APPLICATION NUMBER 2-
Natural History Museum of Utah, University of Utah
Project Title: Enhancing Habitat Quality for Seasonal Movement of Mule Deer within the Red Butte Corridor in Research Park and Fort Douglas

UTAH DIVISION OF WATER QUALITY
195 North 1950 West
PO Box 144870
Salt Lake City, Utah 84114-4870

Red Butte Creek Project Proposal Form

NOTE: Proposal must be no longer than 6 pages. Supplemental documents such as letters of support, information to demonstrate previous project implementation and other relative supportive documents may be submitted in addition to this form.

Applicant Name: **William D. Newmark**

Co-Applicant Name(s) (if applicable): **Eric A. Rickart**

Project Title: **Enhancing Habitat Quality for Seasonal Movement of Mule Deer within the Red Butte Creek Riparian Corridor in Research Park and Fort Douglas**

Agency or Business Name (if applicable): **Natural History Museum of Utah, University of Utah**

Mailing Address: 301 Wakara Way City: Salt Lake City State: UT Zip: 84108

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☐ Individual ☐ Non-Profit ☐ Govt. Agency **X** Academic ☐ Commercial ☐ Other

1. Estimated Project Costs:

Labor	$ 67,000
Materials	$ 450
Equipment	$ 72,698
Administration	$ 15,392
Miscellaneous	$ 13,770
TOTAL	**$169,310**

Other sources of project funding:

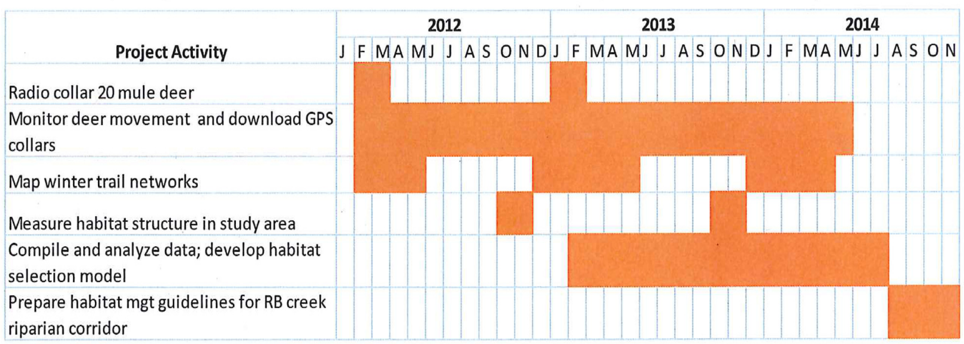
_____ Source	$_____ Amount	_____ Source	$_____ Amount
_____ Source	$_____ Amount	_____ Source	$_____ Amount
_____ Source	$_____ Amount	_____ Source	$_____ Amount
_____ Source	$_____ Amount	_____ Source	$_____ Amount

Total project cost including other sources of funding: **$169,310**
(please include bids for labor, equipment, rentals, etc.)

2. Describe the purpose and need of the project:

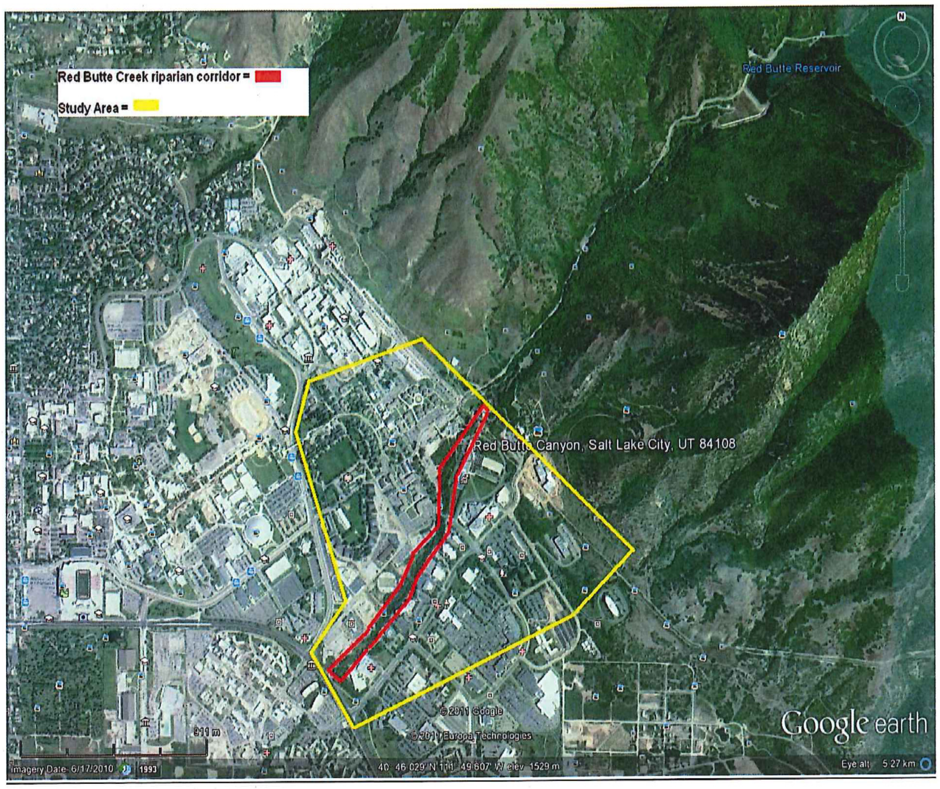
Red Butte Creek is one of the most important seasonal movement corridors for mule deer in the Salt Lake Valley. During the winter when snow in Red Butte Canyon exceeds 40 cm in depth, mule deer move out of Red Butte Canyon and disperse into Research Park and Fort Douglas. This project proposes (1) to identify habitat features that promote or hinder mule deer movement within the Red Butte Creek riparian corridor in Research Park and Fort Douglas; and (2) develop management guidelines for enhancing habitat quality within the Red Butte Creek Riparian Corridor for seasonal movement of mule deer. This work builds upon ten years of research by Drs. William Newmark and Eric Rickart at the Natural History Museum of Utah identifying landscape predictors of mule deer and elk movement in Red Butte Canyon Research Natural Area. Past research in Red Butte Canyon has demonstrated the critical value of riparian corridors for mule deer.

