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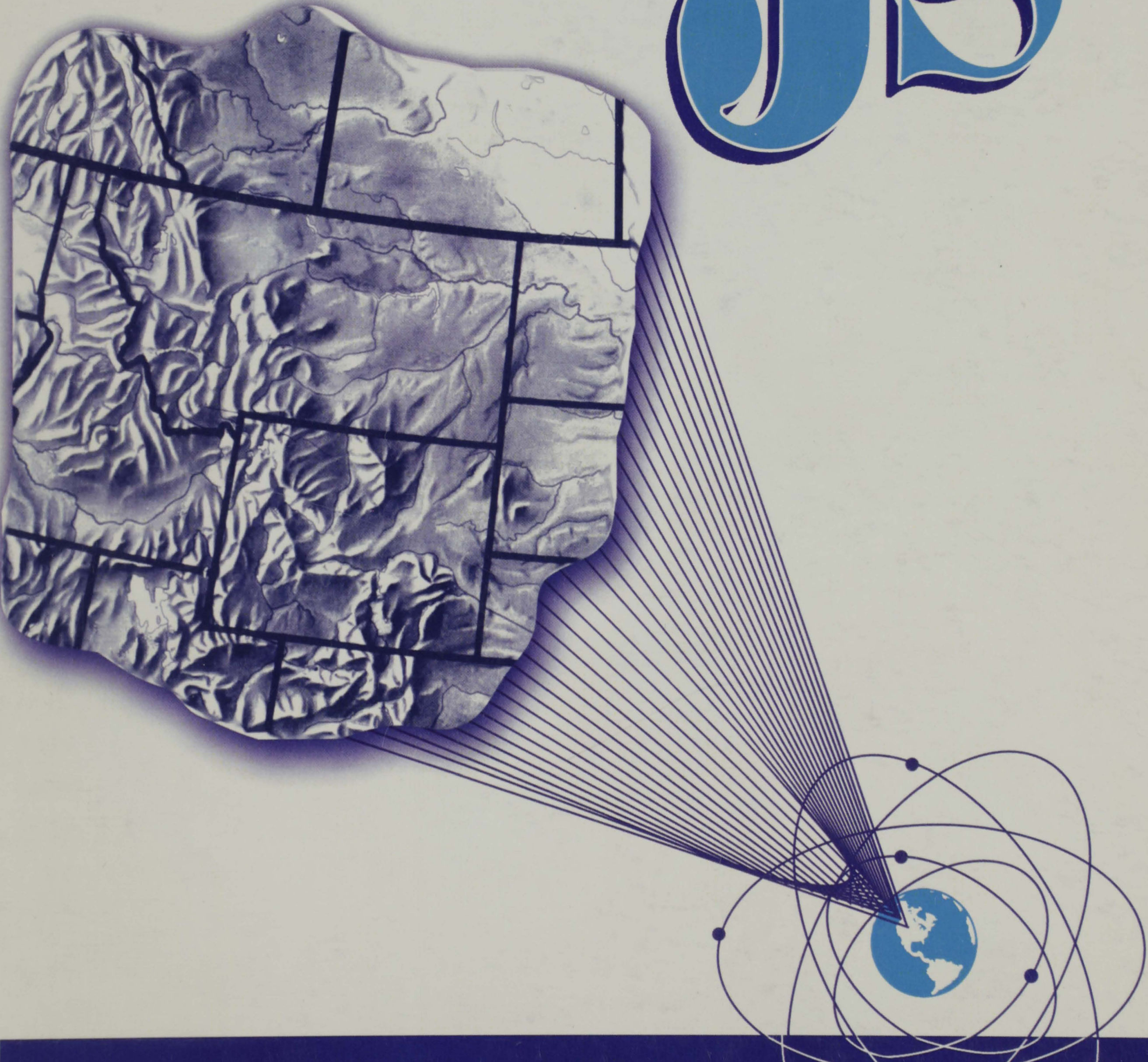

INTERMOUNTAIN JOURNAL OF SCIENCES

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

Co-sponsors/publishers include the Montana Academy of Sciences, the Montana Chapter of The Wildlife Society, and the Montana Chapter of The American Fisheries Society. This journal offers peer review and an opportunity to publish papers presented at annual meetings of the co-sponsor organizations. It is the intent of the governing bodies of the co-sponsor organizations that this journal replace printed proceedings of the respective annual meetings. Therefore, it is the policy of the editorial board that presenters at annual meetings of the co-sponsors be given priority in allocation of space and time of publication, although submission of other manuscripts for review and publication without regard to membership is encouraged.

Initial funding was provided by the co-sponsor organizations. Long-term funding will be derived from page charges assessed authors, sponsoring organizations or agencies at $60 per printed page upon acceptance of each manuscript and from annual subscriptions: student $6; regular member $15; patron member $25; overseas member $25; library $25; life member $150; and, sustaining subscriber $2,500.

The intent of the co-sponsors and editorial board is that ***The Intermountain Journal of Sciences*** be expanded to a quarterly journal. Achieving that objective depends upon numbers of acceptable manuscripts received and available funding. It also is the intent of the editorial board that contributing authors be assured of publication within 12 months of acceptance of their manuscript by the managing editor.

The organizational staff is voluntary and consists of an editorial board, an editor-in-chief, a managing editor, associate editors, a business manager and a panel of referees. The editorial board is responsible for establishing policy and the chair of the editorial board serves as liaison to the sponsoring organizations. The editor-in-chief is responsible for determining acceptability and level of revision of manuscripts based on referees' comments and recommendation of an associate editor. The managing editor serves as liaison for layout and printing. Associate editors include but are not limited to the section vice presidents of The Montana Academy of Sciences. Referees are selected on the basis of their field and specific area of knowledge and expertise.

Referees and associate editors judge submitted manuscripts on originality, technical accuracy, interpretation and contribution to the scientific literature. Format and style generally follow the *Guidelines for Manuscripts Submitted to the Intermountain Journal of Sciences, Dusek 1995, revised 2007.** Organization may vary to accommodate the content of the article, although the text is expected to elucidate application of results.

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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, 2007). 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.

The EJC reviews the recommendation and all comment. The EIC then notifies the corresponding author of the resuts of the review and the publication decision.

ACCEPTANCE

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 that is rejected for publication is returned by the EIC to the corresponding author along with the reasons for rejection. The author is also advised that the manuscript may be resubmitted, provided all major criticisms and comments have been addressed in the new manuscript. The new manuscript may be returned to the initial review process if deemed appropriate by the EIC. If the manuscript is rejected a second time by either the EIC or the Associate Editor and reviewers, no further consideration will be given for publication of the manuscript in IJS. The corresponding author will be notified of this decision.

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The identity of all reviewers shall remain anonymous to the authors, called a blind review process. All criticisms or comments by authors shall be directed to the EIC; they may be referred to the ME or the Editorial Board by the EIC for resolution.

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ABSTRACTS

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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, revised 2007. Guidelines for manuscripts submitted to the *Intermountain Journal of Sciences*. Int. J. Sci. 1(1):61-70. Revised guidelines are available on the Intermountain Journal of Sciences web site: (www.intermountainjournal.org)

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INFLUENCE OF LANDSCAPE CHARACTERISTICS ON FISH SPECIES RICHNESS AMONG LAKES OF GLACIER NATIONAL PARK, MONTANA

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ABSTRACT

Studies suggest that abiotic factors at local and landscape scales partially influence patterns of occurrence of fish species in freshwaters. We examined the occurrence of fishes in relation to landscape characteristics and connectivity of habitat among 16 lakes west of the Continental Divide in Glacier National Park, Montana. Ten native and five nonnative species were observed among lakes, including catostomids, cottids, cyprinids, and salmonids. Estimated species richness (based on rarefaction) varied from 1.00 ± 0.00 to 10.22 ± 0.02 (mean ± 95% confidence interval) and estimated native species richness varied from 1.00 ± 0.00 to 7.85 ± 0.02 among lakes. Information-theoretic models indicated that the presence of dispersal barriers had a strong influence on estimated native species richness among lakes. To a lesser extent, lake maximum depth, lake surface area, and distance from study lakes to a common downstream branching point in the hydrographic network influenced estimated native species richness. Nonnative specie specifically lake trout (*Salvelinus namaycush*), have become widespread throughout the Flathead Drainage, but these data show that the upstream extent of their distribution is limited by the presence of barriers to fish dispersal. Our results indicated that habitat connectivity primarily influences, occurrence, and richness of native species in lakes of Glacier National Park.

Key words: fish species richness, landscape characteristics, barriers, native, nonnative

INTRODUCTION

Biogeography is the study of geographic patterns of species distribution and underlying processes that influence those patterns (Cox et al. 1976). At the coarsest scale, patterns of species distribution may be explained by the evolutionary history of species, tectonic activity, continental movement, and glacial events (Tonn 1990, Matthews 1998). At a finer scale, species distribution may be influenced by local environmental conditions, the biology of individual species, and interactions among species (Tonn 1990, Matthews 1998).

Large-scale patterns of native fish distribution in northern North America are largely influenced by glacial history. During the most recent glacial period, the Wisconsinan, with three major glacial expansions spanning ~ 120,000-10,000 years before present (Mathews 1998), glaciers and ice sheets covered much of North America. Glacier National Park, Montana, is located in an area associated with the Cordilleran Glacier Complex, which at its maximum was composed of interconnected valley and piedmont glaciers and an ice sheet centered in British Columbia, Canada (Flint 1957). As Wisconsinan glaciers retreated, fishes likely colonized northern latitudes from Cascadia glacial refugia (Crossman and McAllister 1986, McPhail and Lindsey 1986). Additionally, remnants of Glacial Lake Missoula, which was located directly south of Glacier National Park, may have provided a source of colonizing fishes. At its peak, Glacial Lake Missoula covered an area larger than Lake Erie and Lake Ontario combined, and was formed, drained, and reformed several times as massive ice dams ruptured (Alt 2001). Therefore, regional patterns of fish species distribution in Glacier National Park may be viewed as a legacy of post-glacial colonization. At a more localized scale, distribution of fishes in specific water bodies in this region may be the result of habitat availability, i.e., species area relationships (MacArthur and Wilson 1967, Tonn 1990) and suitability, barriers to movement and colonization, interactions among species, and stochastic events.

Although lakes in Glacier National Park have experienced past introductions and invasions of nonnative fishes, extirpations of native species as a direct result of establishment of nonnative species has not been documented, and the historic data necessary to evaluate assemblage level effects are not available. Additionally, information regarding the basic distribution patterns of fishes in Glacier National Park is not readily available with the exceptions of scientific literature related to species of special concern (e.g., Marnell 1987, Fredenberg 2002, Mogen and Kaeding 2005a, Mogen and Kaeding 2005b) and popular literature related to sport fishing (e.g., Schneider 2002). The first complete scientific account of the fishes of Glacier National Park was written by Schultz (1941), based on systematic sampling of Glacier National Park waters conducted by the U.S. Bureau of Fisheries in 1932 and 1934. Perhaps Morton (1968a, 1968b, 1968c), who summarized available information from 1916 through 1966, provided the most complete body of information available for fisheries of Glacier National Park.

Understanding patterns of species distribution underlies effective management and conservation of ecological communities, species assemblages, individual species, and local populations. The relatively unperturbed habitat of Glacier National Park makes it an ideal system to examine patterns of fish species distribution associated with landscape characteristics in an area that has received little attention in the fishery literature. Additionally, understanding factors affecting species distribution may elucidate the potential for future nonnative species invasions in this area.

We used a landscape ecological approach (see Turner et al. 2001) to examine the influence of landscape characteristics and heterogeneity on native fish species richness among lakes in Glacier National Park, west of the Continental Divide (Fig. 1). Within this framework, we consider lakes within the study area to represent suitable habitat patches within a background matrix of unsuitable habitat. Additionally, we consider these patches to be interconnected to varying degrees by way of the North Fork and Middle Fork Flathead rivers and their tributaries. Therefore, this study examines the influence of both categorical pattern, e.g., patch-level metrics such as lake size and elevation (Turner et al. 2001) and linear network pattern, e.g., stream network connectivity and discontinuity associated with dispersal barriers (Turner et al. 2001) on native fish species richness. Our specific objectives were to (1) examine the influence of landscape characteristics on native species distribution in lakes of Glacier National Park, located in the upper Flathead River Drainage, Montana, (2) summarize distributions of nonnative species, and (3) discuss potential for future invasions by nonnative fishes in this region based on patterns of native species distribution.

METHODS AND MATERIALS

Study Area

Lakes within Glacier National Park, located in northwestern Montana (Fig. 1), represent portions of three major drainages; the Flathead Drainage (west of the Continental Divide), the Hudson Drainage (east of the Continental Divide in the northern portion of Glacier National Park), and the Missouri Drainage (east of the Continental Divide in the southern portion of Glacier National Park). The present study focused on 16 lakes within Glacier National Park west of the Continental Divide, which are part of the North Fork Flathead (U.S. Geological Survey Cataloging Unit:

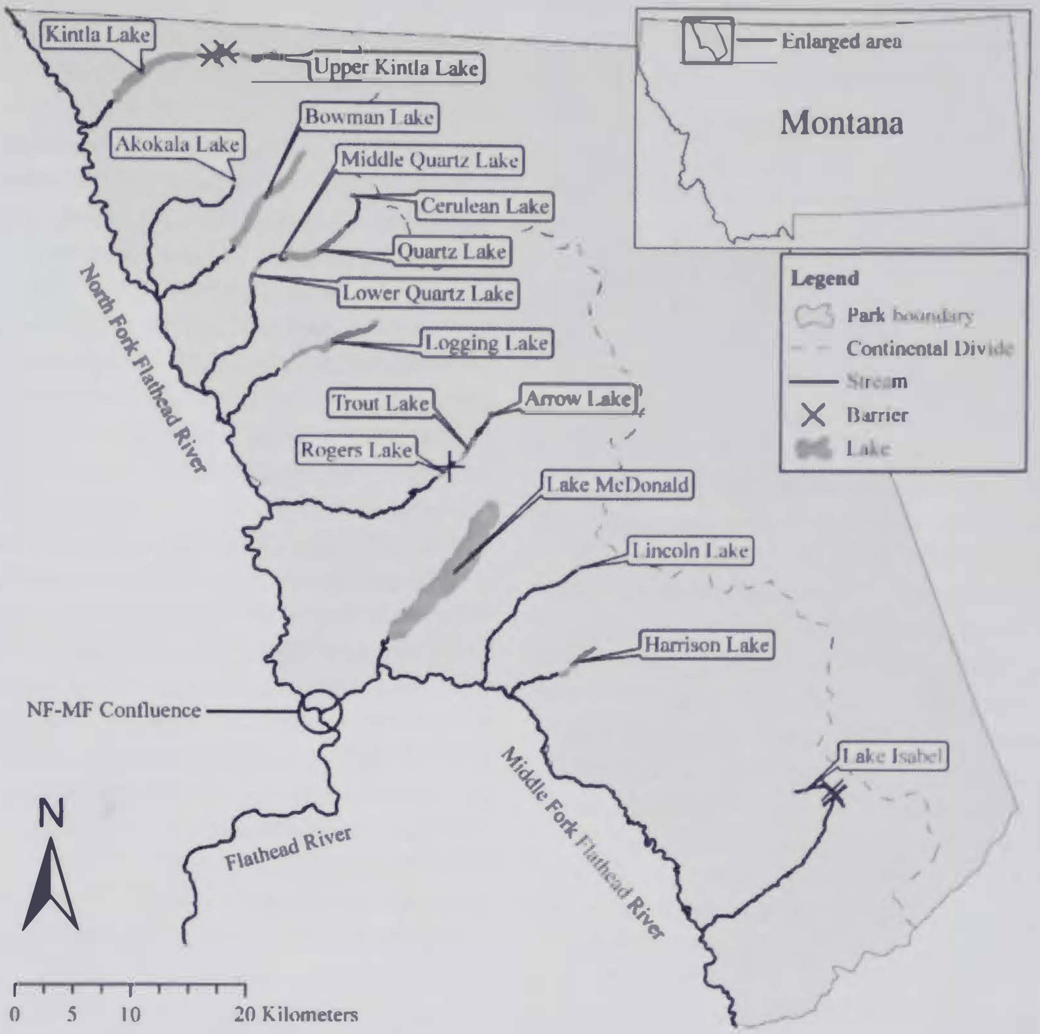

Figure 1. Study area, Glacier National Park, located in northwestern Montana. Sixteen study lakes are labeled, solid line represents the boundary of Glacier National Park, dashed line represents the Continental Divide, and solid bold lines represent the stream system made up of the North Fork and Middle Fork Flathead rivers and tributary streams associated with study lakes. An **X** represents the locations of a barrier.

17010206) and the Middle Fork Flathead (U.S. Geological Survey Cataloging Unit: 17010207) watersheds (U.S. Environmental Protection Agency 2006). Situated in glaciated valleys, lakes within Glacier National Park can generally be classified as cirque and moraine lakes (Gallagher 1999). These glacial lakes vary from round and deep to long and narrow, and are fed by headwater streams originating from glaciers and snowfields (Schneider 2002). Only 10 native fish species are known to occur in the Flathead Lake-River ecosystem, but at least 17 additional species have been introduced or currently inhabit portions of the watershed (Spencer et al. 1991). Fish assemblages within Glacier National Park lakes vary from monospecific to lakes containing intact native fish species assemblages and lakes containing complex fish assemblages marked by multiple nonnative species. Additionally, the study lakes represent the known distribution of adfluvial bull trout (*Salvelinus confluentus*), a species listed as threatened under the federal Endangered Species Act of 1973, in the Columbia River Basin headwaters of Glacier National Park, and a number of headwater populations of westslope cutthroat trout (*Oncorhynchus clarkii* *lewisi*), a species of special concern in all states throughout its native distribution in the U.S. (NatureServe 2007).

Fish Sampling Methodology

We conducted gill net surveys during the summers of 2004, 2005, and 2006 in 16 lakes within Glacier National Park (Table 1). Surveys were conducted with sinking experimental gill nets that were 38 m long, 2 m deep, and constructed of multifilament nylon with five panels· 19-, 25-, 32-, 38-, and 51-mm bar mesh. Gill nets were configured as either a single 38-m net or as a double net, i.e., two 38-m nets tied end-to-end such that the 51-mm bar mesh panel of one net was tied to the 19-mm bar mesh panel of the second net. Number of gill nets set varied among lakes (Table 1) according to scientific collection permit requirements; the collection permit allowed lethal sampling of ≤ 10 bull trout. We set gill nets perpendicular to the lake shoreline with one end anchored near the shore. The near shore end of the net generally consisted of a 19-mm bar mesh panel with the exceptions of three of seven nets in Akokala Lake, five of eight nets in Arrow Lake, three of four nets in Cerulean Lake, one of three nets in Lake Isabel, five of 12 nets in Lincoln Lake, and three of four nets in the 2006 Lower Quartz Lake sample, which were set with the 51-mm bar mesh panel near shore. We set gill nets from a float tube, canoe, or motorboat depending on accessibility and lake-specific boating regulations. Gill nets were set during late afternoon and evening, allowed to soak overnight, and pulled the following morning beginning at sunrise. Gill net set time, soak time, pull time, and depth varied among lakes because of seasonality, i.e., day length in relation to different sampling dates, lake morphometry, i.e., size, depth profile, and accessibility (Table 1).

Fish sampled during gill net surveys were identified to species (with the exception of *Cottid* spp.), enumerated, and returned to the lake. Two species of sculpins are known to occur within the study area—mottled sculpin (*Cottus bairdi*) and slimy sculpin (*C. cognatus*); (Holton and Johnson 2003). Accurate species identification required laboratory examination and dissection (Eddy and Underhill 1978); therefore, we only identified sculpins to

Table 1. Lake, year sampled, number of gill nets (*n*), gill net configuration (single = 38 m; double = 76 m), gill net soak time (hr; mean ± SD), and gill net depth (m· mean ± SD) at the inshore and offshore ends of the gill nets.

Lake	Month and year sampled	*n*	Configuration	Soak time (hr)	Depth (m) Inshore	Depth (m) Offshore
Akokala	July 2004	7	Single	9.4 ± 0.2	1.8 ± 0.4	4.5 ± 1.7
Arrow	June 2004	8	Single	9.3 ± 0.2	1.2 ± 0.7	10.7 ± 3.9
Bowman	August 2005	10	Double	14.1 ± 1.6	3.2 ± 1.7	34.4 ± 9.9
Cerulean	July 2004	4	Single	9.0 ± 1.1	0.5 ± 0.3	17.8 ± 6.1
Harrison	August 2005	10	Single	12.4 ± 0.9	5.0 ± 1.7	18.9 ± 6.4
Isabel	September 2004	3	Single	17.2 ± 1.9	2.6 ± 0.5	8.9 ± 1.0
Kintla	August 2005	10	Double	13.0 ± 1.8	2.1 ± 1.5	25.4 ± 15.2
Lincoln	August 2004	12	Single	10.8 ± 0.7	1.8 ± 1.1	12.3 ± 5.5
Logging	August 2005	10	Double	12.2 ± 1.7	2.7 ± 2.0	20.5 ± 12.0
Lower Quartz	August 2005	8	Single	12.8 ± 2.0	3.3 ± 1.9	13.5 ± 5.0
	June 2006	4	Single	15.0 ± 0.1	4.5 ± 2.4	6.6 ± 1.4
McDonald	September 2005	10	Double	16.1 ± 0.4	12.1 ± 16.4	31.3 ± 14.3
Middle Quartz	August 2005	6	Single	11.5 ± 0.2	4.4 ± 2.2	9.7 ± 1.0
Quartz	September 2005	6	Single	17.8 ± 1.4	2.1 ± 1.5	16.8 ± 4.7
	June 2006	2	Double	8.8 ± 0.0[1]	4.7 ± 3.5	14.2 ± 5.4
Rogers	July 2005	2	Single	11.5 ± 0.6	2.7 ± 0.6	3.5 ± 1.1
Trout	July 2005	4	Single	12.6 ± 1.2	1.5 ± 0.8	12.3 ± 2.7
Upper Kintla	July 2005	4	Single	9.0 ± 0.0[1]	0.8 ± 0.8	18.3 ± 5.4

[1] Standard deviation (SD) value less than 0.05

genera. Westslope cutthroat trout were historically the only native member of the genus *Oncorhynchus* present in the study area (Liknes and Graham 1988); however, rainbow trout (*O. mykiss*) and Yellowstone cutthroat trout (*O. c. bouvieri*) have been introduced to areas of the Flathead Drainage resulting in hybridization and introgression with native westslope cutthroat trout (Hitt et al. 2003, Boyer et al. 2008). Field identification of hybridized westslope cutthroat trout based on morphological and meristic characteristics alone is problematic (Gyllensten et al. 1985, Leary et al. 1987); therefore, we did not identify cutthroat trout based on hybrid status or to subspecies.

