey with prairie voles accounting for 29.9 percent ($n = 288$) (Table 1). Mice were the second most abundant prey representing 12.5 percent (n 120) (Table 1). There were highly significant differences among the proportions of the four species of mammals eaten (X^2 437, df 3, $P <$ 0.001) as prairie voles dominated the diet. Because so few other vertebrate prey species were eaten, they were not included in the analysis. Insect remains were found in 313 (76.2%) of the 411 pellets. A few horned larks (*Eremophila alpestris*) and tiger salamanders (*Ambystoma tigrinum*) represented birds and amphibians in the diet.

In 1991, 118 pellets and various prey remains yielded 218 prey items from seven breeding pairs. Small mammals accounted for 66.5 percent of that prey. Collectively, voles accounted for 55.5 percent ($n = 121$), of the prey with prairie voles accounting for 42.2 percent ($n = 92$) (Table 1). Mice were the second most common prey representing 8.3 percent (n 18; Table 1). Differences among the proportions of the four species of mammals among pellets were highly significant (χ^2 174, df 3, $P < 0.001$) as prairie voles dominated in the diet. Because so few other vertebrate prey species were eaten, they were excluded from our analysis. Fifty-one (43.3%) of 118 pellets contained insect remains that accounted for 32.1 percent ($n – 70$) of the diet. Scarab beetles dominated followed by ground

Table 1. Burrowing Owl prey items collected from central Montana in 1990, 1991, and 1992.

	1990 (%)[a]	1991 (%)	1992 (%)	Total (%)
Mammals				
Prairie vole	288 (29.9)	92 (42.2)	538 (40.9)	918 (36.8)
Meadow vole	33 (3.4)	4 (1.8)		37 (1.5)
Vole spp.	504 (52.3)	25 (11.5)	71 (5.4)	600 (24.0
Mice spp.	120 (12.5)			
Northern pocket gopher	5 (0.5)	6 (2.8)	17 (1.3)	28 (1.1)
Subtotal	950 (98.7)	145 (66.5)	708 (53.8)	1803 (72.2)
Birds				
Horned lark	4 (0.4)	2 (0.9)	10 (0.8)	16 (0.6)
Western meadowlark			2 (0.2)	2 (0.1)
Chestnut-collared longspur			3 (0.2)	3 (0.1)
Unidentified	3 (0.3)		21 (1.6)	24 (1.0)
Subtotal	7 (0.7)	2 (0.9)	36 (2.7)	45 (1.8)
Amphibians				
Boreal chorus frog			1 (0.1)	1 (0.1)
Tiger salamander	6 (0.6)	1 (0.5)	5 (0.4)	12 (0.5)
Subtotal	6 (0.6)	1 (0.5)	6 (0.5)	13 90.5)
Insects				
Coleoptera				
Caribidae (ground beetles)		19 (8.7)	5 (0.4)	24 (1.0)
Scarabeaidae (scarab beetles)		33 (15.1)	17 (1.3)	50 (2.0)
Silphidae (carrion beetles)			8 (0.6)	8 (0.3)
Orthroptera				
Acrididae (short-horned grasshoppers		18 (8.3)	498 (37.8)	516 (20.6)
Subtotal		70 (32.1)	566 (43.0)	636 (25.5)
Total	963	218	1316	2497

[a] The column of parentheses is percent of prey from the grand total.

beetles and short-horned grasshoppers.

In 1992 1367 pellets and various prey remains yielded 1316 prey items from 17 breeding pairs and two single adults. Small mammals accounted for 53.8 percent of the prey. Collectively, voles accounted for 46.3 percent ($n = 609$) of the prey, and prairie voles accounted for 40.9 percent ($n = 538$) (Table I). Mice represented 6.2 percent ($n = 82$) (Table 1). Differences among proportions of the four species of mammals eaten were highly significant ($X2 = 1224$, df = 3, $P < 0.001$) as prairie voles continued to dominate the diet. Because so few other vertebrate prey species were eaten, they were not included in the analysis. Interestingly however, two western meadowlarks *(Sturnella neglecta)* were eaten. Insect remains occurred among 719 of 1367(52.6%) pellets and made up 43.0 percent ($n = 566$) of which shortr-horned grasshoppers accounted for 37.8 percent ($n = 498$) followed by scarab beetles.

Seasonal Diets Across Years

Of 2497 prey recorded from 1896 pellets and various prey remains collected during 1990-1992, mammals clearly dominated among prey eaten. Cumulatively, small mammals accounted for 72.2 percent ($n = 1803$) of the total prey over the three seasons. Numerically, prairie voles were the abundant item among pellets followed by mice ($X^2 = 96.14$, df = 6, $P < 0.001$). All other vertebrates were eaten in numerically insignificant proportions (Table 1). Insects were most often identified from remains found at the nests and roosts but were commonly eaten and in large numbers when quantified in 1991 and 1992. Pellets that were made up of predominately insect remains were fragile and when teased apart were generally a conglomerate of small bits of chitin with few identifiable parts. Although tiger salamanders were brought to nests, interestingly, they apparently were not fed upon.

Prey items ranged in body mass from <1-g insects to 104-g northern pocket gophers *(Thomomys talpoides)*. Voles occurred most frequently among vertebrate prey and dominated *overall* biomass. The prairie *vole* weighed about 35 g and meadow vole about 49 g. Mice weighed about 24 g and the Northern Pocket Gopher about 104 g. Although these estimates of body mass are conservative, they probably overestimate the actual size of free-ranging individuals among various sex and age classes, and thus, skew biomass estimates.

DISCUSSION

Our results generally agree with those from others reporting on the burrowing owl diet. Prey availability, vegetative cover, and weather among other variables might influence annual and seasonal variation in the diet of burrowing owls (Thomsen and Anderson 1988, Haug et al. 1993). Gleason and Craig (1979) and Green (1983) reported that burrowing owls ate rodents in early spring and switched to insects as they became available. Schmutz (1991) also suggested that small mammals and insects are very important to burrowing owls in Alberta. Insects were the most numerous prey reported from other burrowing owl studies as well although small mammals dominated by biomass (Maser et al. 1971, Marti 1974, Konrad and Gilmore 1984, Haug 1985, Rich 1985, Brown et al. 1986). Seasonal variation in prey use also might be attributed to different stages of brood development and nutritional needs (Haug and Oliphant 1990, Thomsen 1971).