3. Estimated time frame of the project with significant milestones (Note: Project must be completed with final reports filed by November 10, 2014:



4. Describe the location of the project with attached location map, including details on the total area that will be directly enhanced by the project:

The study area includes all of the Red Butte Creek riparian corridor beginning immediately below the oil spillage site to the east and extending to the western edge of Research Park. The study area also includes adjacent open areas in Research Park and Fort Douglas which are important winter range feeding sites for mule deer. The total area along the Red Butte Creek riparian corridor that will be directly enhanced by the project is 53,382 m^2 or 13.2 acres.



5. Describe how the project will specifically enhance and protect waterways affected by the Red Butte releases and improve the conditions of one or more of the following: wildlife, habitat, natural vegetation, water quality or emergency response:

   This project will develop a habitat selection model for mule deer in the Red Butte Creek riparian corridor and use this model to develop management guidelines for enhancing habitat quality for mule deer movement in the Red Butte Creek riparian corridor. Habitat selection models are used to examine (1) whether a species uses habitats available to it at random; (2) to rank habitats in order of relative use; (3) to compare habitat use by different groups of animals, e.g., males and females; and (4) to relate habitat use to variables such as temperature, food abundance, distance to water, predation risk, and habitat structure. We will develop habitat selection models for mule deer in the Red Butte Creek riparian corridor that incorporate these four components.

6. Describe project's connectivity to other natural areas or projects that further enhance wildlife, habitat, natural vegetation, water quality or emergency response:

   The Red Butte Creek riparian corridor is an important seasonal movement corridor for mule deer moving between Red Butte Canyon Research Natural Area and the Research Park and Fort Douglas area. It is also an important winter range watering site for mule deer.

7. Describe any additional social benefits of implementing this project:

   This project provides a unique opportunity to enhance habitat quality for ungulate movement within an urban setting in Utah. We also propose to provide opportunities for students and community volunteers to participate in the gathering of field data.

8. Project plans and details, including rights to work on specified piece of land:

Since 2001, Drs. William Newmark and Eric Rickart have studying ungulate movement in Red Butte Canyon Research Natural Area through the mapping of permanent and seasonal wildlife trail networks. The objective of this research has been to identify important fine-scale landscape predictors of ungulate (mule deer *Odocoileus hemionus* elk and *Cervus elaphus*) movement in the central Rocky Mountains.

Specific questions that we are attempting to address include:
(1) How do landscape features such as slope, aspect, elevation, cover, food availability, snow depth, and distance to high risk predation zones and water influence ungulate movement at a fine spatial scale?
(2) How do non-landscape features such as predator distribution and abundance interact with landscape features to affect ungulate movement?
(3) How does the relative importance of landscape and non-landscape features vary seasonally?
(4) How does the relative importance of landscape and non-landscape features vary with scale of movement?

Results to date of this study indicate that fine spatial scale landscape features highly influence patterns of ungulate movement. Theses results have important implications for the design of movement corridors for ungulates. Currently there are few criteria or guidelines available to conservation practitioners to select and design movement corridors. To date most proposals to link habitat isolates and protected areas worldwide with corridors have been based upon habitat availability – that is areas that are currently undeveloped and could potentially link existing protected areas -- rather than an understanding of how animals move through the landscape. Finally results of this research indicate that the Red Butte Creek riparian corridor is an important seasonal movement corridor for mule deer.