Electrofishing surveys were conducted in the summers of 2004, 2005, and 2006 at sites located in wadeable portions of the littoral zone of study lakes (Table 2). We selected electrofishing sites based on presence of large substrates, e.g., cobble and boulder, which was considered likely to provide fish cover. Electrofishing sites were open to movement, i.e., block nets were not used, 100-m in length, and ~ 3-m wide, and number of sites varied among lakes (Table 2); two sites were surveyed in Arrow Lake with site lengths of 106 and 173 m. Sites were sampled using a backpack electrofishing unit (model LR-24 Electrofisher, Smith-Root, Inc., Vancouver, Washington) using a single pass. The LR-24 Quick Setup option was used to produce a 30Hz, 12-percent duty cycle at 25 W power output with the exception of Arrow Lake where a 10-percent duty cycle was used. Output voltage was increased if fish were not exhibiting galvanotaxis and varied from 296 ± 17 V (mean ± SD) to 810 ± 0 V among lakes (Table 2). Electrofishing time varied among sites (Table 2) based on number of fish sampled and habitat complexity. Fish sampled during electrofishing surveys were identified to species (as above), enumerated, and released.

Electrofishing surveys were not conducted in Cerulean Lake due to logistical constraints associated with its remote location and at Rogers Lake because of an apparent fish kill prior to scheduled sampling. On the scheduled date for sampling Rogers Lake, dead fish were observed along the shoreline and floating in the lake. Lake surface temperature on the scheduled sampling date was 21 °C, mid-day 2 August 2006. Additionally, temperature data from the period 22 August 2006 to 13 July 2007 indicated that mean daily temperatures reached 21 °C in the inlet stream and 23 °C at the outlet stream of Rogers Lake (unpublished).

Table 2. Lake, year sampled, number of 100-m electrofishing sites (*n*), electrofisher voltage setting (V; mean ± SD), and electrofishing time (min; mean ± SD).

Lake	Month and year sampled	*n*	Voltage (V)	Electrofishing time (min)
Akokala	July 2004	4	547 ± 78	19.6 ± 5.1
Arrow[1]	June 2004	2	800 ± 0	23.0 ± 8.8
Bowman	June 2005	6	392 ± 21	23.2 ± 6.7
	June 2006	4	296 ± 17	22.3 ± 4.7
Harrison	August 2005	3	500 ± 0	13.2 ± 2.2
Isabel	September 2004	2	785 ± 35	18.0 ± 8.9
Kintla	June 2005	6	420 ± 0	31.0 ± 6.7
	June 2006	3	310 ± 0	25.4 ± 3.7
Lincoln	August 2004	4	685 ± 0	15.1 ± 2.2
Logging	August 2005	6	600 ± 0	15.1 ± 4.0
Lower Quartz	August 2005	6	550 ± 0	15.4 ± 4.3
McDonald	June 2006	5	327 ± 11	20.3 ± 3.8
Middle Quartz	August 2005	6	567 ± 26	10.7 ± 2.4
Quartz	June 2006	6	397 ± 40	18.4 ± 2.5
Trout	July 2005	6	467 ± 26	13.7 ± 1.7
Upper Kintla	July 2005	6	545 ± 10	17.7 ± 3.5

[1] Electrofishing sites for Arrow Lake were 106 and 173 m in length.

Landscape Characteristics

Landscape characteristics, including lake morphometrics, i.e., patch-level metrics (Turner et al. 2001), were measured either on-site during the summers of 2004, 2005, and 2006, or determined from previously recorded data. Lake morphometrics included lake surface area, maximum length, and maximum depth. Other landscape characteristics included lake elevation, distance from the study lake to the confluence of the North Fork Flathead River and the Middle Fork Flathead River (hereafter referred to as NF-MF distance; Fig. 1), and presence of putative fish dispersal barriers (hereafter referred to as barriers) located within the drainage downstream of the study lake.

We determined lake surface area, maximum length, and elevation (Table 3) from a geographical information system (GIS) lake layer (simple polygon; NAD 1983 UTM projected coordinate system). Lake maximum depth (Table 3) was measured from available bathymetric maps (Bowman Lake, Harrison Lake, Kintla Lake, Lake McDonald, Logging Lake, Lower Quartz Lake, Quartz Lake, and Upper Kintla Lake; see USDI Fish and Wildlife Service 1977) or on-site (Akokala Lake, Arrow Lake, Cerulean Lake, Lake Isabel, Lincoln Lake, Middle Quartz Lake, Rogers Lake, and Trout Lake) using a handheld depth finder (model LPS-1, VEXILAR, Inc., Minneapolis, Minnesota). NF-MF distance (Table 3) was measured from a GIS stream layer (simple polyline; NAD 1983 UTM projected coordinate system). This metric represents the distance from individual study lakes to a common branching point in the contemporary hydrographic network (Fig. 1) and likely path of post-glacial colonization from Flathead Lake and Cascadia glacial refugia. Barriers were located by walking stream reaches between each study lake and either the North Fork Flathead River or the Middle Fork Flathead River. We measured barriers, defined by vertical drops of ≥ 1.8 m (Evans and Johnston 1980), for width and height and recorded their locations.

STATISTICAL ANALYSIS

To make comparisons among lakes where both gill net and electrofishing surveys were performed, we used a rarefaction method (Sanders 1968, Simberloff 1972) to estimate species richness that included nonnative species and native species richness excluding nonnative species. Rarefaction estimated expected

Table 3. Presence and absence of barriers downstream of lake, maximum lake depth (Depth; m), lake surface area (ha), distance from lake to the confluence of the North Fork Flathead River and the Middle Fork Flathead River (NF-MF; km), maximum lake length (Length; km), and elevation (m) for 16 study lakes in Glacier National Park, Montana.

Lake	Barrier	Depth (m)	Surface area (ha)	NF-MF (km)	Length (km)	Elevation (m)
Akokala	Absent	6.9	9.5	73.3	0.7	1443
Arrow	Present	16.5	23.9	55.1	0.8	1241
Bowman	Absent	77.1	697.5	63.9	10.5	1228
Cerulean	Absent	35.9	20.3	63.8	0.7	1423
Harrison	Absent	41.1	162.6	28.5	2.3	1126
Isabel	Present	16.0	18.3	82.2	0.6	1742
Kintla	Absent	118.9	694.1	84.3	6.8	1222
Lincoln	Absent	22.7	13.9	35.0	0.7	1401
Logging	Absent	60.4	450.6	48.3	7.9	1161
Lower Quartz	Absent	18.9	67.5	58.4	2.0	1277
McDonald	Absent	141.4	2780.9	11.6	15.2	961
Middle Quartz	Absent	12.5	19.0	60.3	0.7	1340
Quartz	Absent	83.2	351.8	60.7	4.8	1346
Rogers	Absent	4.3	34.5	51.7	1.0	1156
Trout	Present	49.8	87.4	52.7	2.8	1190
Upper Kintla	Present	55.8	189.5	88.0	3.7	1332

species richness standardized to the smallest sample size (Simberloff 1972) to make statistical comparisons among lakes where different numbers of fish were sampled. Although rarefaction methods are useful for comparing among samples of different sizes, we note that rarefaction-based species richness estimates may be sensitive to small sample sizes and to samples with highly variable species specific relative abundances (Hurlbert 1971).

Because species composition varied between gill net surveys (generally dominated by salmonid and sucker species; Table 4) and electrofishing surveys (generally dominated by minnow and sculpin species; Table 5), gill net and electrofishing data were rarefied separately. For each lake we drew a random subsample of 34 individuals from the total sample of individuals observed during gill net surveys and drew a random subsample of seven individuals from the total sample of individuals observed during electrofishing surveys. Based on this procedure, the species identity of randomly-drawn individuals was known, unlike methods that use rarefaction algorithms to predict species richness (see Hurlbert 1971, Kwak and Peterson 2007); therefore, two random subsamples, i.e., gill net and electrofishing, of individuals could be combined and number of species present could be determined. We repeated this procedure 10,000 times and used the mean value as an estimate of species richness for statistical comparisons.

We used simple linear and multiple linear regression (PROC REG; SAS Institute 2004) to model the effect of landscape characteristics on native species richness (rarefaction estimate). Lake surface area and maximum length were $\log_{10}$ transformed to normalize data; normality was determined based on a Kolmogorov-Smirnov test (Sokal and Rohlf 1995) for normal distributions (PROC UNIVARIATE; SAS Institute 2004). We used an indicator variable to represent the presence of a barrier located within the drainage downstream of the study lake. The three-lake morphometrics were highly correlated ($P < 0.0001$); therefore, no models were examined that contained a combination of these variables. Elevation and NF-MF distance were highly correlated ($P = 0.008$); therefore, no models were examined that contained both of these variables.

We examined three groups of models. The first group consisted of five simple linear regression models used to examine the influence of five individual landscape characteristics (excluding the presence of barriers) on native species richness The second group consisted of five multiple linear regression models used to examine additive effects of barriers and (a) each of the three lake morphometrics individually, (b) lake elevation, and (c) NF-MF distance on native species richness. The third group consisted of three multiple linear regression models used to examine additive effect of barriers, NF-MF distance, and each of the three lake morphometrics individually on native species richness.

An information-theoretic approach using Akaike's Information Criterion adjusted for small sample sizes (AIC , Hurvich and Tsai 1989) in conjunction with Δ_i values was used to select appropriate approximating models supported by the empirical data (Burnham and Anderson 2002). We excluded models with Δ values > 10.00 from consideration (Burnham and Anderson 2002). The model likelihood given the data [$L(g_i|x)$], Akaike weights (weight of evidence for a given model; w), and evidence ratios (w_1/w) were calculated to assist in comparisons among appropriate approximating models (Burnham and Anderson 2002). For appropriate approximating models with greater than one independent variable, we calculated reduction in error sums of squares associated with inclusion of each independent variable, i.e the marginal contribution of each independent variable, in the model (Neter et al. 1996).

RESULTS

Ten native and four nonnative fish species were sampled among 16 lakes during gill-net and electrofishing survey in Glacier National Park (Tables 4 and 5

Table 4. Sample size (*n*) and percent of sample made up of 14 species among 16 lakes sampled using gill nets in Glacier National Park, Montana. An asterisk (*) denotes nonnative species.

Lake	*n*	BLT	CUT	MWF	PWF	BRK*	KOK*	LKT*	LWF*	LNS	LSS	NPM	PEM	RSS	SCU
Akokala	103	12.6	3.9	83.5											
Arrow	73	19.2	30.8												
Bowman	543	3.1	4.2	74.8				9.6		6.8				0.9	0.6
Cerulean	54	11.1		88.9											
Harrison	424	2.1	2.8	79.7		0.2	0.9	2.1		12.0					
Isabel	150	38.0	62.0												
Kintla	626	1.9	7.5	60.5				5.4		17.7			5.6	1.3	
Lincoln	278	3.2	2.5	23.4		3.6				67.3					
Logging	984	0.7	4.2	50.0				2.5		17.8		24.3		0.5	
Lower Quartz	441	2.9	13.2	53.3				0.5		29.5				0.7	
McDonald	478	1.7	0.4	14.2	2.1		1.7	6.9	15.3	8.6	4.8	24.1	18.8	1.5	
Middle Quartz	210	5.2	5.7	66.7						20.0				2.4	
Quartz	493	11.0	5.7	67.3				0.2		12.6	1.8			1.4	
Rogers	130	0.8	6.9	59.2				0.8		28.5		3.8			
Trout	125	20.8	78.4												0.8
Upper Kintla	34	100.0													

BLT = bull trout, CUT = cutthroat trout, MWF = mountain whitefish, PWF = pygmy whitefish, BRK = brook trout, KOK = kokanee, LKT = lake trout, LWF = lake whitefish, LNS = longnose sucker, LSS = largescale sucker, NPM = northern pikeminnow, PEM = peamouth, RSS = redside shiner, SCU = sculpin *spp.*

Table 5. Sample size (*n*), and percent of sample made up of nine species among 14 lakes sampled using electrofishing gear in Glacier National Park, Montana. An asterisk (*) denotes nonnative species.

Lake	*n*	BLT	CUT	MWF	BRK*	LNS	NPM	PEM	RSS	SCU
Akokala	76	2.6								97.4
Arrow	39	46.2	53.8							
Bowman	212					8.5			10.4	81.1
Harrison	7		14.3		14.3	28.6				42.9
Isabel	12	75.0	25.0							
Kintla	259		0.4			88.8		7.5		79.8
Lincoln	20									100.0
Logging	46						45.7		21.7	32.6
Lower Quartz	76		2.6	1.3		26.3			43.4	30.3
McDonald	76					3.9	26.3	17.1	21.1	27.6
Middle Quartz	11					9.1			90.9	
Quartz	97					60.8			20.6	18.6
Trout	7									100.0
Upper Kintla	9	100.0								

BLT = bull trout, BRK = brook trout, CUT = cutthroat trout, LNS = longnose sucker, MWF – mountain whitefish NPM = northern pikeminnow, PEM = peamouth, RSS = redside shiner, SCU = sculpin *spp.*

Native species included bull trout, cutthroat trout, mountain whitefish (*Prosopium williamsoni*), pygmy whitefish (*Prosopium coulterii*), largescale sucker (*Catostomus macrocheilus*), longnose sucker (*C. catostomus*), sculpin, northern pikeminnow (*Ptychocheilus oregonensis*), peamouth (*Mylocheilus caurinus*), and redside shiner (*Richardsonius balteatus*). Total number of species observed within lakes varied from one to 13, and number of native species varied from one to 10 (Table 6). Following rarefaction, estimated species richness varied from (mean ± 95% CI) 1.00 ± 0.00 to 10.22 ± 0.02 and estimated native species richness varied from 1.00 ± 0.00 to 7.85 ± 0.02 (Table 6). All nonnative species were in the family Salmonidae, including brook trout (*S. fontinalis*), kokanee (*O. nerka*), lake trout (*S. namaycush*), and lake whitefish (*Coregonus clupeaformis*).

Maximum lake depth varied from 4.3 to 141.4 m, lake surface area varied from 9.5 to 2780.9 ha, NF-MF distance varied from 11.6 to 88.0 km, maximum lake length varied from 0.6 to 15.2 km, and lake elevation varied from 961 to 1742 m (Table 3). Barriers were located in Camas Creek, Kintla Creek, and Park Creek (Table 3, Fig. 1). The barrier in Camas Creek was a waterfall measuring 7.2 m high and 23.2 m wide in a steep canyon. This waterfall was downstream of Trout Lake and therefore also influenced Arrow Lake located upstream of Trout Lake (Fig. 1). Multiple barriers were located in Kintla Creek downstream of Upper Kintla Lake (Fig. 1). The most substantial barriers in Kintla Creek were a waterfall within a bedrock constrained canyon measuring 2.8 m high and 2.7 m wide, and a waterfall measuring 6.7 m high and 14.3 m wide. Three waterfalls were located in Park Creek downstream of Lake Isabel measuring 2.7 m high and 3.0 m wide, 2.4 m high and 3.4 m wide, and 1.8 m high and 2.9 m wide.

Five simple linear regression models examining the influence of the individual landscape characteristics had no support given the data, i.e., $\Delta_i > 10.00$, and were therefore not presented. All supported models included presence of barriers (Table 7). The weight of evidence against alternative models relative to the top ranked model increased rapidly for models ranked 5 through 8 based on evidence ratios (Table 7). For models best supported by the empirical data (Δ values less than or equal to 2.00; Burnham and Anderson 2002), the top ranked model included presence of barriers and maximum lake depth (Table 7). For this model, inclusion of barriers reduced model error sums of squares by 76 percent and inclusion of maximum lake depth

Table 6. Study lake, observed native species richness and mean native species richness (± 95% CI) based on rarefaction, and observed species richness and mean species richness based on rarefaction. Richness estimates were based on samples from gill-net and electrofishing surveys.

Lake	Native species richness Observed	 Mean (± 95% CI)	Species richness Observed	 Mean (± 95% CI)
Akokala	4	3.80 ± 0.01	4	3.80 ± 0.01
Arrow	2	2.00 ± 0.00	2	2.00 ± 0.00
Bowman	6	5.18 ± 0.01	7	6.15 ± 0.02
Cerulean[1]	2		2	
Harrison	5	4.54 ± 0.01	8	5.44 ± 0.02
Isabel	2	2.00 ± 0.00	2	2.00 ± 0.00
Kintla	7	5.71 ± 0.01	8	6.58 ± 0.02
Lincoln	5	4.30 ± 0.01	6	5.04 ± 0.02
Logging	7	5.81 ± 0.01	8	6.39 ± 0.02
Lower Quartz	6	5.91 ± 0.01	7	6.10 ± 0.01
McDonald	10	7.85 ± 0.02	13	10.22 ± 0.02
Middle Quartz	5	4.76 ± 0.01	5	4.75 ± 0.01
Quartz	7	6.30 ± 0.01	8	6.40 ± 0.01
Rogers[1]	5		6	
Trout	3	3.00 ± 0.00	3	3.00 ± 0.00
Upper Kintla	1	1.00 ± 0.00	1	1.00 ± 0.00

[1] Incomplete data for Cerulean and Rogers lakes is a result of incomplete sampling, i.e., no electrofishing surveys.

Table 7. Model rank (Rank) based on Akaike's Information Criterion values adjusted for small sample size, variables entered into the mode, Akaike's Information Criterion values adjusted for small sample size (AIC_C), change in AICc (Δ_i), likelihood of the model given the data [$L(g_i|x)$], Akaike weights (w_i), the evidence ration (w_1/w_j) relative to the highest ranked model for models with ΔAIC_C values less than 10.00.

Rank	Variables in model	AIC_c	Δ_i	$L(g_i|x)$	w_i	w_1/w_j
1	Barrier, depth	1.37	0.00	1.00	0.34	
2	Barrier, surface area	2.11	0.73	0.69	0.23	1.48
3	Barrier, depth, NF-MF distance	3.10	1.73	0.42	0.14	2.43
4	Barrier, length	3.41	2.04	0.36	0.12	2.83
5	Barrier, NF-MF distance, surface area	4.32	2.95	0.23	0.08	4.25
6	Barrier, NF-MF distance, length	5.12	3.74	0.15	0.05	6.80
7	Barrier, elevation	6.24	4.87	0.09	0.03	11.33
8	Barrier, NF-MF distance	7.94	6.57	0.04	0.01	34.00

reduced model error sums of squares by 49 percent in the linear model. The second highest ranked model included presence of barriers and lake surface area (Table 7). For this model, inclusion of the presence of barriers reduced model error sums of squares by 75 percent and inclusion of lake surface area reduced model error sums of squares by 46 percent in the linear model. The third highest ranked model included the presence of barriers, maximum lake depth, and NF-MF distance (Table 7). For this model, inclusion of the presence of barriers reduced model error sums of squares by 75 percent, inclusion of maximum lake depth reduced model error sums of squares by 51 percent, and inclusion of NF-MF distance reduced model error sums of squares by 21 percent in the linear model.

DISCUSSION

Presence of barriers and some metric of habitat size, i.e., lake depth and lake surface area, best explained patterns of estimated native species richness in Glacier National Park. We did not detect cyprinids and catostomids in lakes located upstream of barriers (Arrow Lake, Lake Isabel, Trout Lake, and Upper Kintla Lake), and of lakes located upstream of barriers, we only detected cottids in Trout Lake. All regression models with Δ_i values less than 10.00 included the presence of barriers. Additionally, inclusion of barrier in the top three approximating models reduced error sums of square by 74-76 percent. Our combined results revealed that barriers limit dispersal of fishes in this system, but in the absence of barriers estimated native species richness generally increased with increasing habitat size, i.e., positive parameter estimates for lake depth and lake surface area.

The observed pattern of native fish distribution among study lakes may have occurred if the most successful, early post-glacial colonizers were primarily salmonids and, to a lesser extent, cottids. In this situation specific species assemblages may have colonized the study system prior to or during formation of dispersal barriers that we documented in this study. Alternatives to this hypothesis exist. For example, structures that we identified as migratory barriers may not be true barriers, but allow limited passage of fish that are powerful swimmers or that are capable of navigating complex or high-velocity habitat. However, absence of nonnative salmonids and native cyprinids and catostomids in all lakes located upstream of migratory barriers, despite their widespread presence in other study lakes, provided little support for this hypothesis. Structures identified as barriers in this study may not have been true barriers at all times in history, but may have allowed limited, sporadic, or seasonal passage during some past colonization. Additionally, the barriers may have been breached sometime in the past following colonization by fishes in downstream lakes. These alternatives are plausible; however, absence of native cyprinids and catostomids and nonnative salmonids would still suggest that native salmonids were early colonizers from downstream sources. Alternatively, local extirpations following colonization of more diverse fish assemblages may have occurred in lakes located upstream of barriers; however, no available historic data were available to provide insight into this hypothesis.