In Montana Restani et al. (in press) identified insects to family and found them numerically dominant in the burrowing owl diet whereas vertebrates dominated by biomass. Our results for the three most abundant insect families (acrididae, carabidae, scarabaeidae) followed a similar pattern and suggested these insect families are important to Montana burrowing owls. Greater numbers of insect families reported by Restani et al. (in press) probably reflected involvement of an entomologist for insect identification. Few small mammal prey reported by Restani et al. (in press) might reflect regional differences in burrowing owl diet, the manner in which prey were quantified, or simply only one season of study. Prey biomass for birds and Richarson's ground squirrel as reported by Restani et al. in (press) could be misleading if the entire body mass of these individuals was calculated. Our observations suggested that entire carcasses of birds and large mammalian prey are rarely eaten.

Although we had difficulty quantifying insects, we felt that small mammals probably were more important to these burrowing owls, particularly when considering mammal biomass. Our data also suggested that food habit studies only utilizing pellets may not truly represent numbers or species of insect prey eaten because pellets composed of insects often are flakes of chitin that break down rather quickly in the environment. This was consistent with findings of Thomsen (1971) who stated that burrowing owls pick at their food that results in pellets that are poor indicators of prey eaten. Coulombe (1971) reported that pellets containing fur preserved longer than those comprised of insect chitin. In contrast Marti (1974) felt that pellets did accurately reflect prey eaten even though many were badly broken or crushed. However, we believe that while pellet remains sufficed for vertebrate prey, they did not accurately reflect total numbers of insects eaten.

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HABITAT SELECTION AND SEXUAL SEGREGATION OF ELK IN NORTHERN WYOMING

Hall Sawyer, Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, WY 82071
Frederick G. Lindzey, Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, WY 82071

ABSTRACT

We examined spring and summer habitat use patterns of adult male and female elk (*Cervus elaphus*) on the Bighorn National Forest in north-central Wyoming. Radio-collared elk were located twice in each of three sampling periods during June and July of 1995 and 1996. Habitat selection was examined at three spatial scales (13 ha, 52 ha, 112 ha) using a geographic information system (GIS). Selection ratios developed from use-availability data were used to detect habitat selection. Selection patterns of male and female elk significantly differed in both spring and summer. Males preferred forested habitats with larger patch sizes and less diversity, whereas females selected for smaller, more diverse foraging areas in open habitats. Our results indicated the value of large, contiguous timber stands for mature male elk are not limited to hunting seasons and also should be considered on spring and summer ranges.

Key words: *Cervus elaphus*, elk, habitat selection, security cover, sexual segregation.

INTRODUCTION

Sexual segregation during the non-breeding period has been documented in a variety of polygynous ungulates, including mule deer *(Odocoileus hemionus)* (King and Smith 1980, Ordway and Krausman 1986, Weckerly 1993), white-tailed deer *(Odocoileus virginianus)* (McCullough et al. 1989), moose *(Alces alces)* (Miquelle et al. 1992), reindeer *(Rangifer sp.)* (Skogland 1989), caribou *(Rangifer sp.)* (Jakimchuk et al. 1987), red deer *(Cervus elaphus)* (Clutton-Brock et al. 1982), bighorn sheep *(Ovis canadensis)* (Geist and Petocz 1977, Bleich et al. 1997), and elk (Geist 1982). Spatial separation of male and female elk may be a result of different habitat requirements or preferences. Because of the important role females play in population dynamics, most ungulate research and management is directed towards this segment of the population. However, knowledge of sex-specific habitat preferences may improve elk management by providing a better understanding of the effects habitat perturbations may have on both sexes. Our objective was to compare habitat selection patterns of adult male and female elk during late spring and summer.

STUDY AREA

Elk habitat use patterns were examined in the Bighorn National Forest (BNF) of north-central Wyoming. The BNF encompassed 6000 km^2 at elevations ranging from 1200 to 4018 m. Vegetation, characterized by juniper (*Juniperus osteosperma*) at low-elevations, ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) at mid-elevations, and lodgepole pine (*Pinus contorta)* and spruce-fir (*Picea engelmannii, Abies lasiocarpa*) dominating the higher elevations, was typical of the central Rocky Mountains. Aspen (*Populus tremuloides*) stands were present but uncommon. Large natural openings and high-elevation gentle slopes were often dominated by big sagebrush (*Artemisia tridentata*) and/or Idaho fescue (*Festuca idahoensis*). Despain (1973) provided a detailed description of vegetation, soils, geology, and climate of the Bighorn Mountains.

METHODS

Helicopter net-gunning was used to capture and radio-collar adult (>1 yr) elk. Thirty radio-collared elk (15 male and 15 female) from separate social groups were monitored during three sampling periods in 1995 and 1996: 1) 30 May-8 June, parturition; 2) 23-29 June, 3-4 weeks post-calving; and 3) 25-31 July, 7-8 weeks post-calving. We located and attempted to sight each elk from the air twice during each period; flights were conducted ≥ 1 day apart to increase independence of relocations. Universal Transverse Mercator coordinates of radio-collared elk were recorded using a global positioning system.

We examined habitat selection at three spatial scales by identifying vegetation types included within 13-ha (200-m radius), 52-ha (400-m radius), and 112-ha (600-m radius) circular areas around each location. Coordinates of elk locations were organized with Map and Image Processing Software (MIPS v.5.2). Buffer zones were created in ARC-INFO and habitat measurements (mean patch size and Shannon Diversity Index) processed in FRAGSTATS (McGarigal and Marks 1994). The Wyoming Game and Fish Department used remote sensing techniques to develop a digital vegetation map that classified every 30 m x 30 m pixel within the BNF into one of 13 different vegetation types (Table 1).

We measured habitat selection by developing selection ratios from use-availability data of male and female elk locations (Manly et al. 1993). Elk locations from 1995 and 1996 were pooled within sexes. Although Thomas and Taylor (1990) and Schooley (1994) identified potential problems with pooling data from different years, it was necessary to meet sample size minimums suggested by Alldredge and Ratti (1986). Used units were defined as the circular areas centered around elk locations and available habitat was delineated as that contained within a minimum convex polygon constructed from all elk locations during sampling periods. However, because snowpack limited habitat available to elk during the first sampling period, data from this period were analyzed using a smaller area delineated by the minimum convex polygon constructed from elk locations from only this period. We assigned selection ratios 90 percent confidence intervals and considered vegetation types selected for if

Table 1. Vegetation types and availability (%) classified by GIS during 3 sampling periods[a] on the Bighorn National Forest, Wyoming, 1995-96.