Field Activities

We propose to radio-collar 20 mule deer with GPS collars during the winters of 2012 and 2013. The GPS collars will be programmed to record location at 15 second intervals so as to be able to examine fine-scale movement and habitat selection by mule deer within the Red Butte Creek riparian corridor and adjacent habitat in Research Park and Fort Douglas. Mule deer movement will be monitored over a 27 month period. Radio-telemetric data will be entered into a GIS database (see below).

We also propose to map during the winter semi-permanent snow trail networks that mule deer create in the Red Butte Creek riparian corridor and in adjacent open areas in Research Park and Fort Douglas as line features with a Trimble ProXL GPS. The line features will be differentially corrected with an accuracy < 1 m and subsequently entered along with the radio-telemetric GPS data into a geographic information system (GIS) database containing a digital elevation model (DEM) and a digital ortho quad (DOQ) of the study area. Elevation, aspect, and slope will be calculated from 10 m DEM and cover type maps will generated from 1 DOQ. Cover type maps will be ground-truthed at 5 m intervals along line transects that are 25 m apart and bisect the entire study area.

To assess the influence of snow depth and habitat structure on mule deer movement in the Red Butte Creek riparian corridor, we will measure snow depth and habitat structure (density and height of woody vegetation) within all study cells (25 m x 25 m) in the study area.

The DIGIT laboratory at the University of Utah will be responsible for managing the GIS database and generating summary statistics for all cells (25 m x 25 m) within our study areas. Spatial regression analysis will be used to identify important landscape predictors of mule deer movement in our study site. Prior to conducting this analysis, we will project a 25 m x 25 m grid over the study site in our GIS database and develop summary statistics of the dependent and independent variables for all cells within a study site. Our dependent variable is trail density.

The relative importance of models and predictor variables will be assessed using Kullback-Leibler information and Akaike's Information Criteria.

Results of the habitat selection model for mule deer will be used to develop management guidelines for enhancing habitat quality within the Red Butte Creek movement corridor.

An application to radio-collar mule deer will be submitted to the Utah Division of Wildlife Resources and permission will be requested from the University of Utah to radio-track mule deer movement in Research Park and Fort Douglas.

9. Describe your experience in implementing projects of similar scope and magnitude:

Dr. William D. Newmark is a research curator and conservation biologist at the Natural History Museum of Utah. He holds a B.A. in Biology from the University of Colorado, an M.S. in Wildland Management from the University of Michigan, and a Ph.D. in Ecology from the University of Michigan. His research specialties include conservation biology, island biogeography, processes of extinction, large mammal movement, understory birds, design of nature reserves, and wildlife corridors. Dr. Newmark has been conducting field research for over 25 years in western North America and East Africa. His findings on patterns of extinction of large mammals in western North American and Tanzanian parks, as well as birds in tropical forest fragments, have highlighted the problems that nature reserves face in conserving biological diversity. They have also provided an important justification for a series of worldwide initiatives to link national parks and related reserves with wildlife corridors. Technical as well as popular reviews of his research have appeared in *Science, Science News, Nature, The New York Times, The Washington Post*, and *The Independent* and his findings have been cited in many undergraduate and graduate ecology and conservation biology textbooks. He also serves as an international consultant in conservation biology to the World Bank and has been a technical adviser on a number of conservation projects in East Africa. He has published over 100 scientific papers and technical reports.

Dr. Eric A. Rickart is a curator of vertebrates at Natural History Museum of Utah. He holds a B.S. in Systematics and Ecology and an M.A. in Biology from the University of Kansas, and a Ph.D. in Biology from the University of Utah.. Following an appointment at the University of Texas, El Paso, he returned to Utah where he has been a curator at the Utah Museum of Natural History since 1985. He holds an adjunct faculty appointment in Biology at the University of Utah and is a research associate at the Field Museum of Natural History in Chicago. For the past 25 years, Dr. Rickart has conducted research on the biogeography, systematic, and conservation of mammals, focusing on the highly endemic and threatened mammal fauna of the Philippine Islands, and mammals of the Intermountain West. He is a former editor of the *Journal of Mammalogy* and has authored more than 70 peer-reviewed publications.

10. Describe how ongoing maintenance of the project will be funded and carried out:

William Newmark and Eric Rickart will conduct all of the field work, analyses, and write up. Opportunities will be provided to students and volunteers to assist in data gathering.

The radio-collaring of mule deer will be sub-contracted to a wildlife biology consultancy firm with extensive experience immobilizing ungulates and fitting GPS radio collars.

The project will be entirely funded through this grant.

