

DEMOGRAPHY OF LEWIS'S WOODPECKER, BREEDING BIRD DENSITIES,
AND RIPARIAN ASPEN INTEGRITY IN A GRAZED LANDSCAPE

by

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ABSTRACT

Aspen (*Populus tremuloides*) riparian woodlands are extremely limited in distribution throughout the western U.S., yet these habitats have a disproportionate value to breeding birds. Aspen habitats are also considered prime sheep and cattle summer range, particularly in the semiarid Intermountain West. Such concentrated use has raised concern about the effects of sheep and cattle grazing on these habitats. We examined the influences of sheep and cattle grazing on aspen riparian woodlands and the associated breeding bird community. We had two objectives: 1) to determine how habitats grazed by sheep and cattle influenced the reproductive biology of Lewis's Woodpecker (*Melanerpes lewis*), and 2) to determine how vegetation differed between sheep and cattle-grazed aspen riparian woodlands and how these differences influenced breeding birds densities. To examine what factors influenced nest-site selection in Lewis's Woodpecker and whether these factors influenced nest survival, we quantified nest-site characteristics and monitored nests to determine nest fate. Lewis's Woodpecker nest-site selection was positively influenced by nest tree diameter and tree density and negatively influenced by increasing amounts of bare ground and woody stems. However, these characteristics were not strong predictors of nest survival. Instead, nest initiation date and daily average temperature had the strongest influence. We then compared several vegetation characteristics between grazing treatments, conducted point transect surveys and used distance sampling techniques to estimate breeding bird densities. Cattle-grazed sites had more bare ground, less herbaceous cover, lower willow (*Salix* spp.) densities, and lower aspen densities than sheep-grazed sites. Differences in breeding bird densities between these grazing treatments reflected these vegetation differences, as ground-nesting species and riparian specialists had lower densities in cattle-grazed areas. Data from this study provide landowners and land managers with information on the habitat requirements of sensitive bird species needed to implement compatible grazing strategies in aspen riparian woodlands.

CHAPTER 1.

INTRODUCTION TO THESIS

The importance of riparian areas throughout the arid and semiarid western U.S. to avifauna has been the focus of considerable attention in recent decades. Many studies have directed attention to the degradation of these habitats as a result of several land use and management practices, particularly the influences of livestock grazing (Ohmart 1994, Dobkin et al. 1995, Saab et al. 1995, Tewksbury et al. 2002, etc.). Livestock grazing is the most common land use in portions of the West, particularly in the semiarid Intermountain sagebrush steppe (West 1983). Aspen (*Populus tremuloides*) is the predominant deciduous tree species in this region (Mueggler 1985), and aspen habitats are considered prime livestock summer range (Sampson 1919). Aspen habitat has declined by as much as 90% in some regions of the West due in part to heavy browsing by domestic and wild ungulates (Schier 1975, Mueggler 1988, Kay 1997, Bartos and Campbell 1998).

Several bird species breed in aspen woodlands more than in any other habitat (Winternitz 1980, Finch and Reynolds 1987, Dobkin et al. 1995, Turchi et al. 1995), and some species may be aspen obligates (Finch and Reynolds 1987, Turchi et al. 1995). Our goals were to assess how several breeding bird species responded to habitats influenced by sheep and cattle grazing. Aspen riparian woodlands of south-central Idaho grazed by sheep and cattle provided an opportunity to examine the influences of these grazing regimes on these habitats and their associated breeding bird community.

Thesis Organization

Chapter 2 focuses on the reproductive biology of Lewis's Woodpecker (*Melanerpes lewis*) in aspen riparian woodlands in the context of sheep and cattle grazing. The investigation of aspen as breeding habitat for this species has been largely unexplored. Reproductive success for many avian species is commonly measured in terms of nest survival. Nest survival, in turn, can be strongly influenced by nest-site choices. Thus, we set out to determine what microhabitat characteristics most strongly influenced nest-site selection, and whether or not these nest-site choices had consequences for nest survival. We predicted that certain nest-site characteristics including nest tree height, diameter at breast height, and woody stem and tree abundance around the nest tree would influence nest-site selection and subsequent nest survival. We also examined the influence of other factors such as temporal and seasonal trends on nest survival.

Chapter 3 focuses on the influences of sheep and cattle grazing on populations and habitats of breeding birds in aspen riparian woodlands of south-central Idaho. Specifically, we examined differences in breeding bird densities, riparian vegetation, aspen regeneration, and the distribution of aspen diameter size classes between sheep- and cattle-grazed aspen riparian woodlands. We expected that differences in breeding bird densities would reflect differences in riparian vegetation between the two grazing treatments.

Chapter 4 summarizes the major findings from the previous two chapters and addresses future research directions. The common theme throughout the thesis is the ecological importance of aspen riparian woodlands to several bird species breeding in this habitat. Because this research was conducted in cooperation with several colleagues, the text is written in the third person throughout the thesis to allow for submission of individual chapters as journal articles with multiple co-authors.

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CHAPTER 2.