Vegetation types classified by GIS		Availability (%) Period 1[b]	Periods 2,3
SHR	Sparse herbaceous rangeland	4.62	7.96
MHR	Medium herbaceous rangeland	16.61	16.38
GHR	Green herbaceous rangeland	5.51	4.42
WIL	Willow/moist site shrubs	2.57	2.62
ASP	Aspen/cottonwood	0.50	0.35
SP/F	Spruce/fir	18.12	19.13
DF	Douglas-fir	10.75	6.26
LP	Lodgepole pine	16.62	24.74
RIP	Riparian moist grass/sedge/rush	3.46	3.23
ES	Early seral lodgepole	2.67	2.38
SB	Sagebrush	16.60	10.49
JUN	Juniper	0.13	0.08
MH	Mountain mahogany	1.56	0.89

[a] Period 1: 30 May-8 June, Period 2: 23-29 June, Period 3: 25-31 July.

[b] Availability of vegetation types was analyzed separately during period 1 due to snowpack conditions at the time (see Methods).

intervals were greater than 1, selected against if intervals were less than 1, and selected in proportion to availability if intervals contained 1 (Manly et al. 1993).

RESULTS

Habitat selection patterns differed between male and female elk during each of the three sampling periods and at all three spatial scales (Table 2). However, patterns were similar within sexes and across spatial scales. Males selected exclusively for timbered areas, while females selected for a mix of forage and cover types.

Mean patch sizes of areas selected by male elk ($\bar{x}$ = 2.15 ha, SE = 0.07) were larger ($t_{318} = 4.69$, $P < 0.001$) than areas used by females ($\bar{x}$ = 1.74 ha, SE = 0.05). Consequently, areas selected by male elk had lower Shannon Diversity Index values

Table 2. Habitat selection[1] by male and female elk for each sampling period at 3 spatial scales (13 ha, 52 ha, 112 ha) on the Bighorn National Forest, Wyoming 1995-96.

Vegetation	30 May-8 June			23-29 June			25-29 July		
types	13 ha	52 ha	112 ha	13 ha	52 ha	112 ha	13 ha	52 ha	112 ha
				FEMALE ELK					
SHR	0	0	0						
MHR	0	0	0	0	0	0	0	0	0
GHR	+	+	+	+	+	+	+	+	+
WIL				0	0	0			
ASP	+	+	0						
SP/F				+	+	+	+	+	+
DF	0	0	0						
LP	0	0	0	0	0	0			
RIP		0	0	+	+	+	+	+	+
ES	0	0	0	0	+	+	0	0	+
SB	+	+	+						
				MALE ELK					
SHR									
MHR				0	0	0	0	0	0
GHR	0	0	0	0	0	0			
WIL					0	0			
ASP	0	0	0		0	0	0	0	0
SP/F				0	0	+	+	+	+
DF	+	+	+	0	0	0			
LP	0	0	0	0	0	0	0	0	0
RIP				0	0	0	0	0	0
ES				0	0		0	0	0
SB	0	0	0						

Selected against (-), selected for (+), or selected in proportion to availability (0).

than those areas selected by female elk ($t_{335} = -4.80$, $P < 0.001$). Landscape measurements; were only calculated for the 112-ha scale.

DISCUSSION

The appropriate scale for any ecological analysis should match the goals of the study (Powell 1994). Selecting the wrong scale or failing to consider scale creates the potential for misleading results or data misinterpretation (Bowyer et al. 1996). Edge et al. (1987) believed that an area larger than just that area adjacent to the radio location influenced elk habitat selection and placed a 200-m radius around elk locations to define sampling unit size. Other research has demonstrated how variable such as forage-cover ratios, patch size, and roads influence the scale at which elk site selection occurs (Wisdom et al. 1986, Thomas et al. 1988, Lyon and Canfield 1991). Of the three scales examined in this study, we believe the 112-ha area was the most appropriate sampling unit size to study elk habitat use. This scale detected the most selection, allowed ample room for potential errors in telemetry (Sawyer 1997), and was most likely to contain habitat features important to elk in a 24-hour period.

We found that habitat selection of male and female elk differed during spring and summer. Females were primarily associated with open foraging areas during parturition, and shifted to a mixture of forage and cover areas as the summer progressed and calves developed. Females selected for sagebrush and green herbaceous rangelands during the parturition period (30 May-8 June) when they had young, immobile calves. Sagebrush communities apparently provided both cover for newborn elk calves and abundant, high-quality forage during early June (Sawyer 1997). Male elk selected exclusively for Douglas-fir during early spring and used open forage areas less than or in proportion to their availability

Female elk continued to select for open vegetation types (GHR, RIP, ES) 3-4 weeks post-calving (23-29 June), as calves became more mobile and less dependent on hiding to avoid predators. Although these foraging areas no longer provided abundant low-level hiding cover for calves, female elk also selected for spruce-fir stands, presumably for the security cover they offered the entire herd. These selection patterns continued through the third sampling period (26-31 July)

Male elk continued to select only for timbered vegetation types during late June and July, using other vegetation types less than expected or in proportion to availability. Their timber or cover preference shifted from the lower-elevation Douglas-fir stands to montane and subalpine spruce/fir stands. The tendency for male elk on the BNF to select for dense timber stands was consistent with Marcum and Edge (1991), who found that male elk in western Montana occupied more heavily forested areas than females during the spring and summer.

Selection for timbered areas rather than open foraging areas suggested that habitat use by male elk on the BNF was based principally on security needs. Males apparently met nutritional requirements within or immediately adjacent to these timber stands. However, this did not necessarily indicate male elk compromise foraging efficiency. Males are often solitary or occur in small groups and do not require the large foraging areas necessary to sustain the larger female calf groups. During the second and third sampling periods in 1995, average male group size was five ($n = 17$, SE=0.73), whereas the average female group size was 50 ($n = 28$, SE = 10) (Sawyer 1997). Foraging alone or in small groups may allow male elk to maximize nutrient intake within security-type habitats. Although male mule deer occupied areas of lower resource quality than females, availability of forage per individual deer did not differ between the sexes because of the low density of males (Bowyer 19 4).

Elk maximize forage intake and minimize their energy expenditures when forage and cover areas are of adequate size and in close proximity (Wisdom et al.

1986). Most habitat effectiveness models incorporate a variable that accounts for size and juxtaposition of forage and cover areas (Witmer et al. 1985, Wisdom et al. 1986, Thomas et al. 1988, Sawyer et al. 1998). Generally, timber stands must be at least 200 m wide to receive optimal use by elk along the cover/forage edge (Witmer et al. 1985). Because areas used by male elk consisted of larger habitat patches, they were more likely to contain timber stands 200 m in width and the valuable edges associated with them.