11. List consultants or agency partners that have participated in project development (below):

Name/Company	Address	Phone
Name/Company	Address	Phone
Name/Company	Address	Phone

Signature ______________________ Date 12/13/2011
Applicant

Signature ______________________ Date 12/13/2011
Co-Applicant (if applicable)

In press, Mammalian Biology

Original Investigation

High-Use Movement Pathways and Habitat Selection by Ungulates

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Abstract
The cumulative movements of large mammals are expressed in many areas as semi-permanent wildlife trails. The mapping of semi-permanent trail networks offers a direct approach to assess habitat selection of high-use movement routes at relatively fine spatial scales across a landscape. Here we examine an ungulate trail network in north-central Utah created and maintained by the repeated movements of mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*). In a resource selection analysis using multivariable spatial regression analysis, we show that at a spatial scale of 70 m open and low cover and distance to water are important predictors of movement pathway density. We also demonstrate at a scale of 10 m that elk and deer movement pathways are less steep than adjacent terrain. The mapping of trail networks should be a particularly useful technique for examining functional connectivity among resource patches across a landscape and identifying important high-use movement routes.

Keywords: elk, GPS mapping, mule deer, spatial regression analysis, ungulate trail network

Introduction

Many issues of wildlife management and conservation are highly dependent upon understanding animal movement, including the assessment of the impact of human activities and barriers on wildlife populations (Preisler et al. 2006), estimating population density from track counts (Stephens et al. 2006), the design of wildlife corridors (Soulé and Terborgh 1999; Chetkiewicz et al. 2006), and enhancing landscape connectivity (Crooks and Sanjayan 2006). Given recent declines both regionally and globally in many large mammal migratory populations (Berger 2004; Bolger et al. 2008; Newmark 2008; Sawyer et al. 2009) and the large area requirements for many large mammals (e.g., Frankel and Soulé 1981; Newmark 1985; Soulé and Terborgh 1999), understanding the influence of environmental heterogeneity on large mammal movement is not only critical for conserving many of these populations but has also a special urgency. Because large mammal dispersal and migration is an accumulation of multiple short and more rapid long distance movements (Johnson et al. 2002; Fryxell et al 2008; Sawyer et al. 2009; Sawyer and Kauffman 2011), understanding the influence of environmental heterogeneity on patterns of movement across varying spatial scales is important.

Ecologists have employed a wide variety of techniques to study large mammal movement including following individually marked animals (e.g., Whitehouse et al. 1977) or animals with unique markings or patterns (e.g., Douglas-Hamilton and Douglas-Hamilton 1975), radio-telemetric tracking (Craighead et al. 1963; Fuller et al. 2005), aerial surveys (e.g, Robel 1960), and the mapping of movement pathways (Murie 1936; Scott 1943; Vanleeuwe and Gautier-Hion 1998). While ungulate movement has been studied using all of these techniques, the mapping of movement pathways has been largely restricted to date to snow tracking (Reichman and Aitchison 1981; D'Eon 2001; Fortin et al. 2005a; Fryxell et al. 2008).

In many regions, the cumulative movements of large mammals, particularly ungulates, are recorded as networks of semi-permanent wildlife trails (Fig. 1). These networks are created by the repeated movement of multiple animals along the same pathway, and thus define at a population-level, high-use movement pathways between important resource patches (e.g., water, food, bedding, thermal, and hiding cover). The mapping of wildlife trail networks offers a direct approach to examine the influence of environmental heterogeneity on large mammal movement and more broadly in linking landscape structure to functional connectivity at relatively fine spatial scales.

In this paper we develop resource selection functions (Manly et al. 2002) using multivariate spatial regression analysis to examine habitat use along semi-permanent movement pathways by mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) in north-central Utah. We conduct this analysis at a population level (design 1; Thomas and Taylor 1990) within the home range of both species (third-order selection; Johnson 1980).

Material and Methods

Study Area

Field work was conducted in a 223 ha study site in Red Butte Canyon Research Natural Area between January 2001 and October 2003. Red Butte Canyon Research Natural Area, which is 18.8 km^2, is located in the Wasatch Range in the central Rocky Mountains in north-central Utah. This research natural area has been protected and closed to livestock grazing for 95 years (Ehleringer et al. 1992), and thus the presence of livestock and their trails did not confound the analysis. Furthermore, this site is closed to the public and therefore human activities such as hiking and hunting have minimal impact on ungulate movements. The study site ranges in elevation from 1642 to 2050 m and is bisected by a perennial stream.

The major vegetation types are riparian woodland dominated by bigtooth maple (*Acer grandidentatum*) and box elder (*Acer negundo*), scrub woodland on upland slopes comprised predominantly of Gambel oak (*Quercus gambelii*), and open meadows dominated by grasses and forbs. Soils are predominantly shallow cobbly loams, silt loams, and dry loams (Ehleringer et al. 1992, Natural Resource Conservation Service undated). Mountain lion (*Puma concolor*) are common and are the principal predator of ungulates at the study site. Secondary predators include coyote (*Canis latrans*) and bobcat (*Lynx rufus*).