FACTORS INFLUENCING NEST SURVIVAL AND
NEST-SITE SELECTION OF LEWIS'S WOODPECKERS BREEDING IN
ASPEN RIPARIAN WOODLANDSIntroduction

Lewis's Woodpecker (*Melanerpes lewis*), a patchily distributed but often locally abundant species, breeds primarily in burned pine (*Pinus* spp.) and cottonwood (*Populus* spp.) forests throughout the western United States (Tobalske 1997). This species is often termed a "burn specialist" due to its high densities and nesting success in burned forests (Bock 1970, Raphael and White 1984, Saab and Vierling 2001). Although used to a lesser degree, aspen riparian woodlands may also provide valuable breeding habitat for this species throughout the Intermountain West. Lewis's Woodpecker has been anecdotally recorded in aspen habitats (Neel 1999, Medin and Clary 1991), but aspen as breeding habitat for this species has been largely unexplored. Aspen is the predominant deciduous tree in the Intermountain West, providing the principal nesting substrate for cavity-nesting bird species throughout the region (Dobkin et al. 1995). Several studies have noted the importance of aspen as breeding habitat for cavity-nesting birds (Harestad and Keisker 1989, Li and Martin 1991, Dobkin et al. 1995, Martin and Eadie 1999, Martin et al. 2004), and the ecological importance of this habitat is well known (Hansen et al. 2000, Campbell and Bartos 2001).

The naturally open character of aspen riparian woodlands likely meets the breeding and foraging requirements of Lewis's Woodpecker. Unlike most woodpeckers

that bore for bark- and wood-dwelling insects, Lewis's Woodpecker is an aerial forager that requires open habitats for hawking and aerial maneuvers involved in fly-catching. Additionally, this species requires a well-developed shrub layer for the production of arthropod prey (Bock 1970), and abundant perch and food storage sites (Vierling 1997). Land use practices such as fire suppression, selective timber harvest, and livestock grazing have degraded suitable breeding habitats throughout the range of Lewis's Woodpecker (Tobalske 1997). The loss of these habitats has been implicated in local and regional declines of Lewis's Woodpecker populations. These declines have prompted several state and federal agencies to include this species among those of conservation concern (Neel 1999, Ritter 2000, USFWS 2002, USDA Forest Service 2004).

Despite the conservation concern for Lewis's Woodpecker populations, few studies have focused on this species. Bock (1970) conducted the most comprehensive study, examining breeding and behavioral characteristics in central California. Estimates of nest initiation and fledge dates are available for nests located in burned pine forests of southwestern Idaho (Dudley and Saab 2003), and information on reproductive success and productivity is available for burned pine and cottonwood riparian forests of Idaho and Colorado (Saab and Vierling 2001). Nest-site characteristics have been described in burned forests (Raphael and White 1984, Linder and Anderson 1998, Saab and Dudley 1998, Saab et al. 2002, and Saab et al. 2004) and cottonwood riparian forests (Vierling 1997). These studies have produced most of the available data for Lewis's Woodpecker, and early natural history reports provided anecdotal information (Bent 1939). Although these studies have contributed valuable information, important data on clutch size, brood

size, and hatching dates are still lacking, as are data on nest-site characteristics in aspen riparian woodlands.

In south-central Idaho, Lewis's Woodpecker populations breeding in aspen riparian woodlands provide an opportunity to fill these information gaps. Data from this habitat coupled with information from burned pine and cottonwood habitats provide habitat-specific demographic parameters needed to make informed management decisions for this species throughout its range. In this study, we determined what habitat characteristics had the strongest influence on nest-site selection of Lewis's Woodpecker in aspen riparian woodlands. We then used recently developed analytical methods (Rotella et al. 2000, Dinsmore et al. 2002, Stephens 2003, Rotella et al. 2004) to examine if these nest-site choices had consequences for nest survival (the probability that a nest survives the nesting period and produces at least one offspring), a commonly used metric of reproductive success for many avian species.

Because nest predation is the leading cause of nest failure (Ricklefs 1969, Martin 1995), birds should select characteristics associated with the nest site that reduce the probability of nest predation and improve the probability of nest survival. Therefore, we expected that Lewis's Woodpecker nest-site characteristics would strongly influence nest survival. As aerial foragers, Lewis's Woodpeckers rely on an ephemeral and often unpredictable food source, and timing the nesting period to coincide with periods of insect emergence may be critical to maximize foraging opportunities. Thus, we expected that temporal and seasonal trends associated with prey availability would also have a strong influence on nest survival.

Methods

Study Area

The study area is located on the Pioneer Mountain Ranch in Butte and Blaine Counties, Idaho in the foothills of the Pioneer Mountains, north of the Snake River Plain. This portion of the state is a mix of private and public lands used primarily for cattle and sheep grazing. Elevation of the study area varies from 1,600 – 2,000 m, and vegetation is characteristic of the Intermountain sagebrush steppe ecosystem (West 1983). The landscape is composed of narrow riparian zones (≤ 50 m in width) dominated by aspen, thinleaf alder (*Alnus incana*), willow (*Salix* spp.), mountain snowberry (*Symphoricarpos oreophilus*), and rose (*Rosa* spp.), surrounded by a matrix of sagebrush steppe (*Artemisia* spp.). Black cottonwood (*P. trichocarpa*) also occurs along some streams. Small stands of aspen occur on sideslopes and in snowmelt pockets at higher elevations of some drainages. Aspen habitat is very limited, comprising $< 7\%$ (900 ha) of the study area (14,000 ha). Aspen communities in these areas are considered “stable” due to the absence of conifers (Mueggler and Campbell 1982, Mueggler 1988). Daily temperature extremes during the breeding season (May – August) range from a low of -3°C to highs of over 38°C , and average monthly rainfall ranges from 5 – 46 mm (weather station, Craters of the Moon National Monument).