Selection patterns of adult male and female elk markedly differed during spring and summer. Males preferred forested habitats with larger patch sizes and less diversity, whereas females selected for more diverse foraging areas in open habitats with smaller patch sizes. The reproductive-strategy theory for sexual segregation in ungulates (Main and Coblentz 1996) provides a useful framework to speculate why sexual differences in elk habitat selection occur. It suggests segregation is due to predator avoidance strategies of females with young and forage optimization by adult males (Geist 1982, Jakimchuk et al. 1987, Skogland 1989, Main and Coblentz 1990, Bleich et al. 1997). The theory predicts that females should select habitats conducive to the survival of their offspring, which they apparently do, by providing newborn calves with protective cover and older calves with abundant, high-quality forage. The theory predicts males should seek out areas that maximize forage intake. Males apparently were able to do this within or near timber stands, presumably because smaller male groups require less plant biomass than the larger female/calf groups, and exploiting feeding areas adjacent to security cover allows them to forage more efficiently.

MANAGEMENT IMPLICATIONS

Managing elk habitat often focuses on the effects different land uses, such as logging, grazing, hunting, and other human disturbances, have on elk populations (Boyd et al. 1986). Most research addressing these and other questions has been restricted to female elk. Sexual segregation between male and female elk occurs most of the year, however, for biological and management reasons, males are less frequently considered in habitat use studies. The habitat needs of females and their young are perceived, either correctly or incorrectly, as a priority in many habitat studies and subsequent management actions. For example, much of the deforestation and fragmentation that has occurred on national forests was often intended to encourage higher levels of elk use (Thomas 1991). Such a management practice often was deemed appropriate because of documented habitat preferences of female elk in the northwest, where Thomas et al. (1979) suggested an optimal forage/cover ratio for elk of 60:40. Groves and Unsworth (1993) cautioned that a forage/cover ratio of 60:40 might be optimal for elk in certain ranges, but clearly does not have wide-ranging applicability. Ironically, the same fragmentation and loss of cover has led to problems associated with elk vulnerability (Hillis et al. 1991, Thomas 1991, Vales et al. 1991, Christensen et al. 1993), including increased road densities and reduced hunting opportunities. Although healthy elk populations occur throughout the western states, managers continue to struggle with maintaining desired sex ratios (Bender and Miller 1999) and lowering elk vulnerability. Although large blocks of security habitat can benefit male elk during the hunting seasons by reducing vulnerability (Hillis et al. 1991), our results indicated the value of large, contiguous timber stands for mature male elk were not limited to that period. Such stands also should be considered on spring and summer ranges.

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USE OF GENERAL GEOMORPHOMETRY IN THE CHARACTERIZATION OF MOUNTAIN TOPOGRAPHY

John Donahue, Department of Geography, University of Montana, Missoula, MT 59812
Mark Jensen, Ecologist, USDA Forest Service, orthern Region, Missoula, MT 59807

ABSTRACT

We characterized mountainous topography by a variety of landform measurements (geomorphometrics) taken across 10 digital elevation models (DEMs) that cover 10 7.5-minute topographic map quadrangles in Idaho and Montana. The eight metrics examined included elevation, slope, aspect, hypsometric integral, bumpiness, roughness, ruggedness, and skyward angle. Principal components analysis (PCA) indicated that roughness, skyward angle, and aspect collectively accounted for an average of 67 percent of the observed morphometric variance within each of the 10 study area quadrangles and, thus, conveyed the bulk of topographic information. Composite images made from the three principal metrics displayed map patterns closely resembling shaded relief (chiarascuro) renditions of the same terrain. The ability to numerically describe and map topographic geometry should help geographers and ecologists establish spatial correlations and other statistical relations between relief and various biophysical patterns and processes.

Key Words: geomorphometrics, digital elevation models (DEMs), geographical information systems (GIS), principal components analysis (PCA), roughness, skyward angle, aspect, biophysical environments, ecological mapping

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INTRODUCTION

Biophysical environment maps are used to describe terrestrial or aquatic ecosystems that behave in a similar manner given their potential ecosystem composition, structure, and function. Such maps also are commonly used to delineate environmental constraints for ecological pattern analysis and land use planning. Biophysical environment maps display areas with similar management response potentials and resource production capabilities and are based on landscape components that do not display high temporal variability at a given mapping scale, e.g, land form, regional climate, and surficial geology. Ecological units (Bailey et al. 1994, Cleland et al. 1997), land units (Zonneveld 1989), ecoregions (Omernick 1987), biogeoclimatic ecosystems (Meidinger and Pojar 1991), and land systems (Christian and Stewart 1968) are examples of biophysical environment mapping systems that delineate ecologically homogeneous environments at different spatial scales based primarily on geomorphologic, climatologic, and biotic criteria.

A problem common to all of these mapping systems is a failure to apply geomorphometrics that describe entire terrains. This failure stems from the fact that to date most geomorphometric descriptions have relied primarily on mapping specific land forms (Evans 1972, 1980, Jarvis and Clifford 1990). In this approach, mappers use aerial photos, topographic maps, orthophotoquads, and other information in the manual delineation of discrete features such as flood plains, cirques, and mountain slopes. This approach is not only costly and laborious but also quite subjective. Different mappers, who apply the same landform mapping criteria in a study area, often achieve different results. Reproducibility and precision of mapped regions are commonly low.

General geomorphometry offers an

alternative to mapping specific landforms (Evans 1987). In this approach, no prior designation of traditional geomorphic features is required. Instead, various metrics reflecting landform geometry and configuration are calculated for pixels, i.e., and cells covering a study area. Based on mapping objectives, pixels are grouped by metric values into contiguous landform areas. These empirically-derived spatial units are referred to in the literature as raster regions, polygons, or patches and are normally constructed from one or several metrics in combination (Evans 1980). The primary advantages of this approach are that reproducibility is very high, i.e., different mappers using the same criteria and source materials obtain identical results, and landform raster region attributes are quantitatively described. Such numerical descriptions may be used in subsequent analysis of landform and biotic-pattern relations, e.g., fish distribution and vegetation types.