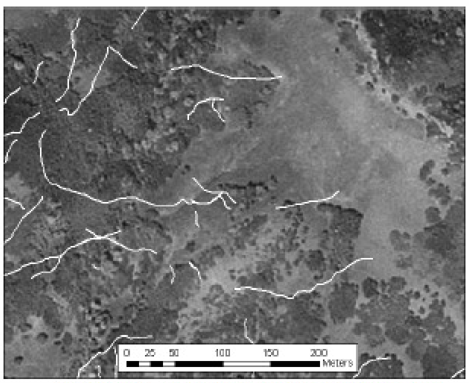

Figure 1. A representative section of an ungulate trail network in Red Butte Canyon Research Natural Area. Mapped trails, shown in bright white, are projected over a 1 m digital orthophoto quadrangle of vegetation with light regions displaying open cover and darker regions displaying low, medium, and high cover.

Ungulate Trail Network

In Red Butte Canyon, mule deer and elk are the large mammals that have created a network of semi-permanent trails. For purposes of this study, we define a semi-permanent trail as a visibly-compacted narrow pathway longer than 10 m, comprising predominantly of bare-ground and containing ungulate tracks. Although both species utilize the same network of trails at this site, as documented through track identification along the trails, their activity patterns vary seasonally. Mule deer, which are non-migratory in Red Butte Canyon and have an average annual home range of 285 ha (Harestad and Bunnel 1979), use the semi-permanent trail network year-round. Elk, which are seasonal migrants and have an average annual home range of 1,293 ha (Harestad and Bunnel 1979), use the semi-permanent trail network during the late autumn, winter, and early spring. During winter when trails are covered by snow, approximately 3 – 4 weeks per year, they are not used by either species; rather both species create new, non-permanent trail networks in the snow which may overlap portions of the semi-permanent trail network. Based upon our encounter rate of mule deer and elk along vegetation transects (see below) we estimate 50 – 100 mule deer and 50 – 200 elk use the study area trail network annually.

In Red Butte Canyon, the repeated movements of deer and elk along established trails are required to maintain trail segments. This was clearly demonstrated in the spring 2007 when deer and elk abandoned the study site because of construction activities on a dam. Much of the wildlife trail network during this period "disappeared" due to trail revegetation. Following the completion of the dam, deer and elk returned to the study area and re-established a trail network within a four month period (mid-June to late-October 2007). The new trail segments that were established were not spatially autocorrelated with each other, i.e., spatially adjacent across a landscape. Based on these observations, we believe that ungulate trail networks in Red Butte Canyon reflect the response of animals to current rather than historical environmental conditions within the canyon.

The creation of individual trails in Red Butte Canyon was influenced by not only the body mass of deer (110 kg) and elk (220 kg) and their frequency of movement along movement pathways, but also slope and soil moisture conditions. We observed that when soils were fully-saturated in the early spring a single pass by a herd of elk (~ 10–40 animals) created a well-defined trail on steep terrain (slope > 35%). On the other hand if soils are dry and terrain is level, a much larger number of animal passes are required to generate a trail.

Response variable

In the analysis, we arbitrarily subdivided the study area into 318, 70 m X 70 m cells which defined resource availability (Thomas and Taylor 2006). Our response variable, which assessed resource use, was sum trail length of trail segments within a cell, i.e., trail density, (Fig. 2) and ranged from 0 – 248.4 m across all cells. Fifty-eight percent (185/318) of cells contained one or more trail segments. We defined our response variable as a continuous rather than a categorical variable so as to better account for the variability in intensity of resource use (i.e., ungulate movement) among study cells. We assume, therefore, that variation in sum trail length among cells does relate to resource use and thus agree with Marzluff et al. (2004) that "a continuous measurement of space use through an animal's range most adequately describes resource use."

All ungulate trails in the study area were mapped as line features with a GPS during two one-week periods during October 2002 and April 2003. While mapping we did not observe any spatial or temporal change in the trail network. Trails were mapped with a Trimble ProXL GPS and differentially corrected to sub-one meter accuracy and GPS data were entered into a GIS database. We are confident that we located and mapped all trail segments longer than 10 m in our study area because we visited all cells in the study area a minimum of two times over the course of the study while either actively searching for trails or assessing cover height and food availability (see below). Trails were located by "search teams" of 4 -12 observers, spaced 10 - 20 m apart, who walked transects across major sections of the study area. After trails were located and mapped, individual trail segments were flagged every 20 – 50 m to indicate that a trail segment had been recorded.

Habitat attributes

Based on behavioral and habitat selection studies of elk and mule deer (e.g., Dasmann and Taber 1956; Reichman and Aitchison 1981; Houston 1982; Nicholson et al. 1997; Unsworth et al. 1998) we selected the following habitat attributes as predictor variables of ungulate movement pathways: aspect, slope, open cover, low cover, medium cover, high cover, food availability, and distance to water.

Mean aspect and slope (percent) were calculated from 10 m digital elevation model (DEM). We transformed aspect (A) following Beers et al. (1966), because 1° and 360° are adjacent but differ greatly numerically:

$$A' = \cos(A_{max} - A) + 1$$

with 180^0 (south) selected as the highest value (A_{max}) on the transformed scale because south-facing slopes are annually snow-free the longest. Transformed values ranged from 0.0 to 2.0.