There are no known populations of nonnative cyprinids, catostomids, or cottids in the Flathead Lake-River ecosystem (Holton and Johnson 2003). Nonnative centrarchids and ictalurids were introduced early in the 20th century into the mainstem Flathead River and Flathead Lake (Spencer et al. 1991), and some were widespread in the lower systems, however, these warm-water species may not have found suitable habitat in the cirque and moraine lake systems we sampled. Yellow perch (*Perca flavescens*) and northern pike (*Esox lucius*), introduced into the Flathead ecosystem in 1910 and 1965, respectively (Spencer et al. 1991), are cool water species with great habitat tolerance and widespread distribution in the Flathead Lake/River ecosystem, but thus far neither species has been detected in Glacier National Park waters west of the Continental Divide.

All nonnative species detected in this study were salmonids. Spencer et al. (1991) documented the dates of first introductions into the Flathead Lake-River ecosystem: lake trout (1905), lake whitefish (1909), brook trout (1913), Yellowstone cutthroat trout (1913), Arctic grayling (*Thymallus arcticus*) (1913), rainbow trout (1914), kokanee (1916), and Chinook salmon (*O. tshawytscha*) (1916). More recent introductions of golden trout (*O. aguabonita*) (1938) and coho salmon (*O kisutch*) (1969) also occurred (Spencer et al. 1991). The only nonnative salmonids Schultz (1941) documented in study lakes were brook trout in Harrison Lake, and kokanee and Arctic grayling in Lake McDonald.

No nonnative species were observed in lakes located upstream of barriers (Arrow Lake, Lake Isabel, Trout Lake, and Upper Kintla Lake). There is a paucity of information regarding early stocking efforts within Glacier National Park. The most complete data is summarized in Morton

(1968a, 1968b, 1968c) for the period of 1916 to 1966. Fish stocking in Glacier National Park lakes has seldom occurred since the 1960s. Along with fish stocking in lakes surveyed in this study, numerous stockings occurred in stream systems within Glacier National Park (Morton 1968a, 1968b, 1968c). The most commonly stocked fish in the lakes represented in this study was Yellowstone cutthroat trout. Yellowstone cutthroat trout were stocked at some time in the past in all study lakes with the exceptions of Cerulean Lake, Lake Isabel, Lincoln Lake, Rogers Lake (although they were stocked throughout the Camas Creek drainage where Rogers Lake is located), and Upper Kintla Lake. However, we did not discriminate between nonnative Yellowstone cutthroat trout, native westslope cutthroat trout, or their hybrids because of difficulty associated with identification based solely on morphology.

Brook trout were historically stocked in Harrison Lake, Lake McDonald, Lake Isabel, and Lake Ellen Wilson, which is located in the same drainage directly upstream of Lincoln Lake. Brook trout were observed in this study in Harrison Lake, but not in Lake McDonald or Lake Isabel. Dux and Guy (2004) recently documented brook trout in tributary streams to Lake McDonald. Based on this study, brook trout also now occur in Lincoln Lake. Brook trout stocked in Lake Isabel in 1927 (Morton 1968b) may not have established a self-sustaining population as we did not detect them, and previous creel surveys indicated only a small number of brook trout that Morton (1968b) considered to be misidentifications. All other intentional stocking efforts among lakes examined in this study occurred in Lake McDonald where Chinook salmon, rainbow trout, and steelhead were stocked in addition to brook trout and Yellowstone cutthroat trout as previously mentioned. Lake whitefish were not detected in Lake McDonald by Schultz (1941) although he mentioned they had been reported there. They now make up the largest share of fish biomass in that lake (Dux 2005).

We did not detect many of the nonnative species in this study previously reported in Glacier National Park (Morton 1968a, 1968b, 1968c) . Kokanee were reported in Bowman Lake, Harrison Lake, and in great abundance in Kintla Lake and Lake McDonald; however, kokanee were only present in samples from Harrison Lake and Lake McDonald in this study. The limited number of kokanee that we detected in Glacier National Park may be partially due to our sampling methods but more likely resulted from the major system-wide decline in kokanee abundance in the Flathead Lake/River ecosystem (see Spencer et al. 1991).

Ongoing and future invasion by nonnative fishes in Glacier National Park is a topic of conservation concern; specifically invasion by lake trout, rainbow trout, and rainbow trout X cutthroat trout hybrids. Although lake trout were introduced into the Flathead River system in 1905 (Spencer et al. 1991), they were not yet documented in Glacier National Park waters west of the Continental Divide in 1941 (see Schultz 1941). Currently lake trout have colonized all of the large moraine lakes in Glacier National Park west of the Continental Divide (Bowman Lake, Harrison Lake, Kintla Lake, Lake McDonald, Logging Lake, Lower Quartz Lake, and Quartz Lake). Fredenberg (2002) detected an increase in lake trout abundance in the four largest lakes in Glacier National Park west of the Continental Divide from 1969 to 2000. Dux (2005) provided documentation of how extensively the aquatic fauna of the largest lake in Glacier National Park, Lake McDonald, is now dominated by a nonnative lake trout – lake whitefish fish assemblage. This invasion has the potential to negatively impact populations of adfluvial bull trout through competitive interactions as both species are generally top-level predators in systems that they inhabit. Donald and Alger (1993) observed that where large-scale geographic distributions of these species do overlap, bull trout and lake trout were generally separated based on elevation. However, elevation did not limit distribution of either species, and Donald and Alger (1993) suggested that post-glacial colonization patterns and competitive interaction resulted in the observed separation. Additionally, bull trout and lake trout may segregate by habitat when sympatric within a stream-lake system. For example, bull trout may adopt a stream-dwelling life history whereas lake trout will occupy lake habitat, e.g., Saint Mary Drainage, Montana and Alberta.

In an analysis of hybridization between native westslope cutthroat trout and nonnative rainbow trout in the Flathead River system (including portions of Glacier National Park), Hitt et al. (2003) found that rainbow trout introgression was spreading rapidly and in an upstream direction from the mainstem Flathead River and that environmental factors alone would probably not restrict further spread of hybridization and introgression. Additionally, Boyer et al. (2008) found that spatial patterns of population admixture for rainbow trout X westslope cutthroat trout follow stepping stone and continent island models of dispersal. These data suggested that further invasion of rainbow trout and rainbow trout X westslope cutthroat hybrids might occur and likely increase the conservation priority of isolated headwater populations of westslope cutthroat trout populations (Allendorf et al. 2001).

Based on distribution of native species in lakes examined in this study, the presence of dispersal barriers apparently has had a powerful influence on limiting fish distribution. Therefore, these structures may also play an important role in limiting further spread of nonnative fishes. Neither lake trout nor rainbow trout were detected in any study lakes located upstream of barriers; however, both species have expanded their distribution to the edge of these barriers. For example, both species were observed in Rogers Lake located just downstream of the barrier isolating Arrow Lake and Trout Lake. Of the study lakes not isolated by barriers, lake trout were also not detected in Akokala Lake, Cerulean Lake, Lincoln Lake, and Middle Quartz Lake. These lakes are relatively shallow (with the exception of Cerulean Lake), have a small surface area, and are located a considerable distance from mainstem Flathead River habitat, which may be a surrogate variable associated with the distance from the study lakes to the confluence of the North Fork Flathead River and Middle Fork Flathead River. A qualitative assessment of lake trout distribution in the study lakes indicated that lake trout occurred in large, deep lakes located in close proximity to mainstem Flathead River habitat. Therefore, Akokala, Cerulean, Lincoln, and Middle Quartz lakes may represent less preferred habitat for lake trout, are inhabited by lake trout at low levels, or have not been colonized yet

Middle Quartz Lake and Cerulean Lake are part of a chain of lakes in the Quartz Creek and Rainbow Creek drainages.Lake trout were first documented in Lower Quartz Lake (most downstream lake in chain) in 2003 and in Quartz Lake in 2005 (Meeuwig and Guy 2007); therefore, lake trout must have moved through Middle Quartz Lake and may be present in Middle Quartz Lake at levels below which were detectable based on our sampling. Alternatively, Middle Quartz Lake may represent less preferred habitat for lake trout compared to Quartz Lake, which is located in close proximity just 0.40 km upstream of Middle Quartz Lake. Although Cerulean Lake has a relatively small surface area, it is relatively deep; deeper than Lower Quartz Lake and comparable to Harrison Lake of which both contain lake trout. Additionally, lack of any structures believed to significantly reduce fish movement upstream from Quartz Lake to Cerulean Lake suggested that Cerulean Lake may be at risk of invasion by lake trout. Akokala Lake and Lincoln Lake are located a large distance from mainstem Flathead River habitat, which may limit the potential for colonization (Beisner et al. 2006). Additionally, Akokala Lake is relatively shallow and may not be preferred habitat for lake trout, which often, but not exclusively, inhabit deep, cool waters (Scott and Crossman 1973). Although we documented lake trout in Rogers Lake, the shallowest lake we sampled, a fish kill was observed coincident with peak summer temperatures at this lake suggesting that this lake may be subject to frequent local extirpations. Despite the relatively shallow depth of Akokala Lake and the distance of Akokala Lake and Lincoln Lake from mainstem Flathead River sources, potential for nonnative species invasion should not be dismissed.

We did not quantitatively examine the influence of landscape characteristics on distribution of nonnative species because potential interactions between intentional introductions and natural colonization could not be separated based on available data. Additionally, we cannot disregard an influence of nonnative species on native species richness. However, systematic baseline data for the lakes we examined are not available to make an accurate assessment of assemblage level effects of establishment by nonnative species. Therefore, these data provide a baseline for future sampling efforts within the study area.

This study provides information on landscape characteristics that have influenced distribution of native species in Glacier National Park lakes located west of the Continental Divide. The effect of barriers stands out as a dominant factor in shaping distribution of fishes in this system. Protection afforded by those barriers may also be the single most important factor preserving native bull trout and cutthroat trout assemblages on the west side of Glacier National Park. We believe that these data in conjunction with current distribution data on nonnative species can provide insight into the potential for future invasions within this system and help prioritize waters in need of special conservation concern.

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FECUNDITY OF FEMALE WOLVERINE IN MONTANA

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ABSTRACT

We collected carcasses from trapper-harvested wolverine (*Gulo gulo*) in Montana from 1984 through 2005 to evaluate pregnancy rates and corpora lutea production as an estimate of wolverine fecundity in eco-regions and subpopulations of western Montana. Pregnancy rates in the northwest eco-region were 100 percent for adults (n=11) and 30 percent for subadults (n = 15). Pregnancy rates within the southwest eco-region were less than observed in the northwest (67.8 % for adults, n = 28; and 12.5 % for subadults, n=16). We observed similar results in subpopulations from northwestern and southwestern Montana. Median corpora lutea counts for pooled adult and subadult females also differed among eco-regions being greater in northwest (median = 3.0, n = 26) than the southwest (median = 0.0, n = 44). Litter sizes and measurement of recovered fetuses are also presented. Comparisons of our data to similar studies in North America suggested adult pregnancy rates and mean litter sizes observed in the southwestern eco-region of our study area are the lowest reported in the literature.

Key words: corpora lutea, *Gulo gulo*, in-utero, Montana, pregnancy, reproduction, wolverine.

INTRODUCTION

Wolverines (*Gulo gulo*) were once widely distributed across the North American continent. However, recent findings suggest that this distribution may have been disjunct in the Pacific and Rocky Mountain states, being limited to high elevation habitats in the mountain west (Aubry et al. 2007). Habitat loss and over harvest have been cited as causes for the reduction in occupied range observed in the 1800s and early 1900s (Newby and Wright 1955, Wilson 1982, Hash 1987, Aubry et al. 2007). Currently the wolverine's range is believed to be limited to Alaska, northern and western Canada, and the mountainous regions of the northwestern contiguous United States (Wilson 1982, Hash 1987, Aubry et al. 2007). Although once considered to be near extinction in Montana (Newby and Wright 1955), the Rocky Mountain states of Idaho and Montana are considered to have the largest and most stable populations south of Canada, partially due to close proximity to Canada and availability of suitable habitat (Hash 1987, Aubry et al. 2007, Brock et al. 2007). Legal harvest has been eliminated in the lower 48 states with the exception of Montana, which still maintains a limited trapping season.

Information regarding population parameters such as age, Sex structure, and reproduction is limited for populations in the wolverine's southern range due to their low relative abundance and secretive nature. The majority of information available on population parameters in North America has come from Alaska and northern Canada where wolverine abundance has been maintained (Rausch and Pearson 1972, Liskot et al. 1981, and Banci and Harestad 1988). Studies conducted in the lower 48 states focused on basic ecology, movements, habitat use, and genetics with limited information regarding reproduction and age structure (Hornocker and Hash 1981, Copeland 1996, Cegelski et al. 2003, Cegelski et al. 2006, Aubry et al. 2007, Brock et al. 2007, Copeland et al. 2007, Inman et al. 2007*a*, Inman et al. 2007*b*,

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Inman et al. 2007*c*). Lack of information about southern wolverine population structure led to management decisions based primarily on data extrapolated from populations in Alaska and Canada. Reproductive information from these studies demonstrates variation in reproductive parameters, especially pregnancy rates (Rausch and Pearson 1972, Liskop et al. 1981, and Banci and Harestad 1988). However, management decisions based on information obtained through these studies may not be applicable to wolverine populations occupying habitats in the southern portion of their range.

The objectives of this study were to 1) evaluate the reproductive potential of Montana wolverines based on *a priori* boundaries and for three genetically isolated subpopulations suggested by Cegelski et al. (2003), 2) provide basic information on reproductive and fetal development rates, and 3) evaluate the ability of corpora lutea (CL) counts to estimate number of in-utero fetuses in wolverine.

STUDY AREA

The study area consisted of the mountainous region of western Montana. Montana Fish, Wildlife and Parks (MFWP) manages wildlife populations based on seven administrative regions throughout the state. Wolverine harvest occurs in five of those regions with the majority occurring in regions one, two and three all of which occur in western Montana (Fig. 1).

Climates and habitats vary within the study area across a northwest-to-southeast moisture gradient. Meridian weather patterns influence the climate of the northwestern region resulting in less variation in temperatures and higher levels of precipitation, ranging from approximately 35.5 cm to 55.9 cm annually in the valleys, up to 86.4 cm in the mountain foothills, and 215.9 cm at the upper elevations of the mountain ranges (Montana Natural Resource Information System 1971-2000). Precipitation typically increases with elevation that ranges from ~ 621 m to 1200 m in the valleys to about 1800 m to 2700 m in the mountains. Habitats generally consist of valley forests comprised of *Thuja*, *Picea,* and *Tsuga* species intermixed with grassland openings. *Abies* dominates the mountainous forests of the northwest.

Broad valleys and prairie ecotones interrupt mountain ranges and characterize

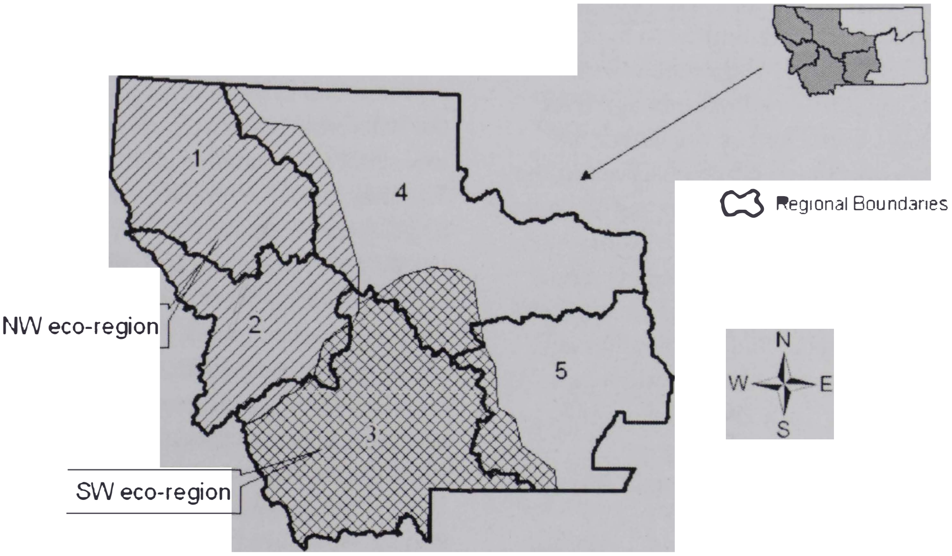

Figure 1. Study area delineating eco-regions of western Montana (inset). The eco-region boundaries were determined using Montana Fish, Wildlife and Parks administrative regions boundaries and ecological considerations. Administrative regions are numbered and eco-regions are identified by cross-hatching.

the southwest and southeast portion of the study area. Valley habitats and prairie ecotones consist primarily of grass and sagebrush habitats containing river and creek riparian areas dominated by willow (*Salix* spp.) and cottonwood (*Populus* spp.). The forested regions of the southern mountains consist primarily of lodgepole pine (*Pinus contorta*), Douglas fir (*Psuedostuga menziesii*) and white pine (*Pinus albicaulis*) interspersed with grass and sagebrush (*Artemisia* spp.) parks.

Annual precipitation varies from ~ 15.24 cm in the dryer valleys to 35.6 cm in the wetter mountain valleys, increasing to > 216 cm in isolated locations of the Absaroka and Beartooth ranges (Montana Natural Resource Information System 1971-2000). As with the northwestern region of the study area precipitation generally increases with elevation that ranges from about 1370 m in the lower valleys to 3350 m in the higher mountains.

The study area was divided into two eco-regions, northwestern (NW) and southwestern (SW) based on general ecological difference and management boundaries. The NW eco-region consisted of MFWP administrative region one, two and the portion of region four containing the Rocky Mountain front. The SW eco-region consisted of MFWP administrative region three, five and the southern half of region four, including the Little Belt, Big Belt, and Crazy Mountains (Fig. 1). Higher precipitation rates, moderate temperatures, and connected habitats generally characterize the NW eco-region. Habitat within the SW unit generally exhibits greater temperature variation, lower precipitation rates and isolated mountain chains separated by open grassland or sagebrush valleys.

The study area was further divided into subpopulations based on the findings of Cegelski et al. (2003) in a study that assessed and evaluated genetic structure producing three subpopulations of wolverine in Montana. The subpopulations were designated as the Rocky Mountain Front (RMF), Gallatin (GAL) and the Crazy/Belts (CB) (Fig. 2). The RMF subpopulation comprises a majority of the mountainous portion of northwestern Montana excluding the extreme western

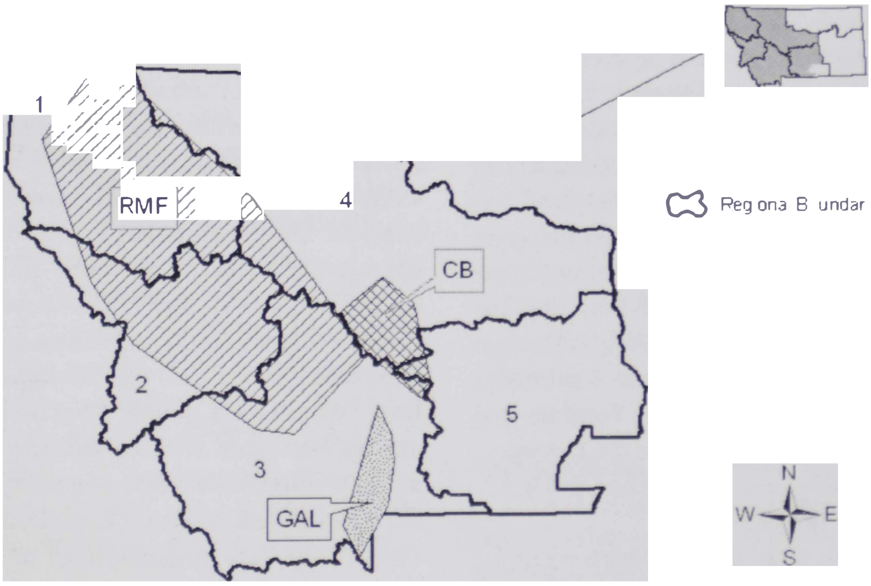

Figure 2. Subpopulation delineations based on home kernel estimates established by Cegelski et al. (2003) for western Montana (inset). Subpopulations are designated as RMF, CB and GAL for the Rocky Mountain Front, Crazy Belts and Gallatin subpopulations, respectively. Montana Fish, Wildlife and Parks administrative are delineated and identified numerically.

edge. The GAL subpopulation resides within the mountainous regions of southwestern Montana and consists of the Bridger, Gallatin, and eastern portions of the Madison Ranges. The CB subpopulation consists of the Little Belt, Big Belt and Crazy Mountain Ranges in south-central Montana.

METHODS

Carcasses were collected from trapper-harvested wolverines from the 1984-85 through the 2004-05 trapping seasons. Trapping seasons ran from early December through mid February. Trappers were required to submit skinned wolverine carcasses to a MFWP official after harvest and complete a harvest form stating harvest date and location as part of a required registration process. Carcasses were frozen at regional collection points and transported to the MFWP Wildlife Research Laboratory in Bozeman, Montana, for examination.

Carcasses were defrosted and examined at the MFWP Wildlife Research Laboratory during which female reproductive tracts and an upper canine were collected. Reproductive tracts were collected and preserved in 10 percent buffered formalin. Ovary pairs were dissected from bursa, packed in distilled water and delivered to Matson's Laboratory in Milltown, Montana, for sectioning and mounting on slides. Ovaries were then serially sectioned at a thickness of 10 microns collected at 0.4-mm intervals across the ovary. Sections were mounted on slides and stained with an aniline blue, acid fuchsin, and orange G solution. We examined slides using a four-power dissecting microscope and identified and counted corpora lutea (CL). Females were considered to be pregnant if CL were present. We totaled the number of CL for both ovaries in the pair.