Until recently, numerical descriptions of relief, the fundation of general geomorphometry (Tricart 1947, Goldberg 1962), have been limited due to the tedium involved in making repetitive manual measurements on topographic maps and aerial photographs. However, recent advances in GIS software, satellite imagery, and digital elevation models (DEMs-matrices or rasters of land surface elevations arrayed as pixels) have enabled researchers to make rapid advances in applying geomorphometric techniques to the characterization of mass wasting and soil erosion processes (Gao 1993, Vertessy et al. 1990), stream and watershed delineation (Band 1986, Moore et al.1991), and surface and subsurface runoff (Tarboton 1997, Montgomery and Foufoula-Georgiou 1993). Despite development of such applications, little research has been directed toward discovering geomorphometrics that are most suitable in describing different kinds of land surface form at different hierarchical levels. and consequently, how a general geomorphometrical approach to landform description can be used to improve biophysical mapping.

The primary objective of this study was to determine geomorphometrics that are most useful in describing the overall topographic complexity of mountainous terrain representative of the Rocky Mountains in Idaho and Montana. A secondary objective was to determine whether raster-maps of these metrics provide visual representations of landscapes that are similar to standard United States Geological Survey (USGS) shaded relief maps commonly used by many land management agencies for biophysical mapping.

BACKGROUND INFORMATION

The interest and research concerning metrics appropriate to general geomorphometric characterization of land surface forms has a long and distinguished history. In a milestone paper, Hammond (1954) suggested that characteristic metrics should include area (surface arrangement). altitude, relief, volume (vertical dimension). profile (vertical arrangement of the surface). texture (horizontal dimension) and slope (deviation of the surface from the horizontal). Through laborious manual measurements Hammond (1964) eventually produced a map of land surface form for the entire United States incorporating three of these metrics. Using new technologies, e.g.. computers, GIS, DEMs, Dikau et al. (1991) automated and tested Hammond's land surface form classification for New Mexico with good results. They showed that many of the metrics Hammond identified could be automated. Brabyn (1997) showed that Hammond's classification could identify macro-landforms across the mountain-plain transition zone of eastern South Island, New Zealand.

Following Hammond's pioneering lead, Van Lopick and Kolb (1959) and Wood and nell (1960) suggested methods appropriate to land form classification using air-photo interpretation methods. Which were subsequently reviewed by Parry and Beswick (1973). Primary metrics considered in these analyses included grain (horizontal distances between major ridges and valleys), relief (elevation difference between major ridges and adjacent valleys) average elevation, elevation-relief ratio, and the number of slope-direction changes. Following this work, Evans (1972, 1980, 1990) suggested four land form metrics calculated from altitude and its mathematical derivataves were most appropriate for land surface relief description. These metrics included point slope gradient, point slope aspect, point vertical convexity, and point plan curvature or rate of slope aspect change. Also, the parameters of average, standard deviation, skewness, and kurtosis were considered to be useful in summarizing metric statistical distributions. In a thorough review of existing manually-derived metrics for land-form description, Mark (1975) suggested that grain (relief wavelength or spacing between major ridges and valleys), texture (smallest desired relief wavelength), local relief (elevation difference between major ridges and valleys), mean slope inclination, roughness factor (a set of unspecified metrics), and hypsometric integral (Strahler 1952) were the "best in the class."

Beginning in the mid-1970's, many manual calculations of general geomorphometrics were considered for digital processing. Collins (1975) was among the first to advocate the use of DEMs in their calculation, suggesting that 14 important metrics could be measured through this technology. Similarly, Nogami (1995) classified many manual measurements into one of three categories (point, window, and basin) for computer application.

Elghazali and Hassan (1986) and Zevenbergen and Thorne (987) provided formulas for the computation of many common metrics based on finite differences between elevations, and Gallant and Wilson (1996) provided computer programs that calculate 12 important metrics such as plan and profile curvature, flow direction, and flow path length. Additionally, morphometric algebraic and calculus equations are included within GIS software packages such as Arc/Info, Idrisi, and Surfer (Anon. 1999a, b).

METHODS

Study Area

In this study we selected 7.5-minute DEMs representing IO quadrangles from a variety of mountainous terrains in the Rocky Mountains of the northern United States (Fig I). These Level I DEMs included Elk Butte, Elk River, Grice Ridge, and Widow Mountain in Idaho and Gable Peak, Glenn Creek, Landowner Mountain, Lozeau, MacDonald Pass, and Mt. Haggin in Montana. The DEMs had 30-m resolutions (arrayed point elevations separated by 30 m on the ground) and spanned elevations ranging from a low of 670 m on Grice Ridge to a high of 3230 m on Mount Haggin. Local reliefs, i.e., elevation differences between the tops and bottoms of valley side slopes, for the quadrangles generally ranged between 300 and 1000 m. Both Lozeau and MacDonald Pass had significant areas containing <300 m of local relief. Low relief occurred primarily along the Clark Fork River in the Lozeau quadrangle and along the comparatively broad and gentle main summit of the MacDonald Pass quadrangle. Alpine glacial landscapes characterized the Gable Peaks, Mt. Haggin, and Widow Mountain quadrangles that were noticeably coarser and had higher reliefs than the other quadrangles that were dominated primarily by fluvial and mass-wasting processes.

Figure 1. Locations of 10 USGS DEMS Used in Study.

Geomorphometrics Considered in This Study

In this study we focused on eight geomorphometrics that we thought could be most descriptive of overall landscape relief and patterns of mountainous topography. Four of the geomorphometrics were introduced or re-defined substantially for computer use (bumpiness, roughness, ruggedness, and skyward angle). These metrics as well as hypsometric integral were programmed in C+ language (Ellis and Stroustrup 1990) and run under DOS commands. Two metrics, aspect and slope, were calculated with the Idrisi Surface module and another, mean elevation, was calculated by the Idrisi Extract module, average option. All metrics were calculated from DEM pixel elevations. In this analysis we moved a 3x3-pane window, i.e., one pixel equals one pane, across each DEM image by placing its central pane over a DEM row's second pixel, calculating a metric based on elevations showing through the nine panes, assigning the result to the DEM pixel underlying the central pane, and moving the window to the next pixel in the row to continue the process (See Lillesand and Kiefer [2000] for more information concerning GIS window-based operations). The moving window was centered over every DEM pixel except for boundary columns and rows. The values of the newly calculated metric images (sometimes called digital terrain models or DTMs in the literature) were standardized across the range of 0 to 255. This normalization of all metric raw values to a common scale greatly reduces adverse statistical effects associated with magnitude differences between the absolute values of the metrics studied. A listing and brief description of the study metrics follows.