Using 1 m digital orthophoto quadrangle, we developed a cover type map of the study area. We classified habitats within each cell into four cover types, expressed as area (m^2): (a) open cover dominated by grasses and forbs < 0.5 m in height; (b) low cover, predominantly Gambel oak ≤ 1.0 m in height; (c) medium cover, predominately Gambel oak > 1.0 m and ≤ 2.5 m in height; and (d) high cover, predominantly Gambel oak, bigtooth maple, and box elder > 2.5 m in height. The number of cover types ranged from 1 – 4 across all cells. For the low, medium, and high cover types, crown shrub and tree cover exceeded 70%. Because of the difficulty in accurately assessing the height of the vegetation from aerial photographs in regions where cover types were patchy, we measured the height of the woody vegetation at 10 m intervals along parallel line transects that bisected the center of all cells in the study area. These data were used to refine the classification of cover types in approximately 20% of all study cells.

To examine whether the density of ungulate movement pathways was associated with food availability, we developed an index of food availability for all cells within the study area. First, important plant species in the diets of elk and mule deer were identified through microscopic analysis of fresh fecal samples (Holechek et al. 1982) that were collected randomly throughout the entire study area in the spring and autumn – the seasons in which we mapped trails (see above). The Wildlife Habitat Nutrition Laboratory at Washington State University conducted the microhistological analysis (Department of Natural Resource Sciences). Secondly, we estimated in all study cells the mean percent cover of the 10 most important food plants (Table 1) in the combined diets of elk and mule deer. In each cell, food plant coverage was estimated in 7, 1 X 1 m^2 quadrats located at 10 m intervals along a line transect that bisected the center of a cell. Thirdly, using the data on food plant coverage we developed an index of food availability for each cell defined as:

$$F = \sum_{i=1}^{n} d_i c_i$$

where F is index of food availability, d is percent of the combined diet of elk and mule deer, c is mean percent cover per cell, and i is food plant.

All habitat variables showed low levels of collinearity ($r < 0.59$) with the exception of open cover and food availability which were negatively correlated ($r = -0.98$). However, we decided to retain these two variables in the analysis because it enhanced model interpretation and did not affect model stability. The exclusion of either variable did not result in a switching of the signs of the regression coefficients or a substantial increase in standard errors.

Table 1. Ten most frequently recorded food plants in the combined diets of elk and mule deer in Red Butte Canyon Research Area as assessed through microhistological analysis of fresh fecal samples.

Plant	Relative frequency in combined diet
Quercus gambelii	0.335
Medicago sativa/Melilotus alba/Trifolium spp.	0.074
Phleum pratense	0.051
Festuca spp.	0.022
Poa spp.	0.021
Balsamorhiza spp.	0.018
Berberis repens	0.005
Equisetum spp.	0.005

Model selection

We developed *a priori* a set of plausible candidate models (N = 20) to evaluate habitat selection along movement pathways by deer and elk. In formulating this set of candidate models, we relied on the literature and our own field observations. We used the difference in AIC_c (Akaike's Information Criteria corrected for small sample size) values (ΔAIC_c) to rank candidate models and AIC_c weights to evaluate the relative support of predictor variables across models (Burnham and Anderson 1998).

Selection of modeling approach

To assess whether an ordinary least squares (OLS) multiple regression or a conditional autoregressive (CAR) model was more appropriate as a resource selection function, we assessed the spatial dependence of residuals of an OLS regression. We checked for spatial independence by plotting a Moran's I_{std} correlogram of the residuals (Legendre and Legendre 1998; Lichstein et al. 2002). Moran's I was standardized and the significance of the correlograms was tested using software written by Lichstein et al. (2002) for S-PLUS. Finally, we examined directional correlograms of the residuals of an OLS regression to detect anisotropy

(Legendre and Legendre 1998; Lichstein et al. 2002).

Since we detected significant ($P <$ 0.05) spatial dependency in the residuals of an OLS multiple regression model, we selected a CAR model (Haining 1990; Legendre and Legendre 1998; Lichstein et al. 2002) to evaluate the relation between the response and habitat variables. Conditional autoregressive models can be thought of as two-dimensional extensions of one-dimensional autoregressive models that are used in time-series analysis (Lichstein et al. 2002). We examined neighbor weights in the CAR model in two ways: $w_{ij} = 1/\text{distance}_{ij}$ and $w_{ij} = (1/\text{distance}_{ij})^2$. We selected a neighbor weight [$w_{ij} = (1/\text{distance}_{ij})^2$] based upon the maximum likelihood model fit. We set the maximum distance for neighbor influence as the maximum distance that residuals of the OLS multiple regression were autocorrelated, which was 140 m. For the CAR models, we calculated the coefficient of determination (R^2) following Nagelkerke (1991).