Because both sheep and cattle grazing occur throughout the study area, we attempted to minimize variation in habitat features that may have been related to differences in grazing regimes by choosing study sites with similarities in timing of

grazing and stocking rates. We chose four study sites; two of the sites were grazed by cattle, and two were grazed by sheep. Each study site was composed of approximately 5 km of linear riparian habitat and all associated aspen stands for a total survey area of 300-500 ha per study site. We were unable to find nearby study sites with comparable habitat characteristics in ungrazed aspen riparian woodlands, thus we were only able to compare cattle- and sheep-grazed sites.

Nest Data Collection

We conducted surveys for Lewis's Woodpecker nests from mid-May to early August during three breeding seasons (2002-2004). We located nests by searching aspen riparian woodlands and isolated aspen stands for potential nest trees and cavities, observing behavior (e.g., courtship, copulation, carrying food, carrying fecal sacs away from nest), and by checking previously used nest sites. A nest was defined as a cavity containing ≥ 1 egg or nestling. We assigned a unique alpha-numeric code to each nest and obtained coordinates with a GPS unit (Trimble GeoExplorer 3). We monitored nests from the time they were found until they either fledged (≥ 1 nestling left the nest) or failed. Upon discovery of the nest and during subsequent visits, we recorded date, time of visit, nesting stage (laying, incubation, nestling), description of nest contents (if observed), parental behavior, and type of prey delivered (e.g., cicada, grasshopper, fruit) during the nestling stage. Interval lengths between nest visits ranged from 1 – 10 days with the most common interval lengths being 2, 3, and 4 days (frequencies of observations of interval lengths of 1, 2, 3, 4, 5, 6, 7, 8, and 10 days were 39, 67, 66, 66, 52, 41, 2, 1, and 2, respectively). Interval lengths were typically longer during the

beginning of the nesting cycle, and nests were visited almost daily as they neared the fledging date. We visited nests on “transition” days (e.g., hatching, fledging) as much as possible. To obtain nest initiation date, clutch size, hatch date, and number of nestlings, we viewed nest contents with a cavity viewer composed of a monochrome pinhole camera mounted on the end of a telescoping pole (TreeTop II; Sandpiper Technologies, Inc.). We were able to view the contents of all cavities ≤ 13 m in height unless prohibited by cavity angle or dense vegetation. When we viewed nest contents, we approached the nest as quickly and quietly as possible and modified our route to the nest tree on each visit to reduce the possibility of predators following our path to the nest tree. We viewed nest contents at every nest visit during the laying period but typically only viewed nest contents once or twice throughout the incubation and nestling periods. To reduce the risk of forcing nestlings to fledge prematurely, we did not view nest contents when nestlings were within 10 days of fledging. For nest visits during which we did not view nest contents, we gathered information on the status of the nest by observing parental behavior from a point ≥ 15 m from the nest tree. We confirmed fledging by observing fledglings near the nest tree. We assumed that a nest failed if the nest was empty or if we observed no parental behavior at the nest before the possible fledge date.

We defined initiation date as the date the female laid the first egg of the clutch and incubation date as the date the female laid the final egg of the clutch. If we did not know initiation date exactly (i.e., we found the nest during the incubation period), then we backdated from the date of observed egg hatching. For example, assuming incubation required 13 days (the average length of the incubation period for Lewis’s Woodpeckers

in our study area), if the eggs hatched on 1 July, then we backdated 13 days to determine the first day of incubation (i.e., 18 June). To determine initiation date, we assumed females laid one egg per day and backdated one day for every egg in the clutch (e.g., 6 eggs = 6 days), so for this example the initiation date would be 13 June. For nests at which we were unable to view nest contents, we estimated nest stage based on observations of adult behavior (e.g., mate switching during incubation, entering the cavity with food during the nestling period). For these nests, we determined initiation and transition dates by using average values for clutch size, incubation, and nestling periods from the literature (Tobalske 1997) and data from other nests in our study area.

Habitat Measurements

At each nest, we established an 11.3-m radius circular plot with a nested 5-m radius circular subplot both centered on the nest tree. Methods and plot design follow Martin et al. (1997) and Saab and Dudley (1998) with some modifications. Within the entire 11.3-m plot, we recorded the number of live trees and snags (dead trees) > 1.37 m in height and ≥ 20 cm in diameter and measured the following characteristics: tree species, diameter at breast height (dbh), and tree height. Within the 5-m subplot, we measured woody stem abundance by counting all woody stems between 0.5 - < 1.37 m in height and estimated bare ground using a point-intercept method. We placed a sharpened dowel every 0.5 m from the center of the plot in four perpendicular directions for a total of 40 measurements. We totaled the number of times the dowel hit bare ground out of 40 measurements and converted this to a percentage of bare ground. For each nest tree, we measured dbh, tree condition (live or dead), nest cavity height, and tree height. In other

studies describing Lewis's Woodpecker nest sites, tree decay was found to be an important nest tree characteristic (Bock 1970, Vierling 1997, Linder and Anderson 1998, Saab and Dudley 1998). We did not include the level of tree decay as a variable in our analysis because the majority of live aspen are infected to varying degrees with heartrot fungus (*Phellinus tremulae*; Hart and Hart 2001). External indicators of decay such as fungal conks may not be reliable indicators of heartrot presence (Schepps et al. 1999 and this study), thus we could not reliably assess the degree of decay for all trees.