Aspect. Aspect is the facing direction of the steepest slope directed through a moving window's central pane. It is the clockwise angle measured from a Universal Transverse Mercator (UTM) grid easting (directed north through the central pixel) and the down-slope direction of the slope gradient or fall line. Many ecologists view aspect as a fundamental geomorphometric because of its effects on solar radiation loadings on the ground. Our calculation of aspect used the following equation:

$$Asp = \arctan\{ -[(V \quad - V \quad)/(2\Delta x)] - [(V \quad - V \quad)/(2\Delta y)]\}$$

where *r*, *c* are the row and column coordinates of a window's central cell; *V* is a pixel value, and resolution –Δx or Δy. For square pixels, Δx Δy.

Bumpiness. Bumpiness indicates the number of pixels at elevations lower than the central pixel elevation in a moving window. Bumpiness values range from 0 to 8 in a 3 x 3 moving window. For example, a value of 8 indicates that a central pixel is a peak or summit, a value of 7 implies a divide, and a value of 0 implies an enclosed depression. Bumpiness was incorporated into the study to serve as a surrogate for the number of changes in the facing directions of slopes in a moving window. Our calculation of bumpiness was based on:

$$Bmp - count(V_{r=2\ c\ 2} \quad V_{r,c}) < 0$$

Mean Elevation. This is the average height above sea level calculated for a moving window. Elevation represents the most fundamental geometrical attribute of the land surface. Elevation changes in mountainous terrain typically lead to the creation of various zones of different bioclimates and geomorphological activities.

Hypsometric Integral.—This value reflects the percentage of total area lying under an area elevation summation curve of pixel elevations. In this study we calculated the hypsometric integral by summing the differences between every pixel elevation and the lowest elevation and dividing the sum by the number of pixels times the maximum elevation difference (window relief) between any two pixels. We included the hypsometric integral to hopefully pick out such slope discontinuities as cliffs and ledges. This metric was introduced by Strahler (1952) and shown by Pike and Wilson (1971) to be the same as the elevation-relief ratio (Wood and Snell, 1960). Our calculation of hypsometric integral used the following equation:

$$\boldsymbol{Hypso} = \{[\sum_{c}^{n}\sum_{r\ 1}^{n}(\boldsymbol{V}_{rc} - \boldsymbol{V}_{l})]/\boldsymbol{n}\}/(\boldsymbol{V}_{u} - \boldsymbol{V}_{l})$$

Roughness. Zakrzewska (1963) defined roughness as the total number of contours intersecting the perimeter of a circle drawn on a topographic map. In essence, this parameter reflects a summation of relief ups-and-downs traced around the circle. We retained this notion of summed elevations by the re-definition of roughness. We define roughness here as the summation of absolute elevation differences between adjacent pixels aligned across rows and down columns in a moving window. Our calculation of roughness used the following equation:

$$\boldsymbol{Ro} = \sum_{c\ 1}^{n-1}\sum_{r\ 1}^{n-1}\left|\boldsymbol{V}_{rc} - \boldsymbol{V}_{r+1\,c}\right| + \sum_{r}^{n-1}\sum_{r\ 1}^{n-1}\left|\boldsymbol{V}_{rc} - \boldsymbol{V}_{r\,c+1}\right|$$

Ruggedness.—Beasom et al. (1983) defined ruggedness in terms of the total length of contours in a unit area. Such a line density depends on the slope and relief of a study area. This dependence is retained in this study, where ruggedness expresses the vertical dimension as a combination of two elements: window relief and window average slope. Strahler's (1958) ruggedness number (HDd) applies only to drainage basin morphometry and cannot be computed within moving windows. We calculated ruggedness as window relief, i.e., the maximum difference in elevation between two pixels in a moving window, and multiplying this difference by the tangent function of average slope in the same window. Window average slope is based on the mean of all pixel slopes encompassed within a moving window. Our calculation of ruggedness used the following equation:

$$Ru = (|V_{\max} - V_{\min}|)(\tan S_{avg})$$

where $V_{\max}$ = maximum value, $V_{\min}$ = minimum value, and S_{avg} is the average of all slope values within the moving window.

Skyward Angle. Skyward angle is defined as the upward angle formed at the center of a moving window by the intersection of two profile slope segments, one directed from the highest elevation to the central pixel and the other from the central pixel to the lowest elevation. Skyward angle values of 180° indicate the junction of two slope segments at the window center; junctions <180° indicate upward concavity, whereas those >180° indicate upward convexity. Skyward angle reflects ground surface curvature, another fundamental surface attribute. Our calculation of skyward angle used the following equation:

$$SA = 360 - \{(180 - \beta) + \alpha\}$$

where α = upper profile segment angle = arctan $\{(V_{\max} - V_{cr})$ / resolution $\}$ and β = lower profile segment angle = arctan $\{(V_{\min} - V_{cr})$ / resolution $\}$, $V_{\max}$ = maximum window pixel value, $V_{\min}$ = minimum window pixel value, and V_{cr} = window central pixel value.

Slope.—This metric reveals the degree of surface inclination through the central pixel. The method used for measurement of slope in this study was the Idrisi's Surface module (Degree-Gradient option). We based computation of slope values of the four closest (side) neighbors of a central pixel. Slope is another fundamental attribute of surface geometry. Indeed, it is generally regarded as the pre-eminent metric (Nogami 1995), principally because of its role in most geomorphological processes that draw materials downhill. Our calculation of slope reflects the following equation:

$$s = \arctan\left\{\sqrt{[(\boldsymbol{V}_{c-1} - \boldsymbol{V}_{c+1})/2\Delta_{x}]^{2} + [(\boldsymbol{V}_{r-1} - \boldsymbol{V}_{r+1})/2\Delta_{y}]^{2}}\right\}$$

Programs for calculating the previous eight geomorphometrics were developed for routine use with ARC/INFO GIS software by Jim Barber of the USDA Forest Service, Northern Regional Office, Missoula, MT. These ARC macro-language (AML) routines are recorded on compact disks and are available through the junior author.

Principal Components Analysis

We used principal components analysis (Dunteman 1989) to assess which of the eight study metrics best explain the overall variability in landform relief and configuration across the 10 DEM quadrangles. This type of analysis has been used successfully in previous research (Mather and Doornkamp 1970, Cadigan et al. 1972) with similar objectives of determining which geomorphometrics best describe topography. In principal components analysis several to many uncorrelated multi-variate linear equations (components) are calculated to account for the observed variation in the parameters (geomorphometrics) being studied. The first component explains most of the variance. This is followed by the second and subsequent components, each of which accounts for progressively less variance. We examined relations from three principal components derived from eight geomorphometrics. Factor loadings were then calculated to represent correlations between individual components and the studied geomorphometrics. The squared value of a factor loading approximates the degree of variance accounted for by a particular geomorphometric and is analogous to the coefficient of determination (r^2) commonly reported in standard correlation analysis. Accordingly, parameters (geomorphometrics) with the highest loading on each principal component and their proportional reduction in the total geomorphometric complexity of a quadrangle were identified through this type of analysis, and those with the highest loading values are referred to below as the principal metrics.