In the CAR models mean slope was not identified as an important habitat attribute of ungulate movement pathway density in Red Butte Canyon, contrary to results from telemetric studies of ungulates conducted at coarser scales (e.g., Fortin et al. 2005b). Therefore, we subdivided all trails within a cell into 10 m trail segments and compared the mean slope of trail segments with adjacent terrain (±10 m of each segment) and overall slope of a cell using a one-way ANOVA. Prior to the analysis, we tested for spatial autocorrelation of these three slope metrics among cells containing wildlife trails, which we did not detect ($P >$ 0.05), using Moran's I_{std} correlograms.

Results

No single *a priori* model had overwhelming support (AICc weight ≤ 0.176, Table 2). However, three variables included in the model with the highest AICc weight had very strong support individually across all models as habitat predictors of ungulate movement pathways: open cover, low cover, and distance to water.

Mule deer and elk movement pathway density (Fig. 2) was positively related to open and low cover and negatively related to distance to water. A combined spatial regression model with these three predictor variables explained 26% of the variation in sum trail length with 15% of the variation explained by fine-scale spatial autocorrelation.

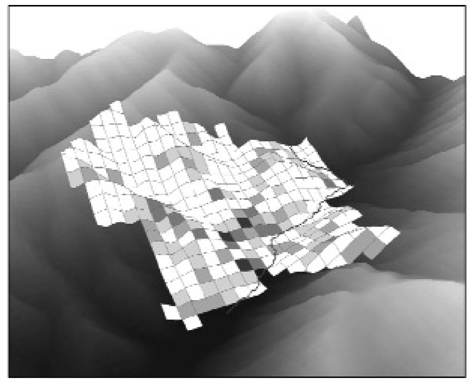

Figure 2. Geographic patterns of movement pathways for mule deer and elk as assessed by sum trail length of trail segments in a 223 ha study area in Red Butte Canyon Research Natural Area. Equal-interval classification is shown with a gray scale color ramp with light indicating minimum values and dark indicating maximum values.

Although mean slope at a scale of 70 m was not an important predictor of the density of ungulate movement pathways, this was most likely because deer and elk were selecting low-gradient movement pathways at a finer scale in steep terrain – a result suggested through an analysis of ungulate pathways at a scale of 10 m. Across our study area, mean slope of 10 m trail segments, adjacent terrain, and the overall slope varied significantly among cells ($F_{2,648}$ = 252.5, $P < 0.0001$). Post-hoc Bonferroni adjusted contrasts revealed that the mean slope of 10 m trail segments was significantly less step than adjacent terrain ($P < 0.0001$) or overall slope of a cell ($P < 0.0001$) (Fig. 3). In our study area mean slope of trail segments was 13.0% whereas mean slope of adjacent terrain and mean overall slope were 41.6% and 37.0%, respectively.

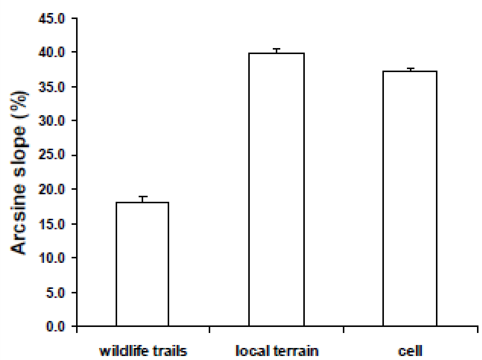

Figure 3. Comparison among cells containing wildlife trails in Red Butte Canyon Research Natural Area of mean (± 1 SE) slope of 10 m trail segments with adjacent terrain and overall slope.

Discussion

Our study reveals that environmental heterogeneity strongly influences high-use ungulate movement pathway density across a landscape at a scale of 70 m. In Red Butte Canyon deer and elk movement pathway density was correlated with open and low cover and distance to water. We speculate that open and low cover were important predictors of movement pathway density for two reasons. First, predation risk for mule deer and elk while moving between habitat patches may be lower in these habitats. In our study area, mountain lion are the dominant predator. In a detailed study of the habitat structure of 52 mountain lion kill sites in northwestern Utah and southern Idaho, Laundré and Hernández (2003) recorded only 3 kill sites in open habitat with the remainder in closed forested habitats, particularly along edges. In studies of ungulate movement conducted at coarser spatial scales, predation risk has also been suggested to be an important predictor of habitat selection for elk in Yellowstone National Park (Fortin et al. 2005b; Creel et al. 2005) and in central Alberta (Frair et al. 2005), and caribou (*Rangifer tarandus*) in north-central British Columbia (Johnson et al. 2002).