Attempts to recover blastocysts were not conducted based on difficulties in recovery rates observed in similar studies and the effects of freezing on recovery (Rausch and Pearson 1972, Liskop et al. 1981, Banci and Harestad 1988). Macroscopically visible fetuses were removed from pregnant wolverines during the examination process. Weight in grams, recorded to the nearest 0.1 g, and crown-rump length, measured in millimeters, were obtained for individual fetuses and, when discernable, sex was determined and recorded. Due to the small number of fetuses collected, crown-rump length, weight, and sex data were pooled for the entire study area. Body measurements were not taken during early fetal development, i.e., embryonic, when gross structure was not apparent.

We collected upper canines for aging using cementum analysis by warming the skull in hot water. The canine was removed and ~ 5 mm of the root tip was cut from the tooth and sent to Matson's Laboratory, Milltown, Montana, for aging. Because harvest occurred from December through mid February, young of the year (juveniles) would have been ~ 0.5 years old when harvested. Therefore, we recorded cementum ages in yearly intervals starting at 0.5 for juveniles. Wolverines were placed into three age classes depending on cementum age, juvenile (0.5 yrs), subadult (1.5 yrs) and adult (> 1.5 yrs).

Corpora lutea (CL) counts were analyzed at both the eco-region and subpopulation level. We compared the percentage of subadults and adults containing CL within the two levels. All female wolverine harvested within the study area were included in the eco-region analysis. Only wolverines harvested within the minimum convex polygons established for the RMF, GAL and CB subpopulations (Cegelski et al. 2003) were considered when conducting analysis at the subpopulation level. We used CL counts from pregnant and non-pregnant females in mean and median comparisons between study areas. CL counts from pregnant females only were used to calculate potential litter sizes. Data for age and CL counts were non-normally distributed requiring non-parametric statistical evaluation at both the eco-region and subpopulation level

The Mann-Whitney W test was used to compare differences in median values of age and CL counts between eco-regions. We determined statistical difference in median age and CL counts among subpopulations with the Kruskal-Wallis test. Two-sample hypothesis analysis was conducted to determine significance in the difference of pregnancy rate between similar age classes of the two eco-regions. Significant differences in pregnancy rates among similar age classes of each subpopulation were determined by Chi-square analysis. A sign test for paired samples was used to test the hypothesis that the difference between the median number of CL and the median number of fetuses did not equal zero based on the number of values above and below the hypothesized median for individuals where fetuses were macroscopically visible. We used a P-value ≤ 0.05 to determine significance for all tests. Mean values ± one standard deviation are presented for comparison to previous studies although statistical analysis was not conducted.

RESULTS

Eco-region Level Analysis

We collected a tooth and reproductive tracts from 83 female wolverines harvested by trappers from December 1985 through February 2005. Thirty-one were harvested in the NW eco-region and 52 were harvested in the SW eco-region. Juveniles, subadults and adults comprised 16.1 percent ($n = 5$), 48.4 percent ($n = 15$) and 35.5 percent ($n = 11$) of the NW eco-region harvests, respectively. Within the SW eco-region juveniles comprised 15.4 percent ($n = 8$), subadults 30.8 percent ($n = 16$) and adults 53.8 percent ($n = 28$) of the harvest. Ages based on cementum analysis ranged from 0.5 to 10.5 in the NW eco-region and 0.5 to 9.5 in the SW eco-region. Although median ages were 1.5 and 2.5 for the NW and SW eco-regions, respectively, they did not differ ($P = 0.2002$, W = 132.5).

We observed no CL in ovaries from wolverine aged as juveniles by cementum analysis. Based on these findings and those of other authors (Wright and Rausch 1955, Rausch and Pearson 1972 and Banci and Harestad 1988), we did not consider juvenile wolverines to be sexually mature and did not include them in analysis of reproductive parameters. As a result, ovaries from 26 NW eco-region wolverines and 44 SW eco-region wolverines > 1 year old were used in analysis of reproductive parameters.

Pregnancy rates based on the presence of CL were higher in the NW eco-region compared to the SW eco-region for subadult ($P = 0.0011$, z statistic = 3.269), adult ($P = 0.0318$, z statistic = 2.146) and pooled age classes ($P = 0.0139$, z statistic = 2.2.458). Likewise, median CL counts were also greater for NW eco-region wolverine when both age classes were pooled ($P = 0.0233$, W = -175) ranging from 0.0 in SW eco-region subadults to 3.0 in both subadults and adults from the NW eco-region. Mean CL counts ranged from a low of 0.4 ± 1.0 in SW eco-region subadults to a high of 3.2 ± 0.6 for NW eco-region adults (Table 1).

CL were present in nine NW eco-region subadult wolverines of which seven (77.8 %) contained three CL and two (22.2 %) contained four CL. The number of CL observed in adult ovaries of wolverine harvested in the NW eco-region ranged from two (9.1 %) to four (27.3 %) with the majority (63.6 %) containing three CL. Three CL were present in the ovaries of both pregnant SW eco-region subadults. CL were present in 21 adult ovaries ranging from one (9.1 %) to four (36.4 %), with the majority (54.5 %) containing three. When only pregnant females were evaluated mean litter sizes were 3.2 ± 0.4 ($n = 9$) for subadults and 3.2 ± 0.6 for adults in the NW eco-region and 3.0 ± 0.0 ($n = 2$) for subadults and 3.1 ± 0.8 ($n = 19$) for adults in the SW eco-region.

Subpopulation Level Analysis

We evaluated age composition and reproductive parameters for 69 wolverine harvested within the 95-percent home-range kernel delineation established by Cegelski et al. (2003) (Fig. 2). Number of female wolverine carcasses examined in the RMF, GAL and CB subpopulations were 27, 30 and 12, respectively. Median age did not

Table 1. Reproduction of female wolverine for eco-regions of western Montana, 1984-2005. Pooled samples combine both subadult (age=1.5) and adult (age>1.5) samples. Calculations of mean and median corpora lutea counts include pregnant and non-pregnant animals.

	NW eco-region					SW eco-region				
			CL Count						CL Count	
Age Class	n	% Pregnant	Median	Mean	SD	n	% Pregnant	Median	Mean	SD
Subadult	15	60.0	3.0	1.9	1.7	16	12.5	0.0	0.4	1.0
Adult	11	100.0	3.0	3.2	0.6	28	67.8	3.0	2.1	1.6
Pooled	26	76.9	3.0	2.5	1.4	44	47.7	0.0	1.5	1.6

differ among subpopulations ($P = 0.8055$, test statistic = 0.4327) being 1.5 for RMF, 1.5 for GAL and 2.5 for CB and ranging from 0.5 - 9.5 for both the RMF and GAL and 0.5 - 5.5 for CB.

Pregnancy rates and CL counts were evaluated for subadult and adult wolverine within each subpopulation (Table 2). Juveniles were excluded resulting in a total of 25, 24 and 10 ovary pairs available for analysis from the RMF, GAL and CB populations, respectively. Pregnancy rates did not differ when similar age classes of subadult ($P = 0.1995$, $X^2 = 3.22$, df = 2), adult ($P = 0.1080$, $X^2 = 4.45$, df = 2) and pooled age classes ($P = 0.1381$, $X^2 = 3.96$, df = 2) of all subpopulations were compared. Median CL counts for pooled age classes were 3.0 for the RMF, 1.0 for the GAL and 0.0 for the CB subpopulations, but did not differ ($P = 0.1559$, test statistic = 3.7164). Although not tested, mean CL counts for pregnant adults were 3.0 ± 0.5, 2.2 ± 1.6 and 1.6 ± 1.7 for the RMF, GAL and CB subpopulations, respectively. When CL were present, counts ranged from 2 to 4 in the RMF and GAL and 1 to 4 in the CB.

Fetal analysis

Due to the small number of females with macroscopically visible fetuses or embryos, fetus measurements and comparisons of CL to fetuses from all study areas were pooled. Fetuses were observed in 21 female wolverine harvested during the study period that ranged in age from 1.5-9.5 years. We detected CL in ovaries in all instances where fetuses were observed. A total of 60 fetuses were collected resulting in an average of 2.8 fetuses/pregnant female with litter sizes ranging from 1 - 4. We obtained crown-rump length and weight measurements for 35 fetuses from 13 females. Twenty-five fetuses from eight females were in early stages of development and were thus classified as embryonic and not measured or weighed. Crown-rump lengths ranged from 24-132 mm and weights varied from 1.0-113.2g. The first date that we observed macroscopically visible fetuses occurred on 5 January in a single female, pregnant with three embryonic fetuses. Sex was determined for 19 fetuses collected from the reproductive tracts of six female wolverines resulting in an in-utero fetal sex

Table 2. Age class composition and pregnancy rates of female wolverines within the RMF, GAL and CB subpopulations of western Montana, 1984-2005. Pregnancy rates were determined by the presence of corpora lutea.

Age	RMF		GAL		CB	
Class	n	Pregnant (%)	n	Pregnant (%)	n	Pregnant (%)
Subadult	16	9 (56.2)	10	2 (20.0)	3	0 (0)
Adult	9	9 (100)	14	10 (71.4)	7	4 (57.1)
Pooled	25	18 (72.0)	24	12 (50.0)	10	4 (40.0)

Table 3. Date of death, litter size, fetus measurements and corresponding numbers of corpora lutea (CL) in ovaries from pregnant wolverine harvested in Montana, 1985-2005. Fetuses without macroscopically apparent features were considered embryonic and measurements were not obtained.

Date of Harvest (mm/dd/yy)	Litter Size	Mean crown-rump length (mm)	Mean weight (g) of fetuses	Sex Ratio	Number of CL
1/5/95	3	Embryo	Embryo	Unknown	3
1/13/94	3	Embryo	Embryo	Unknown	3
1/17/96	2	71.5	15	Unknown	3
1/19/02	1	Embryo	Embryo	Unknown	3
1/19/03	3	Embryo	Embryo	Unknown	3
1/20/01	2	Embryo	Embryo	Unknown	2
1/21/87	2	92.5	43.5	1M:1F	3
1/23/01	2	88.0	28.0	0M:2F	2
1/23/97	2	Embryo	Embryo	Unknown	3
1/26/92	3	29.7	1.2	Unknown	3
1/29/05	3	Embryo	Embryo	Unknown	3
2/02/97	4	80.3	19.5	1M:3F	4
2/03/96	2	37.5	3.0	Unknown	3
2/03/02	4	Embryo	Embryo	Unknown	4
2/04/96	2	26.5	1.0	Unknown	3
2/04/98	4	Embryo	Embryo	Unknown	4
2/07/04	3	40.0	2.6	Unknown	3
2/08/98	4	43.5	2.7	Unknown	4
2/12/93	4	130.2	100.0	2M:2F	4
2/12/04	4	101.5	45.2	3M:1F	4
2/14/03	3	74.0	18.2	0M:3F	4

ratio of 7 males:12 females. Mean crown-rump lengths, mean weights, litter size, date the pregnant female was trapped and the number of CL detected in ovaries for individual females appear in Table 3.

CL counts were consistent with the number of fetuses present in 66.7 percent (14/21) of pregnant females. In six cases, number of CL exceeded number of fetuses by one, and in one case number of CL exceeded number of fetuses observed by two. Median number of CL and fetuses observed was 3.0, however, the number of CL and fetuses above and below 3.0 differed ($P = 0.0133$, test statistic = 2.4749). Although not evaluated statistically, mean litter size based on the number of fetuses was 2.8 whereas mean number of CL present was 3.2. A direct linear relationship suggested that potential litter size was 87.5 percent of the CL counted/individual.

Estimating mean number of fetuses based on linear interpolation of a relationship between number of CL and fetuses yielded an average litter size in the NW eco-region of 2.6 ($n = 9$) for pregnant subadults and 2.8 ($n = 11$) for pregnant adults. Estimated litter size for the SW eco-region was 2.6 ($n = 2$) for pregnant subadults and 2.7 ($n = 19$) for pregnant adults. At the subpopulation level, estimated mean litter size for pregnant subadults was 2.6 and 2.8 for the GAL ($n = 2$) and the RMF ($n = 9$), respectively. We observed no pregnant subadults in the CB subpopulation. Estimated litter sizes for pregnant adult females were 2.6 ($n = 9$) for the RMF, 2.7 ($n = 10$) for the GAL and 2.5 ($n = 4$) for the CB.

DISCUSSION

We did not detect evidence of breeding activity based on presence of CL among juvenile wolverine during our study, which was consistent with observations in previous studies of North American wolverine (Rausch and Pearson 1972, Liskop et al. 1981, and Banci and Harestad 1988). Fecundity differed significantly between the eco-regions of western Montana with higher pregnancy rates and CL production in the NW eco-region.

Nutritional status is often theorized as the main reason for differences in age of first reproduction (Mean and Wright 1983, Banci and Harestad 1988), but habitat quality and food resources may also influence overall productivity. In our study the NW eco-region generally receives more precipitation and has moderate temperature fluctuations compared the SW eco-region. Mountain goats (*Oreamnos americanus*) occupy alpine habitats and moose (*Alces alces*) are present in habitats ranging from riparian to alpine throughout much of both the NW and SW eco-regions offering scavenging opportunities for wolverines. Food sources, such as marmots (*Marmota* spp.) and other small prey, are well distributed across the study area (Foresman 2001) although densities may vary. The NW eco-region is dominated by smaller ungulates (white-tailed deer [*Odocoileus virginianus*] and mule deer [*O. hemionus*]), while elk (*Cervus elaphus*) represent less of the ungulate biomass. Conversely, elk represent a higher percentage of the ungulate biomass in the SW eco-region.

Availability of food during winter may be directly related to reproductive success. Persson (2005) observed increased birth rates and reproductive frequency in females provided with food supplement during mid-winter as compared to non-supplemented females. Ungulate carrion is believed to be an important food source for wolverines with live prey, small mammals and vegetation of less significance particularly during winter (Hornocker and Hash1981, Rausch ad Pearson 1972, Banci 1994, Copeland 1996, Packila et al. 2007). Although precipitation, temperatures, and some food resources differed between the two eco-regions, a relationship of reproduction to overall habitat quality is not well understood in our study area.

Perhaps related to habitat quality, wolverine density within a given area may also have influenced reproductive success. Although wolverines in mountainous areas of western North America typically occupy large home ranges (Hornocker and Hash 1981, Copeland 1996, Inman et al. 2007*a*) and are capable of long-range movements (Gardner et al. 1986), low densities may result in a reduced likelihood of contact between sexually mature individuals. Adequate density projections for wolverines throughout our study area were not available, but we generally assumed that densities may have been higher in the NW eco-region than the SW eco-region. If our assumption proves true, it may partially explain some differences observed in pregnancy rates between the two eco-regions.

In our study, pregnancy rates in the SW eco-region were lower for both subadult and adults. Assuming that age groups have similar patterns of sexual maturity within both the NW and SW eco-regions, the difference in reproduction suggests reduced access to sexually mature males during breeding season in the SW eco-region. Squires et al. (2007) suggested that harvest of reproductive-aged adults may have suppressed observed reproduction in western Montana wolverines. The number of wolverines harvested during this study was only slightly greater in the SW eco-region (n =101) than in the NW eco-region (n = 97) (Montana Fish, Wildlife and Parks, unpublished data). Adult females comprised a larger proportion of the harvest in the SW eco-region (n = 28) compared to the NW eco-region (n = 11). The higher percentage of adult females harvested in the SW eco-region suggested possible increased vulnerability and perhaps contributed to differences in reproduction.

Dispersal of wolverines from source populations may be important in maintaining populations in harvested regions (Krebs et al. 2004, Lofroth and Ott 2007). Information from recent studies indicates that populations in southwestern Montana, i.e. the SW eco-region and the CB and GAL subpopulations, demonstrated significant genetic differentiation compared to populations in northwestern Montana, i.e. the NW eco-region and the RMF subpopulation, (Cegelski et al. 2003, Cegelski et al. 2006). Increased genetic differentiation observed in subpopulations of the SW eco-region suggested limited dispersal of wolverines from source populations into southwestern Montana. The effect harvest and apparent limited dispersal into the SW eco-region had on pregnancy rates and overall reproduction is unknown. If winter harvest can reduce male/female interactions during mating season, then a reduction in pregnancy rates may be expected. However, Inman et al. (2007*a*) observed that wolverine territories quickly refilled when the occupant was removed due to death. This suggested that wolverines are able to refill suitable unoccupied habitat from adjacent areas and are present during mating season, but did not indicate that mating occurs. Other social factors may influence mating behavior.

Genetic variability in the wolverine populations of North America has been addressed in numerous papers (Wilson et al. 2000, Kyle and Strobeck 2001, Chappell et al. 2004, Tomasik and Cook 2005, Cegelski et al. 2006). Cegeski et al. (2003) described the three genetically differentiated subpopulations in Montana used in this study. Of the subpopulations, the CB was the most genetically isolated, followed by the GAL and the RMF was least (Cegelski et al. 2003). Percentage of pregnant subadults and adults and mean CL counts, although not analyzed statistically, were lowest in the CB, higher in the GAL and highest in the RMF. Differences in habitat, food availability, harvest effects, connectivity or some combination of these factors may have influenced reproduction in the GAL and CB subpopulations. Median CL production and pregnancy rates of all subadult and older wolverine within these subpopulations were evaluated and the differences observed were not considered to be significant at the $P < 0.05$ level. However, this result may be influence by small sample sizes, particularly in the CB subpopulation.

Subpopulation boundaries were based on the genetic evaluation of Montana wolverines and not a priori values. However, subpopulations were subunits of the eco-regions: the RMF was a subunit of the NW eco-region and the GAL and CB subpopulations were subunits of the SW eco-region. Reproductive differences at the subpopulation level likely influenced differences in fecundity observed at the eco-region level. Factors that influence gene flow and levels of genetic isolation observed by Cegelski et al. (2003) may also have attributed to reduced reproduction observed in the CB and GAL subpopulations and subsequently the SW eco-region. Further investigation is needed to understand variables related to the limited reproductive capabilities of the CB and GAL subpopulations and the SW eco-region and the role of reduced genetic variability.

Differences in wolverine reproduction may occur at different spatial scales. Information presented in studies on wolverine in Alaska (Rausch and Pearson 1972), British Columbia (Liskop et al. 1981) and the Yukon (Banci and Harestad 1988) suggest that difference in reproduction occurs between widely separated wolverine populations at northern latitudes. Our data suggested such differences may also occur on a finer scale as observed between eco-regions and possibly subpopulations of western Montana. Our study also showed that adult pregnancy rate and mean litter size observed in the SW eco-region, the periphery of this species' range, is the lowest reported for North American wolverine. Our findings were consistent with the relatively low reproductive rates observed in a study of wolverines in the greater Yellowstone area although sample size for that study was small (Inman et al. 2007*c*).

Age composition of a population may contribute to reproductive differences. Banci and Harestad (1988) found the percentage of pregnant or post partum females was highest for 3- and 4-year-old females, and mean number of CL increased with age, which was highest (4.4 ± 1.1) in females ≥ 6 years old. Pregnancy rates and CL production in the subadult age class were critical factors in reproductive differences observed between eco-regions in this study. Nearly 58 percent of the wolverines from the NW eco-region were subadults, whereas only 36 percent were subadults in the SW eco-region. Despite a predominance of subadults in the NW eco-region, pregnancy rates for wolverines ≥ 1 year old were much higher (76.9 %) than those observed in the SW (47.7 %). We also observed higher median CL counts for the NW eco-region despite the disparity in subadults. We included both pregnant and non-pregnant females in our analysis of median CL counts and pregnancy rates between the two eco-regions. If age was a primary factor influencing reproduction, the predominance of subadults in the NW eco-region should produce lower CL production than observed in the SW eco-region, provided that harvested wolverines and cementum age analysis are unbiased estimators of fecundity and age structure for each eco-region. Our data did not support the conclusion that age structure of the wolverines used in this study was a primary factor influencing difference in reproductive performance between eco-regions in Montana.

Comparisons among our study and other studies of North American wolverines may provide insight into the fecundity of wolverine populations in the southern reaches of their distribution. However, differences in aging techniques and age classification methodologies made direct comparison of age-related reproductive parameters difficult. A completely accurate aging technique has not been developed for wolverine to date. Although cementum analysis has been used in prior studies (Rausch and Pearson 1972, Liskop et al. 1981 and Banci and Harestad 1988), some error using this method may occur (Banci 1982). Rausch and Pearson (1972) and Liskop et al. (1981) used cementum analysis as an age estimate, whereas Banci and Harestad (1988) used cementum annuli to determine ages but established age class based on skull characteristics. Rausch and Pearson (1972) defined subadults as individuals of 16-28 months, and we defined a subadult as a yearling ~ 1.5 years old. Despite the assumption that some misclassification of age class likely occurred in prior studies as well as ours, and differences in methodology used for determining age classes, comparison of our data to similar studies still yields insight into potential differences in reproductive parameters. We observed CL in 60 percent of the subadults in the W eco-region and only 12.5 percent in the SW eco-region, whereas all ovaries from adult females in the NW contained CL as opposed to 67.8 percent in the SW. Results similar to our NW eco-region were found in Alaska with 50 percent (*n* = 40) of female wolverines 16-28 months of age being pregnant and ~ 91.8 percent (*n* = 98) of adults ≥ 29 months being pregnant (Rausch and Pearson 1972). Liskop et al. (1981) observed that 84.6 percent (*n* = 13) of subadults and 88.5 percent (*n* = 26) of adults ≥ 2 years old were pregnant in British Columbia. However, Banci and Harestad (1988) observed that only 7.4 percent (*n* = 27) of subadult and ~ 73.4 percent (*n* = 79) of adults classified as ≥ 2 years old were pregnant in the Canadian Yukon. Although all the wolverines examined for our study from the NW eco-region were considered pregnant based on CL presence in ovaries, this was likely an overestimation of true pregnancy rates. Hornocker and Hash (1981) found that only two of eight wolverines they tested within our NW eco-region boundaries appeared pregnant when first captured. However, the method of determining pregnancy and age of the wolverines examined in their study was not discussed and may have underestimated true pregnancy rates. They also reported a mean CL production of 2.93 in 15 reproductive tracts in pre-implantation condition from northwestern Montana, whereas the mean number of fetuses from six visibly pregnant females was 2.17. These findings are similar to those observed in our study, but Hornocker and Hash (1981) did not provide the age composition of their sample.