RESULTS

For the 10 study area quadrangles, the first three principal components accounted for an average 75.0 percent of the total variance inherent in the geomorphometric data (Table 1). The lowest explained variance was 72.7 percent for the Widow Mountain quadrangle, whereas the highest was 77.1 percent for the Lozeau quadrangle. The proportion of variance accounted for by the first component ranged from 30.1 percent for the MacDonald quadrangle to 42.8 percent for the Glenn Creek quadrangle. The second principal component ranged from 20.8 percent for the Gable Peak quadrangle to 25.7 percent for the MacDonald quadrangle, and the third principal component ranged from 12.1 percent for the Lozeau quadrangle to 18.8 percent for the Widow Mountain quadrangle.

Analysis of coefficients of determination associated with principal metrics and components (Table 2) suggests

Table 1. The Principal Metrics Identified across 10 DEM Quadrangles Arrayed by Three Principal Components. Numbers Indicate the Quadrangle Count for which a Given Metric had the Highest Loading.

Metric	Principal Component 1	Principal Component 2	Principal Component 3
Aspect			8
Bumpiness			
Elevation	1 (Mount Haggin)		
Hypsometric Integral			1 (Widow Mountain)
Roughness	9		1 (MacDonald Pass)
Ruggedness			
Skyward Angle		9	
Slope		1 (Widow Mountain)	
Total Count	10	10	10

Table 2. Coefficients of Determination (r^2) Associated with Individual Principal Components and Land Form Metrics.

	Aspect	Bump.	Hypso. Elev.	Integral	Rough.	Skyward Rugged.	Angle	Slope
Principal Component 1								
Average	0.011	0.117	0.391	0.059	0.860	0.739	0.072	0.767
Std. Dev.	0.022	0.097	0.257	0.066	0.132	0.245	0.099	0.261
Principal Component 2								
Average	0.007	0.273	0.111	0.494	0.032	0.140	0.714	0.132
Std. Dev.	0.112	0.134	0.196	0.159	0.032	0.221	0.225	0.228
Principal Component 3								
Average	0.667	0.019	0.133	0.066	0.080	0.036	0.069	0.037
Std. Dev.	0.402	0.043	0.134	0.124	0.130	0.073	0.132	0.075

that roughness accounted for most of the explained variance (r^2 0.86) for the first principal component, followed by slope ($r^2 = 0.77$) and ruggedness ($r^2 = 0.74$). This is not surprising given the high degree of correlation between these three metrics. Skyward angle ($r^2 = 0.71$) explained the most variance in the second principal component, and aspect ($r^2 = 0.67$) accounted for the most variance in the third principal component. These three principal metrics (roughness, skyward angle, and aspect) accounted for an average of 67.0 percent of the total geomorphometric variability across all 10 quadrangles. The amount of variance explained by these principal metrics ranged from a low of 52.4 percent for MacDonald Pass to a high of 72.8 percent for Glenn Creek.

In Figures 2, 3, and 4 we present a six class, 30 m, raster-based classification for each of the three principal metrics described

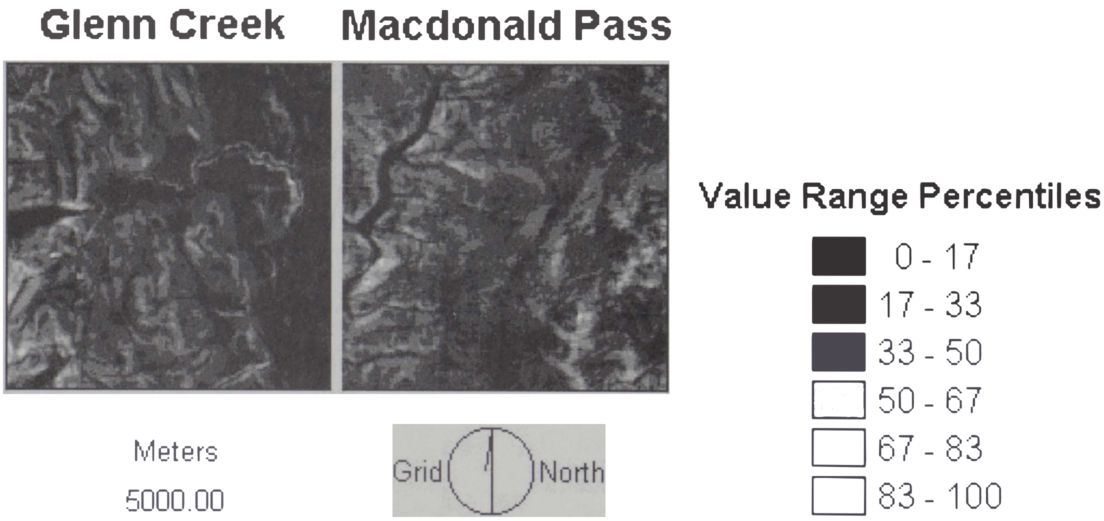

Figure 2. Six-class Representation of Landform Morphomerty Based on the First Principal Metric: Roughness