We characterized available habitat by establishing 60 non-nest random points placed at least 200 m apart throughout riparian habitat on our study sites. Plots established at random points had the same design as those established for nest plots. To compare nest tree characteristics, we randomly chose an available tree from each random 11.3-m radius plot. We defined an available tree as any tree (live or dead) ≥ 20 cm in diameter, as Lewis's Woodpeckers did not nest in trees < 21 cm in diameter. The same measurements taken at the nest tree (other than those specific to the nest cavity) were taken on each randomly selected tree. Because non-nest plots were randomly selected, they did not necessarily contain a tree available for nesting.

Data Analysis

Nest-site selection. We used logistic regression to determine the habitat variables that most strongly influenced nest-site selection. We developed a list of *a priori* candidate models that allowed us to model the odds that a tree contained a Lewis's Woodpecker nest as a function of several covariates based on biological hypotheses from published literature (Bock 1970, Vierling 1997, Linder and Anderson 1998, Saab et al.

2002, Saab et al. 2004; Table 2.1). Our list of candidate models included a global model containing all covariates. We incorporated five continuous habitat variables into our models: tree height (HT), diameter at breast height (DBH), woody stem abundance (STEM), tree abundance (TREE), and percent bare ground (BARE). We included a categorical treatment variable (TRT) to assess the influence of any habitat differences associated with cattle and sheep grazing. We estimated the differences in mean values (i.e., effect sizes) for habitat covariates between nest-site plots and random plots and their corresponding 95% confidence intervals. We provide effect sizes because they allow us to estimate the magnitude of the difference between nest-site and random plot habitat covariates (Anderson et al. 2001).

We predicted that Lewis's Woodpeckers would select nest trees that were taller and larger in diameter than randomly selected trees. Taller nest trees would allow for higher nests, and these higher nests may be less accessible to tree-climbing nest predators (Li and Martin 1991, Saab et al. 2004). Larger diameter trees may provide warmer and more stable nest cavity temperatures (Wiebe 2001). We also predicted that nest-site plots would have higher woody stem and tree abundances than random plots. Higher stem abundance would provide increased substrate for arthropod prey (Bock 1970), and higher tree abundance would provide increased perching and food storage sites. We also expected nest sites to have more bare ground than random sites. Although Lewis's Woodpecker spends the majority of its foraging effort fly-catching, it also spends a considerable amount of time searching for insects on the ground (Bock 1970, Tobalske 1997), and increased bare ground would increase visibility of prey. To test for

multicollinearity among continuous habitat covariates, we calculated Pearson correlation coefficients (Table 2.2).

Table 2.1. Biological predictions for the factors affecting nest-site selection of Lewis's Woodpecker nests in aspen riparian woodlands and the resulting model structure.

Prediction	Model Structure
Global model: Tree height + Dbh + Stem abundance + Tree abundance + Bare ground + Treatment	$\beta_0 + \beta_1(\text{HT}) + \beta_2(\text{DBH}) + \beta_3(\text{STEM}) + \beta_4(\text{TREE}) + \beta_5(\text{BARE}) + \beta_6(\text{TRT})$
Tree height + Dbh + Stem abundance + Tree abundance + Bare ground	$\beta_0 + \beta_1(\text{HT}) + \beta_2(\text{DBH}) + \beta_3(\text{STEM}) + \beta_4(\text{TREE}) + \beta_5(\text{BARE})$
Tree height + Dbh + Treatment	$\beta_0 + \beta_1(\text{HT}) + \beta_2(\text{DBH}) + \beta_3(\text{TRT})$
Tree height + Dbh	$\beta_0 + \beta_1(\text{HT}) + \beta_2(\text{DBH})$
Stem abundance + Tree abundance + Bare ground + Treatment	$\beta_0 + \beta_1(\text{STEM}) + \beta_2(\text{TREE}) + \beta_3(\text{BARE}) + \beta_4(\text{TRT})$
Stem abundance + Tree abundance + Bare ground	$\beta_0 + \beta_1(\text{STEM}) + \beta_2(\text{TREE}) + \beta_3(\text{BARE})$
Stem abundance + Tree abundance + Treatment	$\beta_0 + \beta_1(\text{STEM}) + \beta_2(\text{TREE}) + \beta_3(\text{TRT})$
Stem abundance + Tree abundance	$\beta_0 + \beta_1(\text{STEM}) + \beta_2(\text{TREE})$
Dbh + Tree abundance + Treatment	$\beta_0 + \beta_1(\text{DBH}) + \beta_2(\text{TREE}) + \beta_3(\text{TRT})$
Dbh + Tree abundance	$\beta_0 + \beta_1(\text{DBH}) + \beta_2(\text{TREE})$
Treatment	$\beta_0 + \beta_1(\text{TRT})$

We evaluated support for our models using an information theoretic approach (Burnham and Anderson 2002). For our global model, we conducted the Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000), and calculated the overdispersion parameter, \hat{c} , (Pearson's χ^2 divided by degrees of freedom) to determine if quasi-likelihood corrections were necessary (Burnham and Anderson 2002). We used Akaike's Information Criterion (AIC) corrected for small sample size AIC_c to evaluate our candidate models. If we found evidence of overdispersion ($\hat{c} \geq 1.2$; Burnham and Anderson 2002), we used QAIC_c to compare our candidate models. We calculated

ΔAIC_c (the difference in AIC_c between each candidate model and the model with the lowest AIC_c) or $\Delta QAIC_c$ to determine the strength of support for each model.