Litter sizes based on CL counts from this study were only compared to results presented by Banci and Harestad (1988) for Canadian Yukon wolverine because researchers conducting similar studies did not state whether they included ovaries containing no CL in calculations. Mean CL counts for pregnant adult wolverine in our study were consistent between eco-regions (3.2 ± 0.6 for the NW, 3.1 ± 0.8 for the SW) and varied slightly by subpopulation. The lowest adult mean CL counts were in the CB subpopulation (2.8 ± 1.2) and the greatest were in the RMF subpopulation (3.1 ± 0.4), but both were less than those observed in the Yukon for similar ages. Banci and Harestad (1988) reported mean CL counts for pregnant females of ages ≥ 2 years that ranged from 3.1 to 4.4. However, both Banci and Harestad (1988) and our data demonstrated that CL counts tend to overestimate the number of in-utero fetuses in paired studies. Our findings indicated that in paired samples, the number of fetuses present were 87.5 percent of the total number CL counted, a higher percentage than observed in the Yukon (82.1%, Banci and Harestad 1988). Estimating the potential number of fetuses using linear interpolation produced an average potential litter size of 2.7 for adult wolverine in the SW eco-region, which was lower than true litter sizes observed in Alaska (3.5, Rausch and Pearson 1972) and the Canadian Yukon (3.2, Banci and Harestad 1988), but greater than the average reported in British Columbia (2.6) by Liskop et al. (1981). However, only five pregnant adult females were examined from British Columbia and the reported average may not be representative of the population due to small sample size. Comparisons of wolverine reproductive data from various studies across the North American are challenged by small sample size and some of the observed variation may be artifacts of such limitations.

Corpora lutea counts and other variables including placental scars, the presence of blastocysts, and presence of fetuses have been used to determine potential reproductive activity for wolverine (Rausch and Pearson 1972, Liskop et al. 1981, Banci and Harestad 1988). We detected CL in ovaries from all of the females harvested from 5 January-14 February in which in-utero fetuses were present. We found no evidence of macroscopically apparent fetuses prior to 5 January, although variation may exist that was not detected in our sample. Rausch and Pearson (1972) observed nidation in two of 41 females killed in November and December. Macroscopically visible fetuses were present as early as 5 January with no evidence of parturition occurring prior to 14 February. Variation in fetal crown rump measurements and fetal weights occurred temporally suggesting variation in implantation and parturition as observed by Rausch and Pearson (1972) and Banci and Harestad (1988) although fetuses were recovered as early as November in Yukon wolverine (Banci and Harestad 1988). Embryonic fetuses were observed in reproductive tracts from 5 January to 4 February in our study that further demonstrated variation in the timing of implantation. Rapid regression of CL postpartum (Wright and Rausch 1955, Rauch and Pearson 1972), presence of CL in ovaries of females harvested in December, and presence of CL in ovaries from all females with macroscopically visible fetuses in our study suggested that CL serve as an adequate indicator of pregnancy from December through mid-February in Montana wolverine. Based on data from this study, parturition dates of Montana wolverine generally occur after mid-February and are temporally variable, but less so than observed in wolverine occupying northern latitudes of their range in North America.

Prior studies of wolverine reproduction in Alaska, the Canadian Yukon, and British Columbia have demonstrated differences in pregnancy rates in subadults and adults and variation in litter size (Rausch and Pearson 1972, Liskop et al. 1981, Banci and Harestad 1988). Although CL and in-utero fetal counts tend to overestimate actual reproduction, these data can provide managers with baseline information for wolverine reproduction. Our results indicated that significant differences in pregnancy rates and CL counts existed between wolverines in northwestern and southwestern Montana; differences in reproduction parameters can occur at fairly small geographical scales. Habitat quality, food availability, population density, harvest, and population genetics have all been suggested as possible influences on reproductive parameters evaluated in this and other studies. A combination of these elements likely contributed to differences in fecundity observed in this study. More information is needed to understand the relationships and effects these parameters have on wolverine populations.

Reproductive capability should be a primary consideration when modeling wolverine populations or making decisions affecting management. Within the southern portion of the wolverines range, basic information on reproduction is lacking, yet critical for management decisions. This study provided insight into basic fecundity parameters of wolverines in Montana and the southern extension of their range.

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WINTER DIET OF SNOWSHOE HARES IN MANAGED FORESTS, SOUTHWEST MONTANA

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ABSTRACT

We followed snowshoe hare tracks during winter months from 2000 through 2003 to locate feeding sites to study snowshoe hare (*Lepus americanus*) diet in a portion of the Greater Yellowstone Ecosystem (GYE) near Gardiner, Montana. We observed browsing on 18 different forbs, shrubs, and trees, but 83 percent of the diet consisted of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*). When we compared hare diet with plant availability in the different cover types within our study area, we found a significant correlation in only young regenerating stands of lodgepole pine. Plant availability greatly influenced hare diet as shown by a reduction in the number of different species being utilized by hares as winter progressed, and smaller plants became buried under accumulating snow pack. Hares also took advantage of fallen branches from mature trees laying on the snow pack, especially in more open cover types where food sources were less abundant.

Key words: diet, Greater Yellowstone Ecosystem, *Lepus americanus*, lodgepole pine, snowshoe hare, winter

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INTRODUCTION

Researchers and managers have directed their attention towards mid-sized forest carnivores in recent years—in particular, the Canada lynx (*Lynx canadensis*). In 2000, lynx were listed as a threatened species in the contiguous United States under the Endangered Species Act. A more complete understanding of snowshoe hare ecology, including their diet, is needed (Ruggiero et al. 2000) due to its importance as a prey species of lynx as well as other mid-sized forest carnivores. Such an understanding applies especially at regional scales, e.g., the GYE, where a knowledge of snowshoe hare ecology had not been developed.

Snowshoe hare diets vary widely across their geographic range and among seasons within a specific area. Hares typically feed on succulent herbaceous vegetation during summer. In winter they browse on trees and shrubs (de Vos 1964, Wolff 1978). Although hares eat a wide variety of plants, including conifers and deciduous shrubs, they often show preference for certain species (de Vos 1964) that varies greatly among regions and depend on the local plant community (Hodges 2000). Wolff (1978) and others have noted that density and frequency of occurrence of plant species within different habitats greatly affect composition of snowshoe hare diets, but several studies have shown that, where present, pines are often the preferred coniferous winter browse (de Vos 1964, Pietz and Tester 1983).

Winter plant availability is greatly influenced by snow accumulation. Grasses, forbs, and small shrubs that are important components of the summer diet are often unavailable to hares during winter. High snow levels also allow hares to reach branches well above the ground that are typically unreachable during other periods of the year (de Vos 1964, Smith et al. 1988). During winter, snowshoe hares feed predominately on woody vegetation and can reach stems ≤ 50 cm above the snow surface (de Vos 1964, Smith et al.1988). Hares feed on woody plants by clipping small diameter twigs and needles or by removing bark on younger trees.

Although studies of snowshoe hare diet are fairly common across North America and Montana (Adams 1959, Malloy 2000, McKelvey et al.2002), relatively little work has been done within the GYE. Since substantial variation in snowshoe hare diet exists among locations, this study represents an opportunity to determine how snowshoe hare diet within a drainage in the northern portion of GYE compares to other populations in the Rocky Mountains.

During the winters of 1999-2003, we monitored snowshoe hare diet in an area heavily impacted by > 50 yrs of silvicultural treatment, including clear-cutting, selective harvesting, and precommercial thinning. Our study objective was to describe variability in hare diets among different cover types and winter months relative to food availability.

STUDY AREA

This study was conducted in the Bear Creek drainage on the Gallatin National Forest northeast of Gardiner, Montana that encompassed ~ 11.7 km^2 (1172 ha) between Yellowstone National Park and the Absaroka-Beartooth Wilderness. For a more detailed description of the study area, see Zimmer et al. (2008). Average snow pack in March over the past 60 yrs on nearby Crevice Mountain (2560 m) was 99 cm (USDA 2003). Snow pack on the upper portion of the study area was very comparable to that observed on Crevice Mountain but lower elevations of the study area received considerably less snow.

Coniferous forests covered the majority of the study area. At elevations below 2280 m, Douglas fir was the dominant overstory species and covered 8 percent of the study area (Table 1). Lodgepole pine was the dominant species above 2280 m. We determined cover type proportions across the study area from a map developed for the cumulative effects model (CEM) by the Interagency Grizzly Bear Study Team (USDA 1990). This map, routinely used by biologists in the Yellowstone Ecosystem to identify habitat types, indicated that different successional stages of lodgepole pine forests covered 62 percent of the study area. Other cover types in the study area included Engelmann spruce (*Picea engelmannii*) and subalpine fir and mixed forest which covered 16 and 8 percent of the study area, respectively.

The forest understory was dominated by birch-leaved spiraea (*Spiraea betulifolia*) and snowberry (*Symphoricarpos albus*) at lower elevations, whereas higher elevations contained predominantly subalpine fir, whitebark pine (*Pinus albicaulis*), buffaloberry (*Shepherdia canadensis*) and twinberry (*Lonicera involucrata*). For this study, understory included all vegetation within ~ 4 m of the ground including lower branches of large trees as well as small trees, shrubs, and forbs.

METHODS AND MATERIALS

Vegetation Availability

We used standard techniques outlined for Forest Service stand exams for timber management (USDA 1986, USDA 2000) to compare species composition and density within different cover types in our study area. We randomly selected 18 sites in each of the cover types. At each site, we established two concentric fixed-radius plots based on standard procedures for Forest Service stand exams. The first was a 3.6-m radius plot. For each live tree rooted within the circle, we determined species, height, diameter at breast height (DBH), height to canopy, canopy ratio, and canopy class. Height to canopy was measured from the ground to where the lowest live branches formed nearly a complete canopy around the tree. We defined canopy ratio as the proportion of total tree height that consisted of live canopy. Canopy class defined how each tree compared to other trees in the area: remnant, dominant, codominant, intermediate, or overtopped.

After all trees were classified, we established a 2.1-m radius plot from the same center point that was used for the 3.6-m radius plot. This plot was divided into two horizontal layers from the ground up to 1 m and from 1 m to 2 m. This provided us with estimates of plant availability in early winter (< 1 m snow depth) and availability during late winter (> 1 m snow depth). We estimated percent canopy cover by species for all trees and shrubs that had canopy within either layer. We did not attempt to quantify herbaceous cover within the plots because most grasses and forbs were buried in snow and served as a minor food source for hares during winter months.

Food Habits

Several methods have been used to look at snowshoe hare diets including stomach content analysis, scat analysis, observing hares, feeding trials, tracking to locate feeding sites, and vegetation monitoring to quantify browsing intensity (Adams 1959, de Vos 1964, Wolff 1978, Sinclair and Smith 1984, MacCracken et al.1988, Smith et al.1988). We chose to follow tracks to locate feeding sites to study winter hare diet within each cover type in our study area from January through March in 2000 through 2003 (Smith et al.1988). We chose this method because it was less expensive, less invasive to hares, coincided with other winter research efforts we were doing in the area, and because the low frequency of observing hares in our area made that method impractical.

Within a cover type we selected a fresh snowshoe hare track or trail and followed it until feeding sites were found. Since it was impossible to follow an individual hare we made a small loop through a particular cover type and followed any tracks that we crossed. We did not record a measure of effort spent searching each cover type for browsed plants. Although hares can feed on conifer needles without affecting stems, we counted only bites where stems were damaged by barking or clipping. Twigs browsed by hares were cut cleanly and at an angle, whereas bites by ungulates were more abrupt or torn (Telfer 1972). At each feeding site we recorded cover type, month, year, species of plant browsed, number of bites on each plant, plant height, and snow depth. Data were collected and summarized as percentages for the total diet over all years and for all years by cover type.

RESULTS AND DISCUSSION

Vegetation Availability

Using circular plots randomly placed in each of eight cover types in the study area (Table 1) during summer months, we found that Lodgepole 3 stands had the highest density of trees > 0.1 m tall (average of

Table 1. Forested Cover Types in the Bear Creek Study Area.

Cover Type	Percent of Study Area	Description
Douglas fir	7.9	Old growth Douglas fir forest. Canopy is broken and the understory consists of some small to large spruce and fir.
Spruce Fir	15.9	Mature spruce fir forest. Stands dominated by Engelmann spruce and subalpine fir in both overstory and understory.
Mixed forest	8.4	Mature mixed forest, late succession to climax stage. Varied structure and age class representation with lodgepole pine, subalpine fir, Engelmann spruce, Douglas fir, and whitebark pine all in the overstory.
Lodgepole 0	14.8	Lodgepole pine 20-30 years post disturbance. Areas of regenerating seedlings and saplings before canopy closure created by logging between 1972 and 1977.
Lodgepole 1	15.6	Lodgepole pine 45-55 years post disturbance. Closed canopy of even-aged, usually dense, lodgepole pine. Stands were clear-cut between 1947 and 1952 and thinned in the mid 1970s.
Lodgepole 2	17.6	Lodgepole pine 100-300 years post disturbance. Closed canopy dominated by lodgepole pine. Understory of small lodgepole pine, whitebark pine, Engelmann spruce and subalpine fir seedlings.
Lodgepole 3	13.3	Lodgepole pine 300 plus years post disturbance. Broken canopy of mature lodgepole pine, but whitebark pine, spruce and subalpine fir also present. Understory of small to large spruce and fir saplings.
Sanitation Salvage	6.4	Sanitation salvages (mature forest partially harvested during 1986). Broken old growth canopy with a dense regenerating understory dominated by lodgepole pine.

18,382 trees/ha) followed by lodgepole 2 and mixed forest. Douglas fir stands had the lowest density with 1,263 trees/ha. As expected, lodgepole pine was the dominant tree species in the two youngest classes of lodgepole pine (Lodgepole 0 and Lodgepole 1), however, as the density of lodgepole pines decreased other coniferous species became more common in older lodgepole pine stands (Lodgepole 2 and 3).

Across all cover types, subalpine fir was the most abundant tree, comprising 55 percent of the total trees counted. Whitebark pine, lodgepole pine, Engelmann spruce, and Douglas fir comprised 21, 12, seven, and five percent of the total, respectively. Although subalpine fir and whitebark pine were the most common trees counted, many were <1 m tall, 89 and 92 percent, respectively, and were typically unavailable to snowshoe hares during late winter.

Lodgepole 0 stands had moderate-to-thick canopy near the ground, and the average tree height was 3 m. Lodgepole 1 stands ranged from 5 to 10 m tall but typically had lower branches within 2 m of the ground. The Lodgepole 2 type consisted of many small trees < 1 m tall and many mature trees with a canopy well above the ground thus providing very little food or cover for hares during winter. Dominant trees in Lodgepole 3 stands had a canopy well above the ground but understory trees and shrubs provided a thicker understory above 1 m than did Lodgepole 2 stands. Douglas fir forests had very little understory cover and a broken overstory well above the ground. Spruce-fir stands had dense overhead canopy that often hung within 2 m of the ground but typically had little or no understory growth more than 1 m tall. Mixed forests were structurally similar to Lodgepole 3 forests but typically had more species diversity, especially in the overstory.

Within 2.1-m radius circular plots divided into two height layers, we detected 15 species in layer 1 (≤ 1 m of the ground) and 12 species in layer 2 (1-2 m above the ground). In layer 1, Lodgepole 0 contained the greatest number of species (13), followed by Lodgepole 1 and Sanitation Salvage with 12 each. Douglas fir stands contained the fewest with only seven detected species (Table 2).

In the second layer, Lodgepole 0, Lodgepole 1, Lodgepole 3, and Sanitation Salvage all had six species present while Lodgepole 2 and Spruce-fir only had three and two species, respectively (Table 2). Layer 1 contained both trees and shrubs. Subalpine fir and twinberry were

Table 2. Top three tree and shrub species present and percent canopy coverage for the two base layers (Layer 1 = 0-1 m, Layer 2 = 1-2 m) for each cover type.

Cover Type	No. of Species	Species 1	% Canopy	Species 2	% Canopy	Species 3	% Canopy
Layer 1							
Sanitation Salvage	12	Subalpine fir	13.3	Snowberry	7.0	Twinberry	3.8
Douglas fir	7	Snowberry	32.8	Common juniper	4.0	Spirea	2.9
Lodgepole 0	13	Lodgepole pine	18.4	Subalpine fir	7.2	Douglas fir	3.8
Lodgepole 1	12	Twinberry	5.5	Snowberry	2.9	Lodgepole pine	2.4
Lodgepole 2	10	Subalpine fir	5.8	Whitebark pine	3.5	Twinberry	1.8
Lodgepole 3	10	Subalpine fir	20.7	Twinberry	3.9	Whitebark pine	2.0
Spruce-Fir	10	Subalpine fir	11.5	Engelmann spruce	5.5	Twinberry	2.7
Mixed Forest	9	Subalpine fir	21.7	Engelmann spruce	6.3	Twinberry	5.7
Layer 2							
Sanitation Salvage	6	Engelmann spruce	6.3	Subalpine fir	5.9	Douglas fir	3.0
Douglas fir	5	Spirea	8.0	Whitebark pine	5.0	Douglas fir	1.1
Lodgepole 0	6	Lodgepole pine	14.0	Whitebark pine	12.2	Subalpine fir	7.0
Lodgepole 1	6	Lodgepole pine	6.1	Whitebark pine	4.5	Subalpine fir	4.0
Lodgepole 2	3	Whitebark pine	2.7	Lodgepole pine	2.0	Subalpine fir	2.0
Lodgepole 3	6	Subalpine fir	5.4	Engelmann spruce	5.0	Whitebark pine	1.2
Spruce-Fir	2	Subalpine fir	6.5	Engelmann spruce	5.8		
Mixed Forest	5	Subalpine fir	7.0	Whitebark pine	5.0	Engelmann spruce	4.3

common in Layer 1 among all cover types except Douglas fir. The second layer (1-2 m) contained mostly coniferous trees. Lodgepole pine was only common in the 1 to 2-m layer in Lodgepole 0, Lodgepole 1, and Lodgepole 2. Subalpine fir was common in all types except for Douglas fir, and whitebark pine was common in all types except Sanitation salvage and Spruce-fir. Douglas fir was only common in Layer 2 in Douglas fir and Sanitation salvage cover types.

FOOD HABITS

While tracking snowshoe hares to locate feeding sites, we counted nearly 5000 bites and detected evidence of browsing on 18 different plant species. Lodgepole pine accounted for nearly 60 percent of bites, followed by Douglas fir and subalpine fir with 12 and 11 percent of total bites, respectively. Six plant species accounted for 1-4 percent of the hare diet; each of the remaining nine species accounted for < 1 percent of the total diet (Table 3). Hares typically clipped off the end of small branches or fed on needles and buds. Occasionally tips of branches were cut but left uneaten lying on top of the snow. Barking of stems by hares was very rare. Hares browsed predominately on coniferous trees (88 % of total diet), but also fed on several shrubs and forbs (12 %), the most common of which were juniper (*Juniperus communis*), annual composites (Compositeae), alder (*Alnus* sp.), and buffaloberry.

Snowshoe hare diet differed among cover types. Within Lodgepole 1 stands, 59 percent of the detected bites were on lodgepole pine, followed by Douglas fir and subalpine fir (Table 4). Lodgepole was the most browsed species in all cover types except for Douglas fir and Lodgepole 3. In Douglas fir stands, Douglas fir was browsed more than any other species and subalpine fir was browsed most often in Lodgepole 3 stands. When comparing percentage of browsing on lodgepole pine in the four successional stages, we detected decreased use from 92 percent in Lodgepole 0 stands to 27 percent in Lodgepole 3 stands.

The diet of snowshoe hares also differed among winter months. We recorded bites on 18 plant species during January but only nine in both February and March. Average snow depth across the study area increased over winter. January averaged 45.2 cm of snow while February and March averaged 69.6 cm and 95.7 cm, respectively.

Although we did not have direct information on plant availability where we collected dietary data, we assessed relative

Table 3. Plant species on which snowshoe hare browsing occurred and the percentage of the total number of bites recorded.

Scientific Name	Common Name	Percentage of Total Bites
Pinus contorta	Lodgepole pine	59.4
Pseudotsuga menziesii	Douglas fir	12.2
Abies lasiocarpa	Subalpine fir	11.3
Juniperus communis	Common juniper	3.7
Pinus albicaulis	Whitebark pine	3.2
Compositae	Annual composites	2.3
Alnus sp.	Alder	2.1
Picea engelmanii	Engelmann spruce	2.1
Shepherdia canadensis	Buffaloberry	1.0
Ribes sp.	Gooseberry	0.6
Salix sp.	Willow	0.6
Heracleum lanatum	Cow parsnip	0.5
Sambucus racemosa	Elderberry	0.4
Symphoricarpos albus	Snowberry	0.4
Lonicera involucrate	Twinberry	0.2
Vaccinium globulare	Huckleberry	0.2
Berberis repens	Oregon grape	0.0
Ceanothus velutinus	Evergreen ceanothus	0.0

Table 4 Comparison of the four most common species used in the hare diet with the availability of those species for each cover type. Availability is based on the percent canopy coverage from both layers combined from the 2.1 m radius vegetation plots.