An alternative yet non-mutually exclusive explanation for a positive correlation between open and low cover and ungulate pathway density relates to landscape resistance (Forman 1995). In our study area, the landscape structure comprised largely of small meadows interspersed among patches of dense shrubby oak (Fig. 1). We believe that the obstruction to horizontal movement for mule deer and elk while moving among resource patches is almost certainly lower in open and low cover than in medium and high cover. Forman (1995) has argued that landscape resistance and structure can play an important role in influencing patterns of animal movement.

Distance to water was also an important predictor of the density of movement pathways in Red Butte Canyon with higher trail density being observed in regions close to water. While the attraction of ungulates to riparian habitat in western North American is often related to food preference (Peinetti et al. 2001; Ripple and Beschta 2004), in Red Butte Canyon ungulate food availability, assessed both qualitatively and quantitatively, was not associated with distance to water ($r = 0.14$). This finding is most likely a result of the widespread distribution throughout the study area of food and particularly Gambel oak, the most important food item in the combined diets of deer and elk (Table 1). Given the aridity of the study site, which has a mean annual precipitation of 500 mm (Ehleringer et al. 1992), we suspect that the high frequency of movement pathways near and leading to water reflects the high water requirements for these animals in this environment (Nichol 1938; Skovlin et al. 2002).

Table 2. A comparison of single and multiple variable resource selection models of ungulate movement pathway density in Red Butte Canyon Research Natural Area. Models are ranked by ΔAICc.

Model	Number of estimable parameters (K)	Log-likelihood	AICc	ΔAICc	AICc weight
OpenCover + LowCover + DistWater	6	-2126	4264.27	0.00	0.176
OpenCover + LowCover + MedCover + DistWater	7	-2125	4264.36	0.09	0.168
OpenCover + LowCover + DistWater + FoodAv	7	-2125	4264.36	0.09	0.168
OpenCover + LowCover + HighCover + DistWater + FoodAv	8	-2124	4264.47	0.20	0.159
Aspect + Slope + OpenCover + LowCover + MedCover + HighCover + DistWater + FoodAv	11	-2121	4264.86	0.59	0.131
LowCover + HighCover + DistWater + FoodAv	7	-2126	4266.36	2.09	0.062
OpenCover + LowCover + MedCover + DistWater + FoodAv	8	-2125	4266.47	2.20	0.059
OpenCover + LowCover + MedCover + HighCover + DistWater + FoodAv	9	-2124	4266.58	2.31	0.055
OpenCover + DistWater	5	-2130	4270.19	5.92	0.009
OpenCover	4	-2132	4272.13	7.86	0.003
OpenCover + MedCover	5	-2131	4272.19	7.92	0.003
OpenCover + FoodAv + DistWater	6	-2130	4272.27	8.00	0.003
OpenCover + MedCover + DistWater + FoodAv	7	-2129	4272.36	8.09	0.003
FoodAv	4	-2133	4274.13	9.86	0.001
HighCover	4	-2139	4286.13	21.86	< 0.001
LowCover	4	-2142	4292.13	27.86	< 0.001
MedCover	4	-2142	4292.13	27.86	< 0.001
DistWater	4	-2143	4294.13	29.86	< 0.001
Aspect	4	-2144	4296.13	31.86	< 0.001
Slope	4	-2144	4296.13	31.86	< 0.001

While previous work at coarse spatial scales has found that slope is an important predictor of elk movement patterns (Fortin et al. 2005b), in Red Butte Canyon at a scale of 70 m slope was not an important predictor of elk and mule deer movement pathway density. We suspect that slope was not an important predictor of movement pathway density because animals were selecting low-gradient movement pathways at a finer (10 m) spatial scale. This latter observation is consistent with broad conclusions from previous studies that energetic costs almost certainly influence ungulate movement patterns (Johnson et al. 2002; Frair et al. 2005; Fortin et al. 2005a; Fortin et al. 2005b; Saher and Schmiegelow 2005).

One advantage of mapping wildlife trail networks relative to more traditional telemetric tracking of individual animals is the near absence of measurement error, and thus we believe this technique is particularly well-suited for studying relatively fine-scale patterns of large mammal movement. On the other hand, unlike telemetric studies, trail networks do not record all movements of an animal within an area. This approach is therefore clearly restricted to species whose activities result in extensive and measurable movement pathways and to areas that receive high use with appropriate substrates. Furthermore, in this analysis we have not differentiated intensity of use among trail segments although it should be possible to do so through track counts and remotely-triggered movement counters.

Enhancing landscape connectivity and conserving critical movement routes are often important conservation objectives in fragmented landscapes. We believe the mapping of high-use movement pathways is highly suited for assessing functional connectivity among important resource patches (e.g., water, food, bedding, thermal, and hiding cover) for selected species (Fagan and Calabrese 2006), and can provide a simple, accurate, and cost-effective means of identifying high-use movement routes at relatively fine spatial scales. Furthermore, combining the mapping of wildlife trail networks with the tracking of individual telemetered animals should be a particularly informative and powerful approach for linking movement of individuals and populations for purposes of identifying and conserving high-priority movement routes.

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