Table 2.2. Pearson correlation coefficients among nest habitat covariates used to predict Lewis's Woodpecker nest-site selection and nest survival in aspen riparian woodlands, south-central Idaho, 2002-2004.

	Nest height	Nest tree DBH	Number of trees	Number of stems	Bare ground (%)
Nest height	1.00	0.54	-0.15	0.09	0.06
Nest tree DBH		1.00	-0.45	0.04	0.02
Number of trees			1.00	-0.02	-0.22
Number of stems				1.00	-0.30
Bare ground (%)					1.00

We used PROC LOGISTIC (SAS Institute, Inc. 2000) to compute adjusted odds ratios and their 95% profile likelihood confidence limits for our best model. Adjusted odds ratios allowed us to evaluate the magnitude of the effect of each predictor variable while holding all other variables constant. We interpreted an adjusted odds ratio for a continuous predictor variable as the odds of a tree containing a Lewis's Woodpecker nest for every n -unit increase in the continuous variable. We chose the unit of increase based upon values of the variable that we thought would be biologically significant. We interpreted adjusted odds for the categorical predictor variable treatment as the odds of one category relative to another (i.e., cattle-grazed vs. sheep-grazed). Note that 95% confidence limits around an adjusted odds ratio that overlap one indicate that particular covariate was not a strong predictor of nest-site selection.

Nest survival. We modeled estimates of daily survival rate (DSR), the probability of a nest surviving a single day, using a generalized linear models approach (PROC NLMIXED; SAS Institute, Inc. 2000) with a logit link that constrained the estimates of DSR between 0 and 1 (Agresti 1996). This procedure allowed us to model: 1) the binomially distributed data as a function of several nest- and time-specific continuous or categorical covariates; 2) non-linear relationships between covariates and DSR; and 3) covariates that varied in a predictable manner (e.g., nest age) for each day. We used AIC_C to rank our models and evaluate the support for each model given our data. Analysis methods are detailed in Dinsmore et al. (2002), Stephens (2003), and Rotella et al. (2004). Despite these advantages, this approach lacks the ability to assess the fit of the global model or to adjust for overdispersion.

We developed a set of models based on *a priori* biological hypotheses (Table 2.3) to explain variation in nest survival of Lewis's Woodpecker. We grouped sources of variation incorporated into our nest survival models into seven categories:

1) Nest-site characteristics. We included nest height (NHT), nest tree diameter at breast height (DBH), percent bare ground (BARE), woody stem abundance (STEM), and tree abundance (TREE) around the nest tree as covariates in our nest survival models. We predicted that DSR would: a) increase for taller nests because these cavities may be less accessible to tree-climbing nest predators; b) increase with increasing nest-tree diameter because larger diameter trees provide more stable nest cavity temperatures; c) increase with increasing bare ground due to increased visibility of ground-dwelling arthropods; d) increase with increasing woody stem abundance around the nest tree due

to increased substrate for free-flying arthropods; and e) have a quadratic relationship with the abundance of trees > 20 cm in diameter around the nest tree. We predicted that too few trees would not provide the necessary perch and food storage sites, but too many trees would not provide an open canopy for foraging.

2) Temperature (TEMP) and Precipitation (PRECIP). We predicted that DSR would increase with increasing daily average temperature because cold temperatures can negatively affect prey availability, onset of incubation, and nestling development (Ricklefs 1969, Conway and Martin 2000, Remes and Martin 2002). Early season temperatures below or near freezing are not uncommon in our study areas. We also predicted that DSR would be lower on days with precipitation because rain can reduce the activity of free-flying arthropods (Bryant 1988).

Table 2.3. Biological predictions for the response of the daily survival rate (DSR) of Lewis's Woodpecker nests to covariates in aspen riparian woodlands and the resulting model structure.

Prediction	Model Structure
<u>Non-habitat models</u>	
Null model	β_0
Year only model	$\beta_0 + \beta_1(2002) + \beta_2(2004)$
Initiation date	$\beta_0 + \beta_1(\text{INITDIS})$
Nest age	$\beta_0 + \beta_1(\text{SAGE})$
Daily average temperature	$\beta_0 + \beta_1(\text{TEMP})$
Precipitation	$\beta_0 + \beta_1(\text{PRECIP})$
Initiation date + Daily average temperature	$\beta_0 + \beta_1(\text{INITDIS}) + \beta_2(\text{TEMP})$
Daily average temperature + Precipitation	$\beta_0 + \beta_1(\text{TEMP}) + \beta_2(\text{PRECIP})$
Initiation date + Daily average temperature + Precipitation	$\beta_0 + \beta_1(\text{INITDIS}) + \beta_2(\text{TEMP}) + \beta_3(\text{PRECIP})$
Initiation date + Daily average temperature + Nest age	$\beta_0 + \beta_1(\text{INITDIS}) + \beta_2(\text{TEMP}) + \beta_3(\text{SAGE})$
Initiation date + Nest age	$\beta_0 + \beta_1(\text{INITDIS}) + \beta_2(\text{SAGE})$
<u>Habitat models</u>	
Nest height + Dbh	$\beta_0 + \beta_1(\text{NHT}) + \beta_2(\text{DBH})$
Stem abundance + Tree abundance + Bare ground	$\beta_0 + \beta_1(\text{STEM}) + \beta_2(\text{TREE}) + \beta_3(\text{BARE})$
Quadratic effect of tree abundance around the nest	$\beta_0 + \beta_1(\text{TREE}) + \beta_2(\text{TREE})^2$
Grazing treatment	$\beta_0 + \beta_1(\text{TRT})$
Stem abundance + Tree abundance + Bare ground + Grazing treatment	$\beta_0 + \beta_1(\text{STEM}) + \beta_2(\text{TREE}) + \beta_3(\text{BARE}) + \beta_4(\text{TRT})$

3) Age (SAGE). We predicted that DSR would increase with increasing nest age. Although nest locations are more obvious due to increased activity at the nest (e.g., begging young, frequent feeding trips by adults), we observed that adults increased vigilance and nest defense as the nest neared fledging. The likelihood that nestlings will fledge increases as they age, and they become increasingly valuable to the fitness of the adults (Montgomerie and Weatherhead 1988).