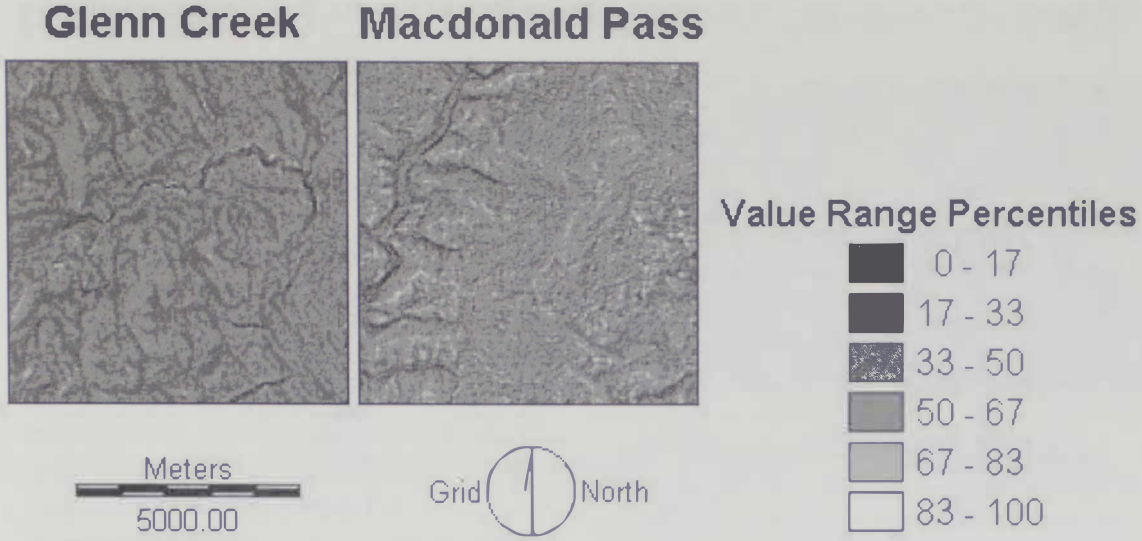

Figure 3. Six-Class Representation of Landform Morphometry Based on the Second Principal Metric: Skyward Angle

above. The two areas presented as examples are from Glenn Creek ($r^2 = 72.8$) and MacDonald Pass ($r^2 = 52.4$). The classes presented in these figures represent equal intervals of the principal metric value ranges. Figure 2 displays a classification of land surface form based on roughness, which represents differences in the vertical dimension of a terrain, i.e., low values indicate regular surfaces, whereas high values indicate irregular surfaces. Figure 3 displays skyward angle classes for the Glenn Creek and MacDonald Pass quadrangles with low values indicating relative concavity and high-values convexity. Figure 4 displays land form aspect which represents slope facing-directions and edges, such as divides and thalwegs (stream bottoms), where different aspect slopes intersect.

In Figure 5, we present composite maps of the Glenn Creek and MacDonald Pass quadrangles synthesized from roughness, skyward angle, and aspect. Six classes for

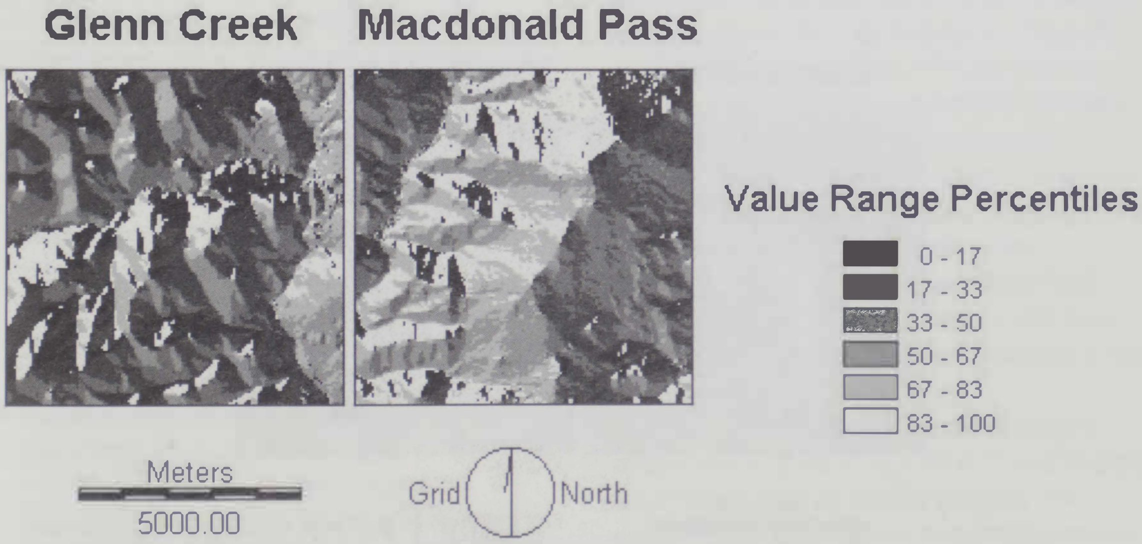

Figure 4. Six-Class Representation of Landform Morphometry Based on the Third Principal Metric: Aspect

Although topographic details in the shaded relief maps are poorly rendered by the composites (Fig 5) in some areas, medium and large components are reliably reproduced. The fact that topographic characteristics can be quantified and displayed on maps suggests that spatial correlations and other types of relations between topography and biophysical factors can be established and examined over comparatively broad areas. Much can be learned at the regional level, and such characterizations can be quite detailed because the metrics used may be represented by small ground cells, currently as small as 30m on a side. In this respect, topographic metrics match the scale of much current and past satellite imagery used by geographers, ecologists, land use managers, and others. In all likelihood, DEM resolutions will increase more or less in step with increases in satellite resolution.

Geomorphometrics convey considerable detail about land surface form nearly everywhere. In many places the form of the land surface discloses the presence of different types and structures of underlying bedrock and residual materials (Tator et al. 1960, Miller 1961). Place-to-place differences in wildland flora and fauna are commonly associated with differences in surface geometry and underlying materials (Howard and Mitchell 1985). Because of such relationships, geomorphometrics and their mapping can be important to the pre-mapping of ecological units or in the mapping of natural species habitats (Canon and Bryant 1997, Nellemann and Fry 1995, Koehler and Hornocker 1989). They also permit the quantitative description and classification of areas important to land managers (Hurley and Jensen 2001). Morphometrics also help provide insight into surface conditions and processes that have shaped such habitats. Much morphometric work has been devoted to geographical aspects of runoff and mass wasting processes and hazards (Quinn et al.1993, Pike 1988).

In the future, other metrics will likely be found to be more informative than those examined in this study. The three principal metrics (roughness, skyward angle, and aspect) identified in this study likely will be superseded but the meanings of the three principal components (vertical dimension, surface vertical curvature and slope face pattern) may not.

CONCLUSIONS

The following conclusions are drawn from this research:

(1) Relief is probably the most essential factor in quantitatively characterizing mountainous topography. The next most important factor may be surface curvature, followed by slope facing pattern;

(2) Mountainous topography can be reasonably characterized for geomorphometric mapping purposes by as few as three metrics: roughness, skyward angle and aspect; and

(3) New metrics may outperform traditional metrics as shown. This was the case for roughness and skyward angle in comparison to aspect, hypsometric integral, average elevation, and slope.

In the future, other metrics will likely be found to be more informative than those examined in this study. The three principal metrics (roughness, skyward angle, and aspect) identified here likely will be superseded, but the essential meanings of the three principal components (vertical dimension, surface vertical curvature and slope face pattern) may not.

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