Cover Type	Rs	*P*-Value	Species	Percent of Diet	Percent Canopy Coverage
Lodgepole 0	1.00	0.00	Lodgepole pine	92.3	29.5
			Subalpine fir	2.4	7.9
			Whitebark pine	1.9	5.6
			Ribes sp.	1.2	0.2
Lodgepole 1	0.40	0.60	Lodgepole pine	59.2	4.3
			Douglas fir	13.7	0.2
			Subalpine fir	12.0	2.4
			Common juniper	4.6	1.6
Lodgepole 2	-0.60	0.40	Lodgepole pine	43.3	0.6
			Douglas fir	32.6	0.5
			Whitebark pine	17.7	4.1
			Subalpine fir	5.7	3.8
Lodgepole 3	0.20	0.80	Subalpine fir	32.4	25.5
			Lodgepole pine	29.6	0.1
			Douglas fir	24.9	0.9
			Whitebark pine	10.4	1.6
Douglas fir	0.82	0.18	Douglas fir	92.0	0.7
			Subalpine fir	8.0	0.0
Mixed forest	-0.21	0.79	Lodgepole pine	46.8	0.0
			Subalpine fir	17.6	27.1
			Composites	10.1	0.0
			Common juniper	5.9	0.8
Spruce Fir	-0.80	0.20	Lodgepole pine	36.1	0.0
			Engelmann spruce	19.8	6.6
			Alder sp.	15.9	0.3
			Subalpine fir	11.1	11.7

availability and use by assuming that the combination of the two layers from the 2.1 m radius vegetation plots recorded during the summer was representative of plant availability during winter. We compared the percentage of diet for the four most commonly browsed species with an index of availability (percent canopy coverage) of those species for each cover type using a Spearman correlation matrix (Table 4). We found a positive correlation between diet and availability in the Lodgepole 0 cover type (Rs = 1.0, P = 0.000) but no significant correlation between diet and plant availability in any other cover type.

Snowshoe hares fed on a variety of plant species and sizes. Plants from which we detected use by hares ranged in size from a few centimeters tall to 21 m tall, but 61 percent of the total bites were taken from plants less than 2 m tall. We commonly observed hares feeding on plants that were barely protruding above the snow, but they also fed on low branches of tall trees that drooped down to the snow level. These low branches provided 28 percent of the total bites.

We never observed hares digging in the snow to uncover food but found hares utilizing branches lying on the snow pack that had broken from the tops of mature trees or had been cut down by squirrels harvesting cones. Approximately 11 percent of the total bites we counted were on fallen branches. Hares fed on these branches in the same manner as a branch attached to a tree. Douglas fir and Lodgepole 2 stands had the highest percentage of their bites on fallen branches, both at nearly 80 percent. Lodgepole 3, mixed forest, and spruce-fir stands had between 20 and 30 percent of their bites on fallen branches. Lodgepole 0 and Lodgepole 1 had 0.5 and 5.7 percent of their bites taken from fallen branches, respectively. The majority of fallen branches eaten by hares were lodgepole pine, whitebark pine, and Douglas fir.

We observed hare browsing on a variety of plants (18 species), but the majority of browsing was on coniferous trees (88%) with lodgepole pine being utilized far more than any other species. Lodgepole pine was a common understory species in only three cover types. Whitebark pine was the fifth most commonly browsed species and was one of the three most abundant understory species in five cover types. Other studies have also reported snowshoe hares utilizing a wide variety of species during winter but also preferences for certain species (de Vos 1964, Wolff 1980, Hodges 2000). Although such preferences vary from place to place, winter hare diets typically consist of coniferous trees, shrubs, and some forbs (Wolff 1978). Where available, pine species are often a preferred winter browse for hares (de Vos 1964). When comparing the diets of hares within the four age classes of lodgepole pine stands, we detected substantially decreased use of lodgepole pine as stands matured. This is not surprising because our vegetation sampling suggested that density of lodgepole trees also declined as lodgepole forests matured.

Engelmann spruce was the eighth most common species in the hare diet (2% of total diet) even though it was common in the understory of four cover types. The majority of bites on spruce trees were taken from the upper branches of trees more than 5 m tall that were bent over under the weight of snow. Only a few bites were taken from spruce trees less than 2 m tall even though 1 to 2 m tall spruce trees were abundant in the study area. In some areas, especially in Canada where there is an absence of pines, spruce trees may be heavily utilized (Wolff 1978, Smith et al.1988). Smith et al. (1988) noticed hares avoiding juvenile spruce branches but found hares using mature side branches during periods of deep snow.

The amount of snowshoe hare browsing on subalpine fir and Douglas fir was very similar even though subalpine fir was much more common across the study area than was Douglas fir. In a study in Northwestern Montana, Adams (1959) found that hares fed heavily on Douglas fir during the winter; ponderosa pine (*Pinus ponderosa*) was moderately used. De Vos (1964) also found heavy browsing on pine species, while balsam fir (*Abies balsamea*) was used very little. Use of subalpine fir is seldom mentioned in literature on snowshoe hare diets.

Hares in our study consumed several species of shrubs and forbs (12% of total diet) including common juniper, annual composites, and alder. Several shrub species were relatively abundant, but all shrubs experienced low levels of use by hares. Due to accumulating snow, availability of these species was typically much lower compared to coniferous trees. Overall, number of species used declined as winter progressed, probably due to decreasing availability of many species as snow depths increased. Others have also noted use of shrubs and forbs by hares in winter (Smith et al.1988, Hodges 2000). Smith et al. (1988) observed hares browsing predominantly on deciduous shrubs, but their study area (Kluane, Yukon) had an abundance of shrub species while spruce was the only common conifer. Adams (1959) observed heavy utilization of Oregon grape (*Berberis repens)* in northwest Montana. We only noticed browsing on this species on one occasion, probably because it was buried under snow for most of the winter due to its short growth stature.

Hares typically feed by clipping the ends off of small twigs, but also may remove the bark of young trees (de Vos 1964). We observed barking on just a few occasions and only on small twigs of coniferous trees, never on trunks of trees or on deciduous shrubs. Barking can be detrimental to young stands of trees by girdling and killing them. Girdling often is associated with high hare density (de Vos 1964, Hodges 2000). We attribute infrequent barking in our study to a relatively low-to-moderate density of hares. Besides clipping small twigs, we observed that hares browsed on fallen branches lying on top of the snow pack (11% of total bites).

Use of fallen branches was most common in Lodgepole 2 and Douglas fir cover types. These types also had the lowest amount of available cover and browse within 5 m of the ground. Due to a lack of available browse growing in these stands, hares appeared to take advantage of this additional food source. Also, fallen branches may have made these less dense habitats tolerable to hares during winter. Use of fallen branches by hares had not been cited in other studies of snowshoe hare diet.

CONCLUSIONS

We found here, as reported for other areas, that snowshoe hares consumed a variety of plants during winter months but fed mostly on coniferous twigs that are available throughout winter, a period in which other plants were buried under snow. Lodgepole pine was an important diet item—common in regenerating lodgepole pine stands. The other two species most frequently consumed by hares, subalpine fir and Douglas fir, were most abundant in dense mature forest types. Mature forest stands and young regenerating stands are essential habitat types needed to ensure healthy populations of snowshoe hares in the northern portion of the GYE.

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Winter Snowshoe Hare Habitat Use Within a Silviculturally Impacted Area

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Abstract

We used snow tracking to monitor snowshoe hare (*Lepus americanus*) habitat use during winter in the Bear Creek drainage near Gardiner, Montana, from 1999 to 2003. Of nine available cover types in our study area, we found the greatest frequency of hare trails in older regenerating stands (~50-55 yrs post-harvest) of lodgepole pine (*Pinus contorta*) that had been pre-commercially thinned. The study area also contained young unthinned stands of lodgepole pine (~25-30 yrs post-harvest) and several middle-age and mature forest types. Older lodgepole stands provided a dense understory and a well-developed overhead canopy as well as plentiful food sources. These three characteristics typically define good snowshoe hare habitat within most of the Rocky Mountain region. Some studies of snowshoe hare habitat needs in portions of the Rocky Mountains indicated that pre-commercial thinning of forest stands may reduce snowshoe hare densities and thus reduce quantity of primary prey for Canada lynx (*Lynx canadensis*). Forest management strategies on USDA Forest Service lands in the Rocky Mountains based on these studies do not allow pre-commercial thinning in areas of potential lynx habitat. Our study showed that thinning portions of regenerating stands may increase the amount of time that lodgepole stands provide suitable habitat for hares.

Key words: snowshoe hare, habitat use, *Lepus americanus*, pre-commercial thinning, silviculture, Greater Yellowstone Ecosystem, forest habitat

Introduction

In 2000, the lynx was listed as a threatened species in the contiguous United States under the Endangered Species Act. Due to its importance in the diet of lynx, a more complete understanding of snowshoe hare ecology has also become a priority (Ruggiero et al. 2000). Currently, biologists and managers are developing management protocols to provide and protect habitat for mid-sized carnivores and their prey. The Canada Lynx Conservation Assessment and Strategy (Ruediger et al. 2000) and the Northern Rockies Lynx Amendment Draft Environmental Impact Statement (USDA Forest Service 2004a) provide the most comprehensive conservation reports to date. They include objectives, guidelines, and standards for resource management, i.e., timber management practices, for 8.4 million ha (18.5 million ac) of occupied and potential lynx habitat in Idaho, Montana, Wyoming, and Utah. These documents, by necessity, apply to large landscapes. Consequently, they may miss important regional differences in snowshoe hare habitat relations. Our research on snowshoe hare habitat use responds to a proposal by the Gallatin National Forest (GNF) to harvest timber in potential lynx habitat. Because little was known about snowshoe hare ecology in the Greater Yellowstone Ecosystem (GYE), the GNF needed baseline data to determine what effects timber sales may have on wildlife, specifically the proposed Darroch-Eagle Creek Timber Sale (USDA 2004b).

Habitat use by snowshoe hares varies greatly across North America, but most studies report that snowshoe hares favor areas with dense understory cover 1-3 m above ground level (Wolfe et al. 1982, Ferron et al. 1998, Hodges 2000). Forest understory density appears to be more important than species composition to snowshoe hares (Pietz and Tester 1983, Litvaitis et al. 1985, Hodges 2000). Although hares seek stands with dense understories, Adams (1959) found that understory density could exceed levels preferred by snowshoe hares. In his study, extremely dense stands were used less than moderately dense areas. Typical hare habitat in the Rocky Mountains consists of montane coniferous forests with well-developed understories (Hodges 2000). This combination of over and understory provides hares with an adequate food supply and protection from both avian and terrestrial predators.

The full effects of modern silvicultural practices on snowshoe hares are not clearly understood. Short-term effects of clearcutting or thinning are usually negative, forcing hares to disperse to other areas (Bull et al. 2005, Homyack et al. 2007, Griffin and Mills 2007). Some recent studies have shown that new thinning treatments may have fewer negative effects on snowshoe hares compared to traditional pre-commercial thinning practices (Ausband and Baty 2005, Griffin and Mills 2007). Sullivan and Sullivan (1988) found that hare activity actually increased immediately after thinning due to increased amounts of cover and food piled on the ground. Use of thinned sites decreased 2 years post-thinning, and unthinned stands were preferred. Several studies reported that hares prefer regenerating coniferous stands 20 to 60 years post harvest, depending on geographic location and the rate of regrowth, due to the dense understories typically found in these successional stages (Monthey 1986, Thompson et al. 1989, Koehler 1990, Koehler 1991).

Since substantial spatial variation exists in snowshoe hare habitat use, this study offered an opportunity to observe how snowshoe hare ecology in the GYE compares to other populations in the Rocky Mountains. This information is critical to understanding the potential of the GYE to support viable lynx populations. Because this study was located in managed forests rather than wilderness, it provided critically needed data on how current silvicultural practices, especially pre-commercial thinning, affect hare habitat use.

Our study objectives were to examine snowshoe hare use of nine cover types in the study area (Table 1) and to compare snowshoe hare use of unthinned regenerating clear-cuts, thinned stands, and uncut mature stands. We conducted snowshoe hare surveys in the Bear Creek Drainage, Gardiner Ranger District beginning in January 1999.

STUDY AREA

Our study area on the Gallatin National Forest encompassed 11.7 km^2 between Yellowstone National Park and the Absaroka-Beartooth Wilderness. Elevation ranged from 2100 to 2600 m. Mountain peaks in the surrounding area exceeded 3100 m. Snow typically covered the study area from late October until May. Average snow pack in March over the past 60 years on nearby Crevice Mountain (2560 m)was 99 cm (USDA Forest Service, Gardiner Ranger District, Gallatin National Forest, unpublished report). Snow pack at lower elevations of the study area was considerably less.

Coniferous forests covered the majority of the study area Douglas fir (*Pseudotsuga menziesii*) was the predominant overstory species below 2280 m elevation and covered 8 percent of the study area (Table 1). Lodgepole pine (*Pinus contorta*) predominated at elevations > 2280 m. Cover type proportions across the study area were determined from a map developed for the cumulative effects model (CEM 4) (USDA, cumulative effects model, Interagency Grizzly Bear Study Team, Bozeman, Montana, unpublished report). This map, routinely used by biologists in the GYE to identify habitat types, indicated that different successional stages of lodgepole pine forests covered 62 percent of the study area. Other cover types in the study area included the Engelmann spruce (*Picea engelmannii*) - subalpine fir (*Abies lasiocarpa*) type and a mixed forest type, which covered 16 and

Table 1. Dominant (>5% of the study area) cover types in the Bear Creek Study Area.

Cover Type	Description
Douglas fir	Old growth Douglas fir forest. Canopy is broken and the understory consists of some small to large spruce and fir.
Spruce - Fir	Mature spruce fir forest. Stands dominated by Engelmann spruce and subalpine fir in both overstory and understory.
Mixed Forest	Mature mixed forest, late succession to climax stage. Varied structure and age class representation with lodgepole pine, subalpine fir, Engelmann spruce, Douglas fir, and whitebark pine all in the overstory.
Lodgepole 0	Lodgepole pine 20-30 years post disturbance. Areas of regenerating seedlings and saplings before canopy closure created by logging between 1972 and 1977.
Lodgepole 1	Lodgepole pine 45-55 years post disturbance. Closed canopy of even-aged, usually dense, lodgepole pine. Stands were clear-cut between 1947 and 1952 and thinned in the mid 1970s.
Lodgepole 2	Lodgepole pine 100-300 years post disturbance. Closed canopy dominated by lodgepole pine. Understory of small lodgepole pine, whitebark pine, Engelmann spruce and subalpine fir seedlings.
Lodgepole 3	Lodgepole pine 300 plus years post disturbance. Broken canopy of mature lodgepole pine, but whitebark pine, spruce and subalpine fir also present. Understory of small to large spruce and fir saplings.
Sanitation Salvage	Sanitation salvages (mature forest partially harvested during 1986). Broken old growth canopy with a dense regenerating understory dominated by lodgepole pine.
Meadow	Non-forested areas supporting primarily herbaceous vegetation at climax.

percent of the study area, respectively. The Bear Creek drainage has been subjected to extensive timber harvesting over the past 60 years with major clear-cuts created during the late 1940s and mid 1970s covering 30 percent of the study area. Sanitation salvage cuts in 1986 removed dead or dying trees but did not remove all mature trees or destroy the understory; these covered 6 percent of the area (USDA Forest Service, timber treatment records, Gardiner Ranger District, Gallatin National Forest, unpublished report). All stands harvested during the late 1940s were thinned in the early to mid 1970s. Forest understories within the study area were dominated by birch-leaved spiraea (*Spiraea betulifolia*) and snowberry (*Symphoricarpos albus*) at lower elevations whereas higher-elevation stands contained predominantly subalpine fir, whitebark pine, buffaloberry (*Shepherdia canadensis*) and twinberry (*Lonicera involucrata*).

Forest Service management allowed timber harvest, motorized travel, and dispersed recreation. Winter recreational activities included cross-country skiing, snow hoeing, snowmobiling, hunting, trapping, and firewood harvest. Three Forest Service roads traverse the study area and are open to vehicles in the summer and used as snowmobile and ski trails during winter.

METHODS AND MATERIALS

Road Track-Intercept Transects

During winters 1999-2003, we determined if snowshoe hares used each cover type in proportion to its availability along transects defined by roads through the study area. Proportions of cover types encountered along the transect did not represent proportions of cover types found across the whole study area because the route followed roads built to access cutting areas; however, the road system allowed us to efficiently replicate our trail counts throughout winter among all years. Roads were split into segments corresponding to changes in cover type (Mattson and Despain 1985). Our methods similarly followed those of Conroy et al. (1979), Monthey (1986), Thompson et al. (1989), and Tyers (2003).

From January through March each year, we traveled the 18-km route via snowmobile 24-72 hrs after each snowfall and counted sets of snowshoe hare tracks, hereafter referred to as hare trails, in each of the segments of the transect. Snowshoe hare trails were recorded each time they crossed the road. If a hare crossed the road several times in an area, it was recorded each time it crossed the road. For runways, defined as multiple trails on top each other, we tried to determine the number of times it was traveled by backtracking away from the road. Often, trails would separate a short distance. We sampled the transect route between seven and 12 times each winter from 1999 through 2003. New snow was needed to erase old trails and create a new tracking surface (Thompson et al. 1989); therefore, our sample size varied annually due to frequency of new snowfall. The number of trails counted was standardized by dividing by the number of nights since the last snowfall.

We grouped data into 11 cover type combinations to account for different cover types occurring on either side of the road and analyzed them using chi-square goodness-of-fit to test the null hypothesis that each cover type was used in proportion to its availability (Neu et al.1974). Statistical significance was accepted at $P < 0.05$. If the null hypothesis was rejected, then a Bonferroni confidence interval was calculated to determine if each type was used more, less, or in proportion to its availability (Neu et al. 1974).

Line Transects

During winters 1999 and 2000, we used systematic line transects (Conroy et al. 1979) to cover the entire study area to determine if the association between hares and cover types observed on the road transects would hold for a sampling system independent of roads. The 1999 transects consisted of meandering lines that started at upper elevations in the study area and followed the fall line of the topography. Lines were independent of the road network, and segment lengths for different cover types sampled were estimated based on field notes and reconstruction of transect routes on aerial photographs. We traveled each line on snowshoes soon after a snowfall once over the course of that winter. For each cover type segment on a line, we classified snowshoe hare trail frequency into one of four categories: absent, low (occasional single trails), medium (many trails and some runways, forms, and feeding sites), or high (many undistinguishable trails and heavily used runways; forms and feeding sites were common) (Conroy et al. 1979). We chose to classify trail frequency into categories instead of counting actual trail intercepts along each line to alleviate a problem with runways where deciphering number of trails was difficult. A total of 30 lines covering 21 km were surveyed.

During winter 2000, we established a set of 51 parallel transects (Conroy et al. 1979) independent of the road network and spread over the entire study area. Endpoints of each line were marked using a GPS unit. These lines covered 390 cover-type segments and a total distance of 56 km. The system used to classify levels of hare use within the different cover type segments during 1999 was also used for this set o fline transects.

For both years we calculated the proportion of segments within each cover type where snowshoe hare trails were present (Monthey 1986). For cover types where snowshoe hare trails were observed, we also calculated the proportion of segments that contained low, medium, and high amounts of trails.

Transect Method Comparison

The consistency between cover type rankings obtained from road-based and non-road-based transect sets was examined using Spearman rank-correlation tests (Zar 1999).

RESULTS AND DISCUSSION

Road Track-Intercept Transects

When we grouped all cover type combinations along roads within the study area into 11 categories and combined data from all winters (1999-2003), chi-square analysis showed that snowshoe hares did not use cover types in proportion to availability ($\chi^2 = 1099.89$, 10 df, $P < 0.001$). Tests of individual cover types indicated that hare use of Lodgepole 1 and Lodgepole 0/Mixed Forest (lodgepole pine regrowth ~25-30 yrs of age on one side of the road and mixed forest on the other) segments was greater than expected, while the Spruce-Fir type was used as expected. All other cover types were used less than expected (Table 2).

Small sample sizes hampered our analysis for individual years in 1999 and 2001, but general trends were apparent. Cover type use varied slightly from year to year, but Lodgepole 1 was consistently used more than other types (Fig. 1). The only consistent change over time occurred in the use of Lodgepole 0, which increased each winter from 1999 through 2003. In the first 2 years of the study, Lodgepole 0 stands were used less than expected. They were used in proportion to availability the last 3 years.

We counted hare trails in January, February, and March. Over all winters (1999- 2003), Lodgepole 1 and Lodgepole 0 contained a majority of use by hares, but use of Lodgepole 1 increased as the winter progressed; however, hare use of Lodgepole 0 stands was highest in January after which it decreased (Fig. 2).

Line Transects

Transects ran independent of the road system closely mirrored proportions of each cover type in the area based on the CEM map. During 1999 we monitored 198 cover type segments of which 82 (41%) contained snowshoe hare trails. In 2000, 193 of 390 (49%) traveled segments contained trails. All cover types except meadows contained some snowshoe hare trails during both years. In 1999, the Spruce-Fir cover type had the highest proportion of segments with trails (63% of segments) followed by Lodgepole 1 (57%), and Mixed Forest (48%). Meadows had the lowest proportion of segments with trails (0%) followed by Lodgepole 0 (5%) and Douglas fir (12%).

In 2000, the cover type with the highest percentage of segments with trails was Lodgepole 1 (77%) followed by Spruce-Fir (73%), and Mixed Forest (57%). The few segments in which whitebark pine dominated also had a high incidence of hare trails (64%). The lowest proportions of segments with trails occurred in the Meadow (0%), Douglas fir (22%), and Lodgepole 0 (26%) cover types.