4) Nest initiation date (INITDIS). We predicted that DSR would decrease for nests initiating later in the breeding season, as early nesters are more likely to succeed (Bryant 1988, McCleery and Perrins 1988). Increased success for early nesters may be related to timing of nesting with food availability, characteristics of the individual birds (e.g., older birds may be more experienced breeders), and higher nest site quality. Lewis's Woodpecker has a weak excavator morphology (Spring 1965) and typically does not excavate new nest cavities (Bock 1970, Tobalske 1997, Saab et al. 2002). Instead it uses existing nest cavities and thus may be nest site limited. Consequently, late nesters may be forced to nest in lower quality nest sites. We did not incorporate a time trend to assess the influence of a general seasonal trend on DSR because time and nest age were collinear variables. This was likely caused by a lack of various ages across the nesting season (i.e., all nests at the beginning of the breeding season were young, and all nests at the end of the season were old).

5) Year (YR). We hoped to account for annual variation in DSR that was not specifically addressed by other sources of variation such as food availability or predator

abundance and distributions. Year was coded as an indicator variable with 2003 set as the reference year.

6) Observer Effect (OB). Viewing nest contents may influence nest survival (either positively or negatively) resulting in potentially biased estimates of DSR (Rotella et al. 2000). To determine if viewing nest contents had an impact on DSR, we incorporated an observer effect variable into our best model. The incorporation of this observer effect allowed DSR to vary for days that nest contents were viewed. This effect was coded as an indicator variable where 1 = contents viewed; 0 = contents not viewed. We assumed that viewing nest contents affected DSR for only the day nest contents were viewed.

7) Treatment Effect (TRT). Sheep and cattle grazing have different impacts on vegetation due to differences in forage preference and utilization of riparian zones (Platts 1982, Ruyle and Bowns 1985). We hoped to account for these differences by incorporating a treatment effect of grazing. This effect was coded as an indicator variable where 1 = cattle grazing; 0 = sheep grazing.

Results

Nests

We found 76 Lewis's Woodpecker nests during the breeding seasons of 2002-2004 and were able to determine the fate of all nests. The number of nests found as well as the proportion of successful nests varied annually (Table 2.4). Overall, 59 nests fledged ≥ 1 young. Of the 17 nest failures, 13 were caused by predation. Potential nest

predators observed in the study area included Long-tailed Weasel (*Mustela frenata*), Least Chipmunk (*Tamias minimus*), Gopher Snake (*Pituophis melanoleucus*), Flammulated Owl (*Otus flammeolus*), House Wren (*Troglodytes aedon*), and Black Bear (*Ursus americanus*). We witnessed a Long-tailed Weasel removing young nestlings from one nest cavity, and we observed Least Chipmunks climbing nest trees on several occasions. Several aspen had claw mark scars from Black Bears, and Black Bears are known nest predators of cavity-nesting birds (Walters and Miller 2001). Flammulated Owl and House Wren each destroyed the contents of one nest and subsequently usurped these cavities. Carpenter ants (*Camponotus* sp.) may have caused nestling mortality in two nests. Two other nests were abandoned, one during incubation and the other during the nestling stage.

We found 45 nests on or before nest initiation (i.e., we found nests when adults were modifying cavities) or during the egg laying stage, 16 nests during incubation, and 13 nests during the nestling stage. The average length of the nesting cycle for successful Lewis's Woodpecker nests in the study area was 51 days \pm 2.7 (1 SD, range 45 – 61 days). During the 2003 breeding season, nests had larger average clutch sizes, more fledglings, and earlier average initiation, hatch, and fledging dates than the 2002 and 2004 breeding seasons (Table 2.4). Clutch size declined for nests initiating later in the breeding season. Average clutch size for nests initiating before 4 June, 6.5 eggs \pm 1.2 (n = 15 nests); between 4 June and 15 June, 5.8 eggs \pm 1.0 (n = 26 nests); and after 15 June, 4.9 eggs \pm 1.1 (n = 11 nests). We considered 23 May to be the first day of the breeding season, as this was the earliest known initiation date. The majority of nests (58%)

initiated on or before 6 June (Figure 2.1). Mean temperature from 23 May through 5 August was $19.1^{\circ}\text{C} \pm 5.9$ in 2002, $20.8^{\circ}\text{C} \pm 4.8$ in 2003, and $17.2^{\circ}\text{C} \pm 5.2$ in 2004 and differed significantly among years ($F_{2,222} = 8.71$, $P < 0.001$). Specifically, pairwise results from Tukey multiple comparison tests suggested daily average temperatures in 2004 were significantly lower than in 2003 ($q = 3.6 \pm 2.0$, 95% CI 1.6, 5.7, $\alpha = 0.05$). Mean temperature during the first 10 days of the breeding season was cooler in 2004 (9°C) relative to 2002 (14°C) and 2003 (20°C), respectively.

Habitat Measurements

Values of Lewis's Woodpecker nest habitat covariates were highly variable (Table 2.5, Figure 2.2). Five of the 76 Lewis's Woodpecker nests monitored for nest survival were located just outside the study area in locations where we did not establish random points, thus we used 71 nests in our analysis of nest-site selection. Two nests were placed in natural cavities in black cottonwood; the remaining 69 nests were in aspen. The majority (54%) of nest trees contained more than one cavity, and 28% of nest trees had multiple species nesting in the same tree. Fourteen nest trees were subsequently reused by Lewis's Woodpecker; ten nest trees were used twice, and four nest trees were used three times during the study. In four of these instances, nests were located in different cavities within the same nest tree in subsequent years. One nest tree fell after only one year of use. Of the 76 nests found, Lewis's Woodpecker was the original excavator of only one cavity. This cavity was excavated in a recently broken branch in a tree that was used for nesting in the previous year.

Table 2.4. Number of nests monitored, apparent nesting success, average initiation, hatch, and fledge dates, and average clutch size and number of fledglings per successful nest for Lewis's Woodpecker nests in south-central Idaho, USA, 2002-2004. Means are followed by 1 SD (*n*, range). SD for initiation, hatch, and fledge dates is expressed in days.

Year	Number of nests monitored	Apparent nest success %	Clutch Size	Initiation Date	Hatch Date	Fledge Date	Fledglings per successful nest
2002	18	78	5.7 ± 1.03 (6, 4 – 7)	8 June ± 9 (23 May – 25 June)	24 June ± 8 (11 June – 9 July)	24 July ± 1.43 (13 July - 31 July)	2.0 ± 0.96 (14, 1 – 4)
2003	33	91	6.2 ± 1.20 (25, 5 – 9)	3 June ± 6 (23 May – 15 June)	21 June ± 5 (10 June – 2 July)	23 July ± 0.95 (13 July – 3 August)	2.4 ± 0.93 (30, 1 – 5)
2004	25	60	5.3 ± 1.20 (21, 3 – 8)	10 June ± 7 (1 June – 25 June)	28 June ± 7 (21 June – 11 July)	28 July ± 1.39 (19 July – 5 August)	2.3 ± 0.49 (15, 2 – 3)
Overall	76	78	5.8 ± 1.24	7 June ± 8	24 June ± 7	25 July ± 0.73	2.3 ± 0.85

Figure 2.1. Frequency distribution of Lewis's Woodpecker nest initiation dates in aspen riparian woodlands, south-central Idaho, 2002-2004.

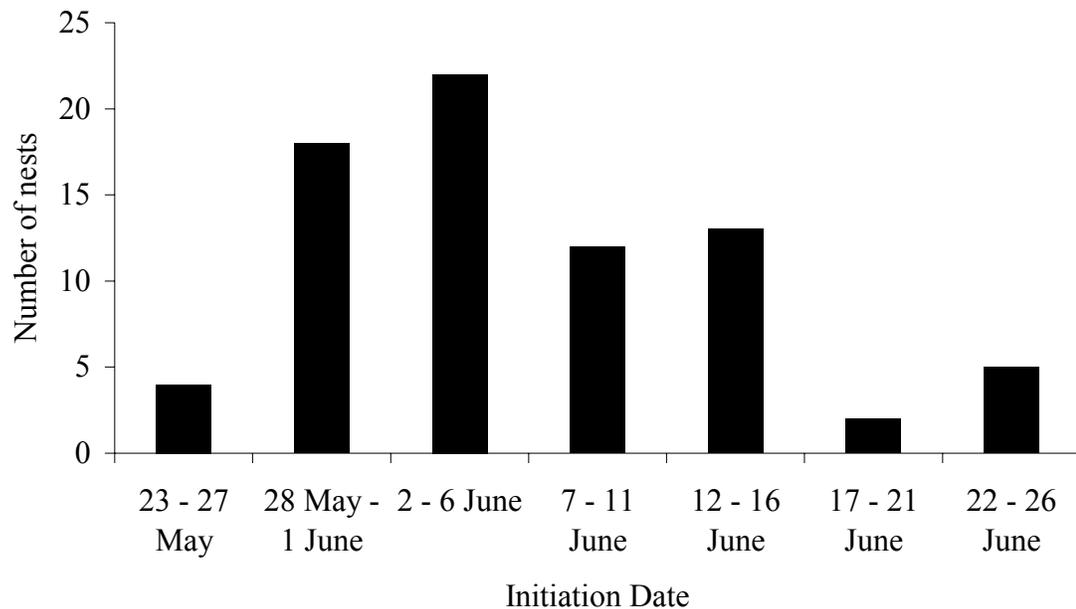


Table 2.5. Summary of nest tree and nest site characteristics of Lewis's Woodpecker nests in aspen riparian woodlands, south-central Idaho, 2002-2004.

Covariate	Mean (\pm 1 SD)	Range
Nest height (m)	6.5 \pm 3.4	(1.9 - 24.5)
Nest tree height (m)	15.6 \pm 5.4	(3.5 - 25.5)
DBH (cm)	41.3 \pm 15.3	(21.0 - 103.5)
Number of trees	9 \pm 6	(1 - 19)
Number of stems	122 \pm 122	(0 - 571)
Bare ground (%)	11.7 \pm 11.7	(0 - 60)

Because birds were not individually marked, we did not know if the same birds were nesting in the same nest tree more than once. Because we were interested only in the odds that a tree contained a Lewis's Woodpecker nest given our set of covariates, we included all 71 nests in our analysis. Nine of the 60 random plots did not contain an available nest tree (≥ 1.37 m in height, ≥ 20 cm dbh), so we incorporated 51 random plots into our nest-site selection analysis.