Method Comparison

When we compared proportions of segments in each cover type that contained at least one hare trail using a Spearman rank correlation, the road track-intercept transect and line transect methods were correlated

Table 2. Chi-square analysis for snowshoe hare cover type use versus availability across all years based on track counts from road track-intercept transects. $\chi^2 = 1099.89$; $P < 0.001$. Cover types are defined in Table 1.

Cover Type	Proportion Available	Number Expected	Number Observed	Proportion Observed	Confidence Interval	Test Result[a]
Douglas fir	0.140	259.42	22	0.012	0.005-0.019	
Lodgepole 0	0.184	341.19	242	0.130	0.108-0.153	
Lodgepole 0/1	0.031	57.89	22	0.012	0.005-0.019	
Lodgepole 0/3	0.009	17.33	7	0.004	0.000-0.007	
Lodgepole 0/Mixed Forest	0.022	41.44	65	0.035	0.023-0.047	+
Lodgepole 1	0.295	545.94	1,157	0.625	0.593-0.656	+
Lodgepole 1/Mixed Forest	0.037	68.11	24	0.013	0.006-0.021	
Lodgepole 3	0.096	178.22	135	0.073	0.056-0.090	
Meadow	0.029	53.39	6	0.003	0.000-0.007	
Mixed Forest	0.149	276.49	165	0.089	0.070-0.108	
Spruce - Fir	0.007	13.24	8	0.004	0.000-0.008	ns

[a] - = use less than expected (P < 0.05), + = use greater than expected, and ns = no significant difference in use and availability.

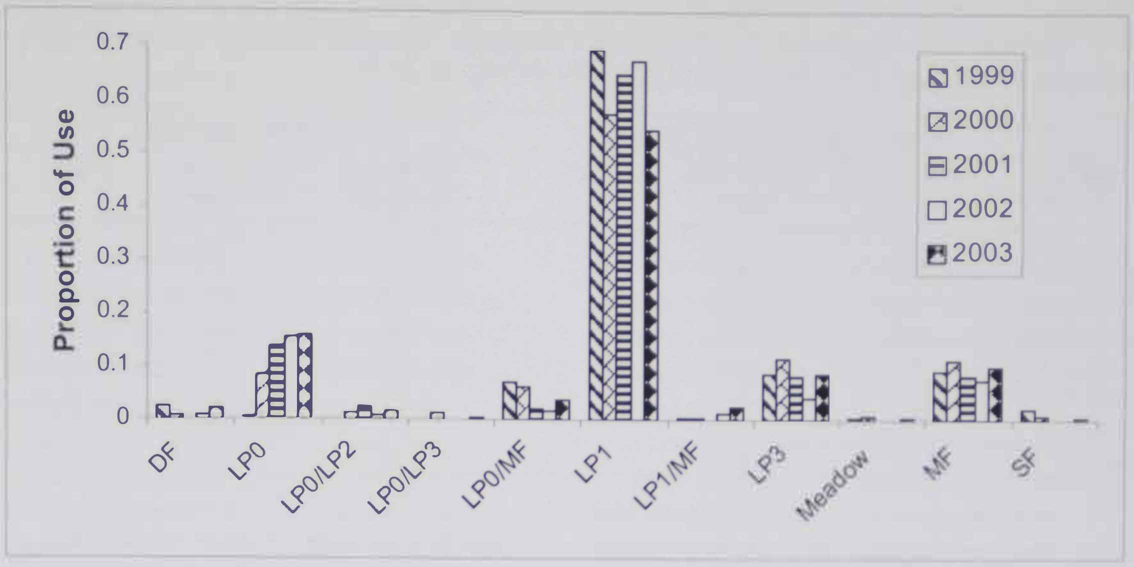

Figure 1. Snowshoe hare cover type use among all years.

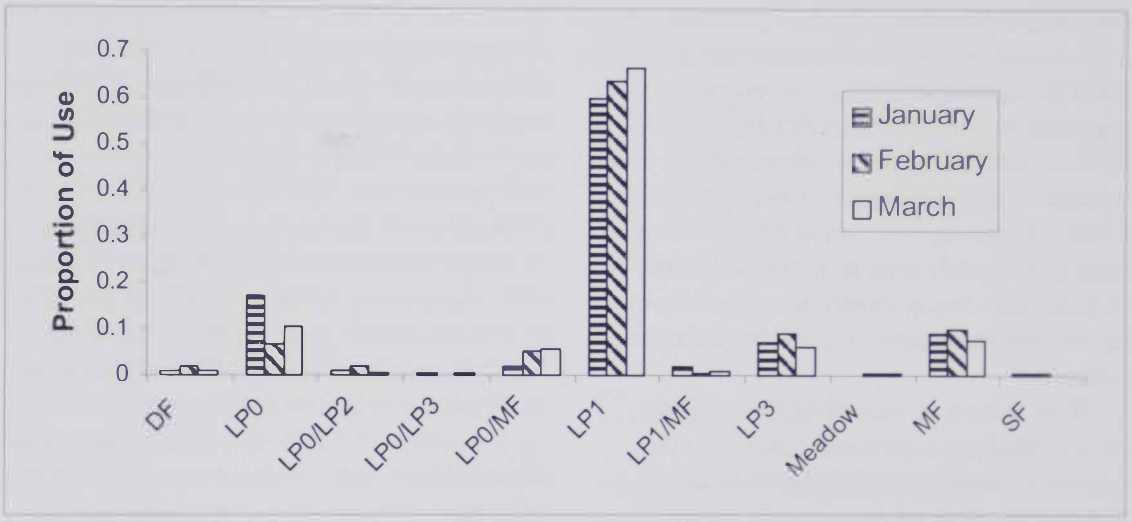

Figure 2. Snowshoe hare cover type use among months for all yers combined.

(Rs = 0.714, $P = 0.047$). Lodgepole 1 had the highest percentage of segments with trails for both methods (Table 3). Both transect types indicated that Douglas fir and Meadow were cover types least frequently used by hares. Ranking of cover types with intermediate levels of use were not consistent. The biggest discrepancy between methods was for Spruce-Fir which was probably an artifact of small sample size. The Spruce-Fir results for the road track-intercept transect were based on one short segment that was bordered on one side by a meadow. Spruce-Fir segments in the line transects were more representative of stands across the study area.

Although our experimental design precluded a definitive test of stand age and thinning vs. non-thinning as treatments (age and silvicultural treatment were confounded), both road transects and line transects indicated that Lodgepole 1 stands, which had been clear-cut ~50-55 yrs prior to our sampling and thinned 20-25 yrs after the cut, contained comparatively high levels of snowshoe hare use during winter months. These stands typically had a closed canopy within 2 m of the snow surface formed by lower limbs on regenerating lodgepole pine and abundant food in the form of accessible lodgepole limbs and palatable shrubs of other species (Zimmer 2004). Cover types

Table 3. Comparison of percentage of segments with tracks for each cover type obtained from the 2 tracking methods. Spearman rank correlation results for road track-intercept versus line transects, Rs = 0.714, P = 0.047. Cover types are defined in Table 1.

	Road Track-Intercept All Years			Line Transect Both Years		
Cover Type	Number of Sections	Percent with Tracks	Rank	Number of Sections	Percent with Tracks	Rank
Lodgepole 0	433	28.2	4	72	19.4	6
Lodgepole 1	556	51.4	1	71	69.0	1
Lodgepole 2	96	21.9	5	73	41.1	5
Lodgepole 3	245	35.9	2	59	49.2	4
Spruce – Fir	57	14.0	6	93	68.8	2
Mixed Forest	403	29.5	3	116	53.5	3
Douglas fir	177	8.5	7	31	19.4	7
Meadow	154	4.6	8	30	0.0	8

in our study area without this combination of cover and food were less heavily used by hares. Mixed Forest and Lodgepole 3 cover types had a developed overhead canopy and understory, but canopy cover between 1 and 4 m above the ground was low compared to Lodgepole 1 (Zimmer 2004. Spruce-Fir stands provided moderately dense over and understory cover, but food species frequently consumed by snowshoe hares in our study area were not abundant. Lodgepole 0 stands offered abundant food but lacked dense cover > 2 m above the ground.

The pattern of snowshoe hare habitat use we observed was consistent with other studies in North America (Wolff 1980, Wolfe et al. 1982, Hodges 2000). Hares can be found in many forest types from pine to spruce to deciduous stands, but hare densities appear to be greatest in areas with thick understory cover (Adams 1959, Wolff 1980, Litvaitis et al. 1985).

From a silvicultural perspective, snowshoe hares in the Bear Creek drainage used older regenerating stands more than mature or young regenerating forests. The youngest regenerating stands showed low to moderate levels of use. Snowshoe hare use of the youngest stands declined as winter progressed possibly due to a loss of available cover as vegetation near the ground became buried under snow. Such a condition perhaps decreased availability of food or directly reduced snowshoe hare density due to over-winter mortality. Use of older regenerating stands increased as the winter progressed. Although both ages of regenerating stands provided plentiful food and thick cover near the snow surface, younger stands lacked thick cover > 2 m above the ground and thus offered only thin overhead cover during late winter when snow depths exceeded 1 m. Mature stands with moderate to very dense understories (Mixed Forest, Spruce-Fir, and Lodgepole 3) had moderate to high levels of use while open middle age and mature stands (Douglas fir and Lodgepole 2) received very little use. Meadows were seldom used by hares during winter due to a lack of food and cover.

Stand uniformity also likely influenced desirability of specific cover types as winter hare habitat in our study area. In general, Lodgepole 0 stands contained higher stem densities and greater ground cover than Lodgepole 1 stands. However, Lodgepole 0 stands typically were not uniform in density or height and often contained small pockets of shorter trees and lower stem densities. Hare use of Lodgepole 1 could be greater due to the more uniform and continuous overhead canopy (Kashain 2002) and to the characteristic of dense cover between 2 and 4 m above ground. We should note that Lodgepole 0 stands may provide good habitat for hares during summer months.

Buskirk et al. (2000) suggested that hares prefer both early and late successional forest types, but late successional stages may provide optimal cover for hares over a longer period of time. Our data suggested that regenerating stands provide optimal cover for hares but only for ~20-30 years. Understory density in a lodgepole forest changes as the stand ages. After a disturbance the understory (low branches as well as shrubs) continue to develop and thicken until the overstory closes and the understory begins to die and the trees self-prune. During this self-pruning stage, the lower edge of the canopy moves progressively higher, but very little regrowth occurs in the understory among later successional species of trees or shrubs. Eventually, the uniform canopy begins to break apart allowing more understory growth of trees and shrubs to take place, which will once again create a thick understory that also offers good habitat for hares.

Several studies have shown snowshoe hares prefer regenerating forest stands to mature forest types (Wolff 1980, Bittner and Rongstad 1982, Monthey 1986, Koehler 1991, Sullivan et al. 2007). These second-growth stands typically provide very dense understory cover important to hares, but the dense understory eventually opens. Exactly when and how long regenerating stands provide suitable habitat for hares will differ among regions due to variable tree growth rates or climate differences. Thinning patterns may also influence the suitability of stands for hares (Bull et al. 2005, Griffin and Mills 2007, Sullivan et al. 2007). Koehler (1991) found that 20-year-old lodgepole stands in Washington had high levels of use by hares; however, Lodgepole 0 stands in our study showed low levels of use by hares compared to other available cover types. Although these forests were of similar age post-disturbance, climatic variation likely influenced different stand characteristics . Also, we encourage caution in interpreting these cover type use results in that our efforts and those of Koehler et al. (1979) and Koehler (1991) compared hare use of a small number of available cover types within a specific study area. In areas with a greater variety of stand types and ages, hares may demonstrate different stand selection patterns than what either Koehler or we observed.

In commercial forests, thinning will likely occur despite negative short-term effects on winter habitat for snowshoe hare. e.g., reduced stem densities and a more open canopy (Sullivan and Sullivan 1988). When viewed from a long-term perspective, thinning delays the self-pruning process, thus keeping understory branches intact longer. Adams (1959) suggested using light thinning in very dense stands to allow more light penetration to promote more growth of ground cover.

Logging during 1972-1976 created Lodgepole 0 stands in our study area that had not been thinned. Hare use in these stands apparently increased throughout our study. If they were thinned now, hare densities may likely remain low for another ≥10 years. However, thinning may create good hare habitat until ~70 years post-harvest. If they are not thinned, hare use would presumably continue to increase, but these stands would self-prune sooner and fail to provide sufficient understory cover for hares by ~50 years post-harvest instead of ~70 years. Hares may only use these regenerating stands for ~ 25 to 30 years whether or not thinning is employed.

CONCLUSIONS

We agree with Buskirk's (2000) contention that hares and lynx may both benefit most from the preservation of large expanses of late successional or mature forests. Mature forests provide stable, long-term habitat for hares as well as for red squirrels, another important prey item of lynx; these stands also provide an abundance of denning habitat for lynx (Buskirk et al. 2000). Mature forest types with dense understories in our study area also showed moderate-to-high levels of use by hares. However, in areas where logging has and will continue to occur, managing early successional forests based on the habitat requirements of hares and lynx should continue to be a top priority. We do not advocate cutting mature stands to provide more regenerating stands for hares.

Although we identified Lodgepole 1 stands as most used by snowshoe hares, trees in this cover type were beginning to self-prune above the snow pack. These stands were logged 50-55 years prior to our study and were subsequently pre-commercially thinned to enhance tree growth. Although they received the greatest use by hares among available cover types, favorable conditions are temporally limited. For example, Lodgepole 1 stands, due to self-pruning, may no longer have lower branches ≤ 5 m of the ground within the following 10-20 years. Without these low branches, hare use will decrease substantially (~ 60 to 70 years post harvest). In contrast, Lodgepole 0 stands (~25 yrs post-harvest at the start of this study) were just beginning to develop a closed canopy > 2 m above the ground. Thus, lodgepole pine stands near our study area provide the best habitat for hares between 30 and 70 years post-harvest. In areas of potential lynx habitat, current Forest Service standards only allow thinning in stands that have self pruned well above the ground and no longer provide suitable hare habitat (Ruediger et al. 2000). Also, the proposed management alternative in the current draft of the environmental impact statement for the Northern Rockies Lynx Amendment would only allow pre-commercial thinning within 200 ft of administrative sites or in stands that no longer provide suitable habitat for snowshoe hares (USDA 2004a). Implementing these thinning standards, at least in locations near our study area, may reduce the amount of time regenerating stands could provide beneficial habitat for hares.

We recommend a combination of thinned and unthinned stands to provide suitable habitat within regenerating forests over a longer period of time. Having multi-aged stands and a mix of thinned and unthinned stands in an area may provide suitable hare habitat over a longer period of time compared to a uniform treatment. Thinning portions of a logged area juxtaposed to unthinned stands may provide hares with additional suitable habitat once the unthinned stands self-prune and no longer provide sufficient cover. This may be especially beneficial for hares in areas that lack mature forests with dense understories.

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MEASURING SOIL WATER POTENTIAL WITH GYPSUM BLOCKS: CALIBRATION AND SENSITIVITY

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ABSTRACT

Gypsum block soil sensors have been a useful tool for measuring soil water for over sixty years. We improve their usefulness by 1) demonstrating a new gypsum block calibration procedure, 2) determining equilibration times for two types of commercial blocks (Delmhorst GS-1, and Bouyoucos) across a range of water potentials (-4.3, -1.2, -0.56, -0.2, -0.08, -0.05, and -0.02 MPa), 3) providing calibration curves for Delmhorst and Bouyoucos instruments, and 4) quantifying the sensitivity of gypsum blocks by finding which soil water potentials are statistically distinguishable. Our procedure yielded calibration curves which are appropriate for Delmhorst and Bouyoucos instruments in well aggregated soils. Dry blocks imbedded in soils reached equilibration (variability of sensor readings stabilized) after ~ 150 hours for Delmhorst, and ~ 300 hrs for larger Bouyoucos blocks. In the water potential series described above, sensor readings of blocks between -4.3 and -0.08 MPa were statistically distinguishable ($\alpha = 0.05$) for both Delmhorst and Bouyoucos blocks. While sensor readings from blocks at the two highest water potentials (-0.02 and -0.05 MPa) were not significantly different for either Delmhorst or Bouyoucos blocks, readings for -0.02 MPa soils were significantly different from soils $\leq$ -0.08 MPa for both blocks types.

Key words: Soil water potential, gypsum blocks, calibration procedure, equilibration time, precision of soil sensor readings, gypsum block sensitivity.

INTRODUCTION

Water availability largely controls plant productivity in both natural and agricultural settings (Lambers et al. 1998). In natural environments availability of water largely determines the distribution and primary productivity of terrestrial ecosystems (Holdridge 1947, Lieth 1975). In agricultural settings crop yield losses from water stress exceed losses from all other biotic and abiotic factors combined (Boyer 1985).

Plant water uptake is largely determined by the water potential gradient from soil to root to stoma to air. As soil water potential drops towards the 'permanent wilting point' (conventionally defined as $\Psi = -1.5$ MPa), a plant will become increasingly unable to extract water from soil. Water stress symptoms may occur including stomatal closure, decreased growth, decreased nutrient uptake, and even cavitation. In flooded soils ($\Psi \cong 0$ MPa) plants may have similar symptoms including stomatal closure and wilting (Lambers et al. 1998). Reliable methods are needed for measurement of soil water potential because of its strong influence on plant physiological processes.

Gypsum block sensors (Bouyoucos and Mick 1940, Taylor et al. 1961) are a time-tested, inexpensive, and reliable tool for measuring soil water across a diversity of field sites (Scanlon et al 2002). Sensor readings of blocks reflect their decreased electrical resistivity with increasing soil water content. Slight dissolution of $CaSO_4$ in blocks creates a weak in-block ion solution which simultaneously controls against the confounding effect of soil salinity on electrical resistance (Weaver 1987, Scanlon et al. 2002). Drawbacks of gypsum blocks include time for equilibration with soils, and an inability to distinguish matric potentials higher than the air entry pressure of the blocks (-0.03 MPa; Scanlon et al. 2002). Other methods for measuring soil water

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potential including piezometry, neutron thermalization, thermocouple psychometry, and time delay reflectometry are reviewed by Reeve (1986), Hignett and Evett (2002), Andraski and Scanlon (2002), and Robinson et al. (2003), respectively.

This paper provides four products that we hope will increase the usefulness of gypsum blocks. We 1) demonstrate a new gypsum block calibration procedure involving equilibration of blocks in soils of known water potentials; 2) determine equilibration times for dry blocks inserted in samples of a sandy loam at seven water potentials; 3) provide calibration curves for two types of commercial plaster blocks (Delmhorst GB-1 and Bouyoucos); and, 4) demonstrate the useful range of both block types by determining what soil water potentials are statistically distinguishable.

MATERIALS AND METHODS

We studied two types of commercial blocks, Delmhorst GB-1 (2.5 cm x 2 cm diameter) available from Forestry Suppliers (205 West Rankin Street, P.O. Box 3897 Jackson, MS 39284-8397), and Bouyoucos (3 x 4 x 1.5 cm) manufactured by Backman Instruments (P.O. Box 3100, 2500 Harbor Boulevard, Fullerton, CA).[2] The blocks were read with a Delmhorst KS-D1 digital soil moisture meter available from Forestry Suppliers. KS-D1 sensor readings corresponding to resistances in the range between 1 and 40,000 ohms were measured by Dr. V. Gerez at the Department of Electrical Engineering at Montana State University.

Block Calibration

To calibrate blocks, we measured their electrical resistance at seven known water potentials and plotted water potential against resistivity. As a calibration medium we chose a homogenized sandy loam (60% sand, 16% silt, 24% clay). We used this soil because its clay/silt components would allow good contact with blocks, while its sand component would facilitate mixing and prevent mudding. Calibration involved five steps.

1) A water retention curve was created for the calibration soil by measuring its water contents at -0.03, -0.1, -0.3, -0.5, -0.8, and -1.5 MPa. Soil water potentials were set with a pressure membrane/ceramic plate apparatus by the Montana State University soil testing laboratory (cf. Gardner, 1986). Water contents of soils at these known water potentials were measured gravimetrically (kg kg^{-1}). A regression of water content and water potential was linear after power transformation (r^2 = 0.992), allowing interpolation of water potential from water content.

2) We compared sensor readings for gypsum blocks over a useful range of water potentials from approximately -0.01 to -5 MPa. To do so we adjusted soil samples to desired water potentials by repeatedly misting them with water and mixing until the correct water content (and corresponding water potential) was reached. Using this method soils were brought to seven evenly spaced water contents (32, 29, 27, 24, 21, 19, and 16% H_2O) corresponding to water potentials of -0.02, -0.05, -0.08, -0.20, -0.56, -1.2, and -4.3 Mpa, respectively. Note that water potential of the -4.3 MPa soil was outside the calibration range created in step 1 and was therefore extrapolated.

3) We stored soils from the seven different water potentials in separate cylindrical containers (16 cm high × 16 cm dia. $\cong$ 3200 cm^3) at room temperature (25 ºC). To quantify sensor variability, three Delmhorst and three Bouyoucos blocks were placed into each of the seven containers, i.e., six blocks were installed / container. Blocks were neither wetted before installation nor placed into slurries since this would have caused confounding from hysteresis (affected block saturation history) and dramatically altered the water potentials of the containers. To prevent water loss by evaporation/condensation, we sealed containers with duct tape, enclosed them in polyethylene bags, and stored them at room temperature. Ports through which gypsum

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block cables extended from the cylinders were sealed with silicon rubber, so drying air did not enter as sensors were read. To demonstrate that no water loss occurred, gravimetric measures were repeated at the end of the experiment.

4) To determine block equilibration time, sensor readings for all blocks were taken 10 times over a 36-day period at 0, 8, 27, 99, 166, 267, 335, 439, 600, 774, and 875 hrs. We assumed equilibration to have been reached when post-equilibration sensor readings within a block type (Bouyoucos or Delmhorst) had an average standard deviation (across water potentials) < 1.

5) To represent an equilibrated sensor reading, all post-equilibration block readings were averaged within a block type (Bouyoucos or Delmhorst) for a particular water potential treatment. We created calibration curves by regressing these seven equilibrated block readings against the seven known soil water potentials using curve fitting software.

ANALYSIS

We determined capacity of gypsum blocks to distinguish distinct water potentials by comparing post equilibration readings from the seven water potentials. A single factor analysis of covariance (ANCOVA) was used for these comparisons with water potential as the main effect and time (hrs) as the covariate. Responses were readings from the time frames after equilibration. Thus, readings from separate post-equilibration time frames were not averaged (as they were in calibrating) but were used instead to quantify sensor variability after equilibration. Due to a lack of independence of blocks within a cylinder, i.e., pseudoreplication, readings within a cylinder were averaged to create a single response for each type of block (Delmhorst or Bouyoucos) for each water potential at each post-equilibration time frame. We used Scheffé's procedure (Neter et al. 1996:1024) for multiple pairwise comparisons of water potentials. The ANCOVA and pairwise comparisons were run using the statistical program R (R development core team 2008). Calibration curves were created using Table Curve 2D® (Systat software 2002).

RESULTS

As the criterion for block equilibration, we required that post-equilibration sensor readings have an average standard deviation < 1 (according to Delmhorst Instrument Co. valid readings for the Delmhorst KS-D1 meter range between 0 and 100). Using this criterion, Delmhorst blocks equilibrated with soils after ~ 150 hrs, whereas the larger Bouyoucos blocks equilibrated after ~ 300 hrs (Fig. 1). After these times the average standard deviation of readings across all water potentials was ~ 0.70 for Delmhorst and 0.96 for Bouyoucos blocks (Fig. 1). Equilibration times were shorter in wetter soils (Fig. 1).

We constructed calibration curves for Bouyoucos and Delmhorst blocks by fitting average post-equilibration block readings against known soil water potentials (Fig. 2). The association between sensor readings and soil water potential was well fit with a simple two-parameter logarithmic model for both Delmhorst ($r^2 = 0.9997$) and Bouyoucos ($r^2 = 0.9991$) blocks (Fig. 2). Exact-model predictions of water potentials at particular sensor readings appear in Table 1. We provide equations for models in Appendix 1. The association between soil sensor readings and soil water potential was asymptotic near field capacity for both types of blocks (Fig. 2).

Differences in readings of equilibrated blocks among water potential levels were highly significant ($F_{6,35} = 6678$, $p < 2.0\times10^{-16}$ for Delmhorst; and $F_{6,21} = 3496$, $p < 2.0\times10^{-16}$ for Bouyoucos). Time and the interaction of time and water potential were not significant for either block type. In pairwise comparisons of readings among water potential treatments, all but the highest water potentials (-0.02 and -0.05 MPa) were distinguishable from each other ($\alpha = 0.05$). This lack of distinguishability at high water potential soils was evident for comparisons of both Delmhorst and Bouyoucos blocks. Note, however, the -0.02 MPa treatment was distinguishable from soils ≤ -0.08 MPa for

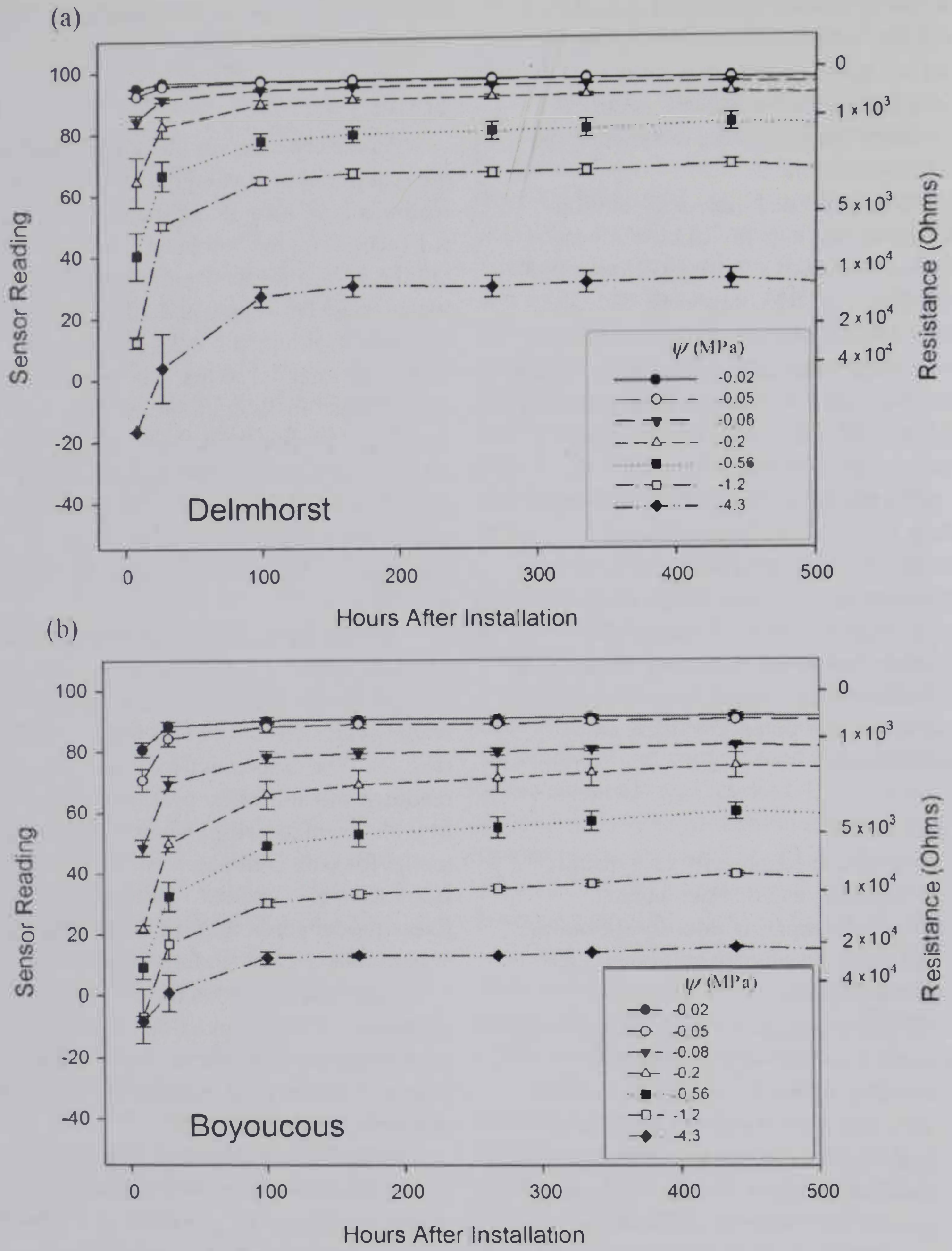

Figure 1. Time required for equilibration of (a) Delmhorst GS-1 and (b) Bouyoucos blocks in soils with water potentials of -0.02 to -4.3 MPa. Bars indicate ±SE

both types of blocks. Pairwise comparisons of water potentials are summarized in Figure 3.

DISCUSSION

Although newer methods with desirable features exist for measuring soil water potential, e.g., zero time for equilibration with time delay reflectometry, gypsum blocks remain a good choice for many applications in terrestrial field ecology. They are time tested, inexpensive, dependable, easy to use, and can quantify water potential soils across different levels of salinity and organic matter content (Weaver 1987, Scanlon et al. 2002). In addition, we show that their readings are repeatable and generally distinguishable in the water potential range of greatest interest

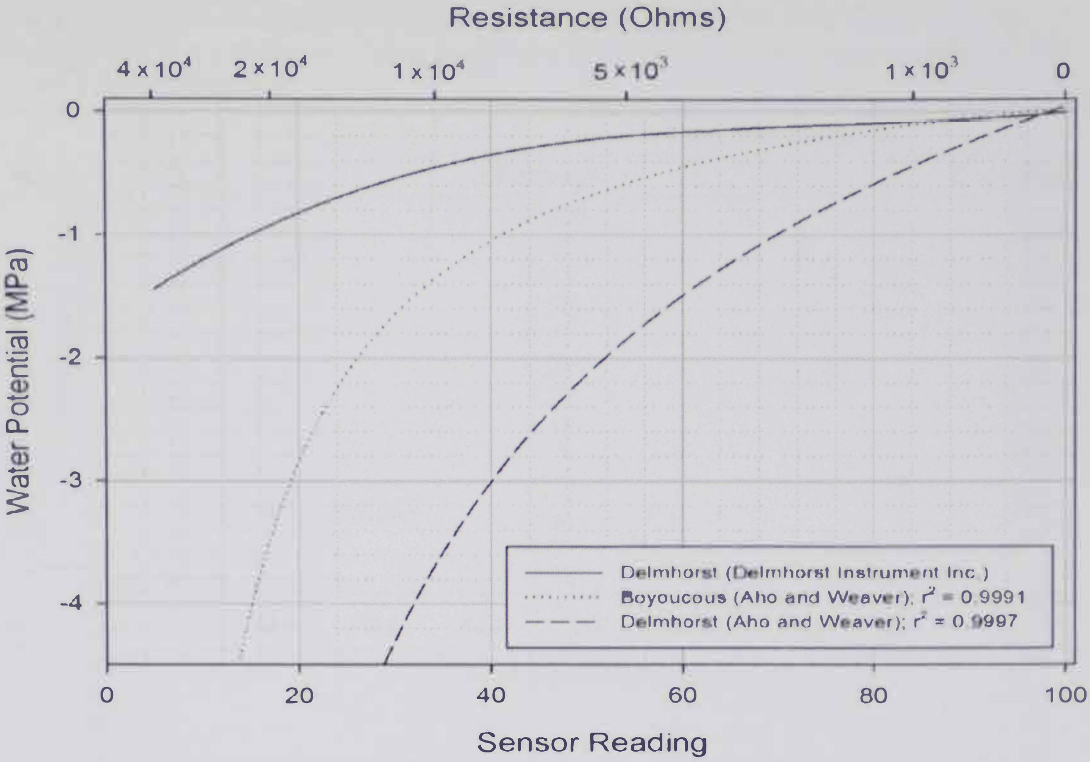

Figure 2. Relationship of soil water potential to meter readings and electrical resistance (ohms) for Delmhorst GS-1 and Bouyoucos blocks (see Appendix 1; Eq. 1). The bottom two curves in the figure were fitted from water potential data gathered for this paper. The top curve is from calibration formulae provided by Delmhorst Instrument Co. for use with their GS-1 blocks and KS-D1 meter (Appendix 1; Eqs. 2, 3).

to ecologists and agriculturists (≅ -0.02 to -4.3 MPa, Fig. 3).

Block Calibration

We introduce a new method for calibrating gypsum blocks in this paper. Our method improved on conventional procedures by simultaneously providing useful measurement units [water potential in megapascals (MPa)] and reducing the time required for calibration.

With regard to measurement units, a common alternative calibration procedure measures block resistivity in soils of known water content (kg kg^{-1}) rather than water potential. Because soils with the same water content may have very different matric potentials, results for this procedure are not general, i.e., they are only applicable to soils used in creating the calibration curve (Gardner 1986).

With regard to time required for equilibration, another alternative procedure involves embedding blocks in soils, reducing water potential incrementally with a pressure plate, and measuring block resistivity at these increments (e.g., Klute 1986, Weaver 1987). While this procedure produces a calibration curve in water potential units, it is very slow (> 6 months, Weaver 1987), and overestimates water potential if the system is not brought to full equilibrium.

Because calibration curves differ among block species, users need curves specific to their brand of blocks (Spaans and Baker 1992). Thus, while some variance may exist among manufacturing runs, our curves (Fig. 2, Table 1) should serve those using either Delmhorst or Bouyoucos blocks inserted dry into well-aggregated soils. While our results were easily read from Figure 2 and Table 1, when working with large data sets it would be more convenient and precise to convert meter readings to water potentials using equations developed for each block type (Appendix A).

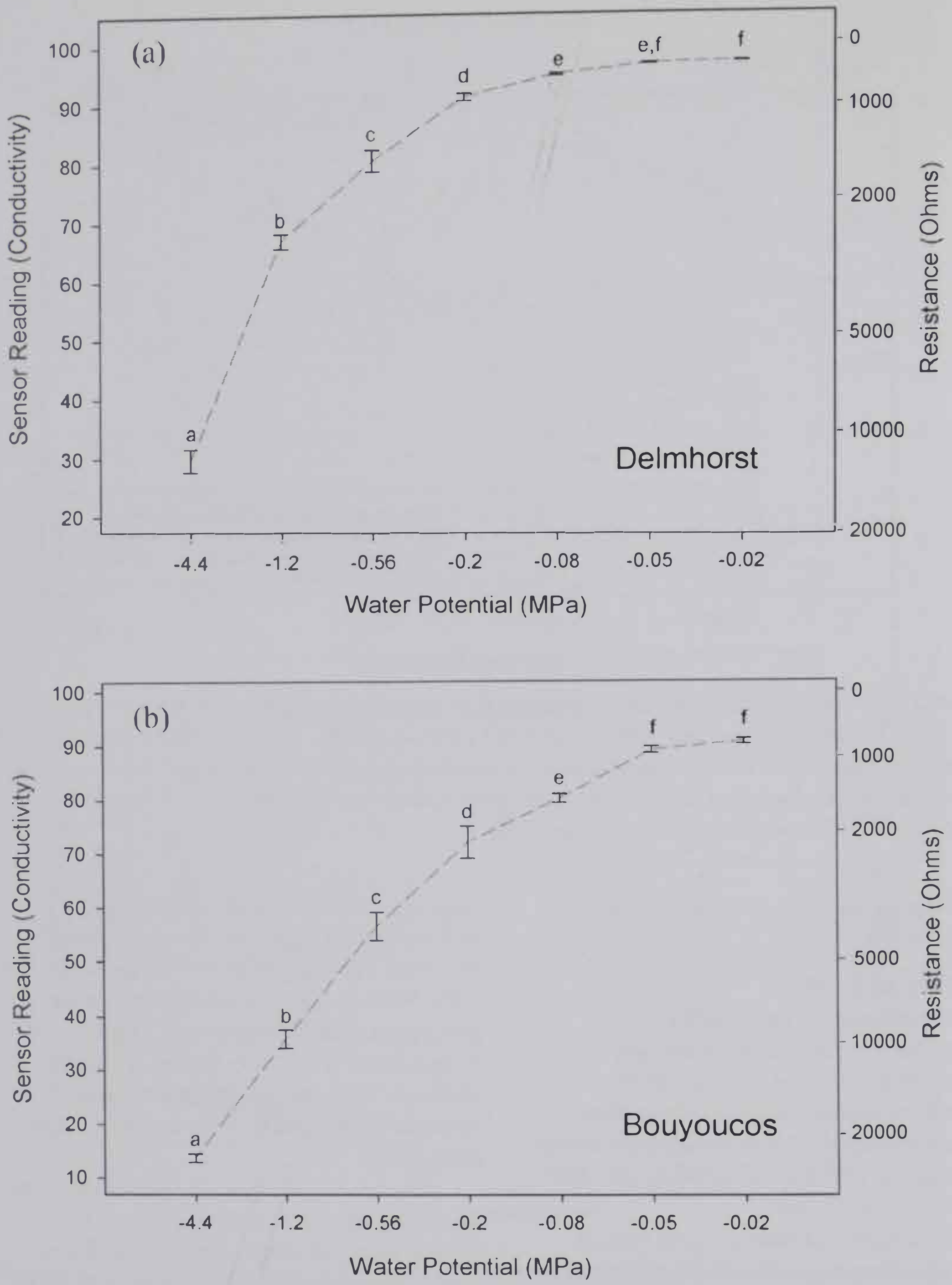

Figure 3. Water potential levels distinguishable with (a) Delmhorst and (a) Bouyoucos gypsum blocks. Water potential levels that are significantly different ($\alpha = 0.05$) are marked with different letters. Scheffé's method was used for simultaneous inference. Bars show 95-percent confidence intervals.

Gypsum block sensor readings will lag behind soil water conditions when blocks are either wetting or drying. Because dry blocks take from 4-8 days to equilibrate (Fig. 1), sensor readings will underestimate soil water potentials if blocks were recently installed or if surrounding soils have been recently wetted. We expect equilibration time to increase with increasing sand content since soil coarseness decreases contact with sensors (cf. Scanlon 2002).

Table 1. Soil water potentials at particular meter readings (Delmhorst KS-D1 meter) for Delmhorst GS-1 and Bouyoucos gypsum blocks. Note that predicted sensor readings below -4.3 MPa are extrapolated.

	Water Potential (MPa)	
Sensor reading	**Delmhorst**	**Bouyoucos**
95	-0.096	-0.009
90	-0.25	-0.051
85	-0.41	-0.098
80	-0.58	-0.15
75	-0.78	-0.21
70	-0.99	-0.28
65	-1.23	-0.36
60	-1.49	-0.45
55	-1.79	-0.56
50	-2.13	-0.69
45	-2.53	-0.85
40	-3.01	-1.05
35	-3.58	-1.31
30	-4.30	-1.65
25	-5.25	-2.13
20	-6.55	-2.85
15	-8.56	-4.05
10	-12.23	-6.44
5	-22.80	-13.63

Conversely, wet blocks inserted in drier soils may equilibrate even more slowly due to the slow loss of moisture from blocks. Equilibration is slow because water moves slowly from a fine-pored (block) to a coarser-pored (soil) medium (cf. Brady 1974). In addition, under field situations, water deep in blocks is removed only slowly by adjacent roots since blocks are impenetrable to them. Thus, recently wetted blocks may overestimate soil potentials for an extended period of time. Such overestimates may occur when soils dry around blocks which were previously saturated by melting snow or flooding. Similarly, overestimation may occur when blocks are installed wet or in a slurry as is recommended by block manufacturers (e.g., Delmhorst Instrument Co. 2000). Although use of wet blocks and slurried soils improve block-soil contact (Scanlon et al. 2002), overestimating water potential from these procedures may persist for weeks or months. We demonstrate evidence for overestimation in a comparison of calibration curves in Figure 2, where the manufacturer's curve predicts lower water potentials through most of the -0.1 to -1.5 MPa range than our curves.

Variability in gypsum block sensor readings is likely to be higher in drier soils (Scanlon et al. 2002). We demonstrated this trend for both types of tested sensors (Figs. 1, 3). As a result, we recommend averaging results from multiple sensors as we have done here to describe water potential with gypsum blocks (cf. Taylor et al. 1961, McCann et al. 1992).

Block Useful Range (Precision/Sensitivity)

We acknowledge that a lack of replication in our experimental design (only one cylinder/water potential treatment) hampers inferential statements concerning block sensitivity. On the other hand, average block reading estimates for water potential treatments were improved by presence of multiple sensors (pseudoreplicates) from each block manufacturer in each cylinder. Independence of readings within cylinders over time (assumed by our analysis) was supported by lack of significance for either time or time x water potential in our analysis of covariance.

Precision of plaster blocks, as indicated by post-equilibration standard deviations of readings, increased as water potential increased (Fig. 3). In contrast, sensitivity of plaster blocks, measured as the capacity of plaster blocks to distinguish different water potentials, decreased in wetter soils (ψ>-0.05 MPa). This is true because the relationship of sensor readings and water potential was logarithmic, and readings were asymptotic as soils approached saturation (Fig. 2; cf. Bourget 1958). Under moist conditions (ψ>-0.05 MPa), where the calibration curve slope approached 0, water potential levels were indistinguishable because differences in readings were small relative to variation around water potential means (Figs. 2 and 3). The limit at which our blocks discriminated water potentials was near the proposed physical upper limit of gypsum blocks ($\cong$ -0.03 MPa, Scanlon 2002). Under drier conditions (ψ < -1.0 MPa), where the calibration curve slope was steepest, water potential levels were readily distinguishable because differences in readings were large relative to variation around water potential means (Figs. 2, 3).

The logarithmic relationship between sensor reading and water potential parallels that of water content and water potential. As a result, soils with higher water content (>27% H_2O) also had very similar water potentials. Recall that our water potentials were -0.02, -0.05, -0.08, -0.2, -0.56, -1.2, and -4.3 MPa, corresponding to evenly spaced soil H_2O contents of 32, 29, 27, 24, 21, 19, and 16 percent. This demonstrated the asymptotic relationship between soil water content and soil water potential near field capacity (Or and Wraith 1999) and the inherent difficulty of distinguishing distinct water potentials among wetter soils.

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Appendix A

Calibration curve equations (Aho and Weaver).

$$\psi = 12.3179 - 56.5354/\ln(D) \quad (1)$$

$$\psi = 0.7476 - 71.9056/B \quad (2)$$

Where: ψ = water potential (MPa), D = KS-D1 meter reading for Delmhorst GS-1 blocks, and B = KS-D1 meter reading for Boyoucos blocks

Calibration curve equation for Delmhorst GS-1 blocks (Delmhorst Instrument Co. 2000)

For $0 > \psi > -0.15$ MPa

$$\psi = -(13.729 - 0.4343R + 0.00524R^2 - 0.0000226R^3)/10 \quad (3)$$

For $-0.15 > \psi > -1.5$ MPa

$$\psi = -(17.09 - 0.05619R + 0.00652R^2 - 0.000024R^3)/10 \quad (4)$$

Where: ψ = water potential (MPa), R = Delmhorst sensor reading

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