We did not incorporate tree condition into our analysis because 75% of nests were located in live trees, and only 18% of trees included in the analysis were dead. In general, nest trees were taller and larger in diameter than random available trees, and nest plots had more trees, fewer woody stems, and less bare ground than random plots, although values were highly variable (Table 2.6). The diameter of nest trees averaged over nine centimeters larger than randomly selected trees (95% CI, 5 – 13), and nest plots averaged three more trees (95% CI, 1 – 5), 80 fewer woody stems (95% CI, -132 - -28), and 7% less bare ground (95% CI, -12 – -2) than random plots. Tree height was similar between nest trees and randomly selected trees, although average nest tree height was greater than random tree height. Habitat characteristics were similar between cattle- and sheep-grazed treatments (Table 2.7).

Figure 2.2. Frequency distribution of nest tree covariates (a. nest height; b. nest tree height; and c. diameter at breast height) and nest site covariates (d. number of trees; e. number of stems; and f. percent bare ground) for 76 Lewis's Woodpecker nests in aspen riparian woodlands, south-central Idaho, 2002-2004.

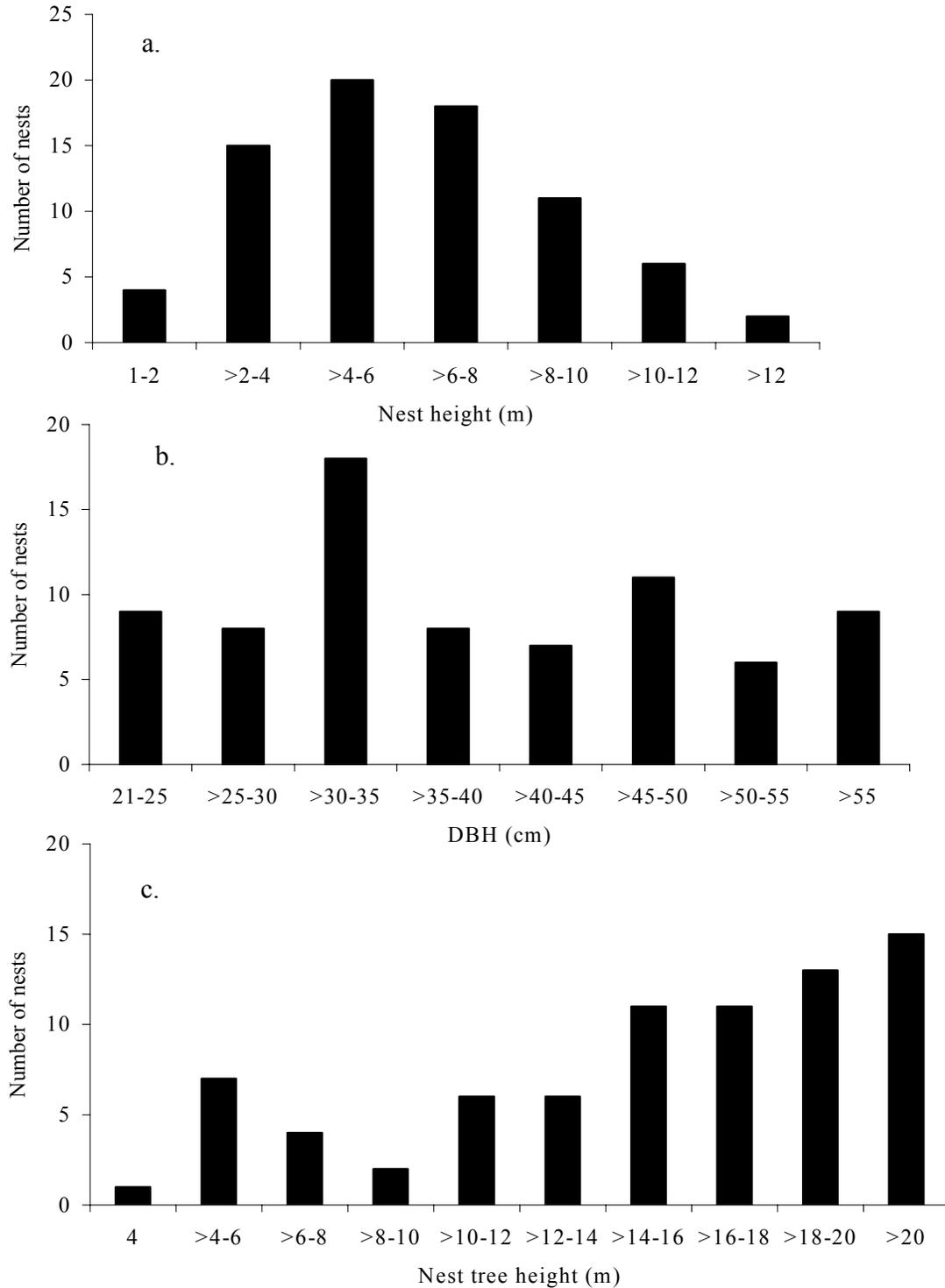


Figure 2.2 continued.

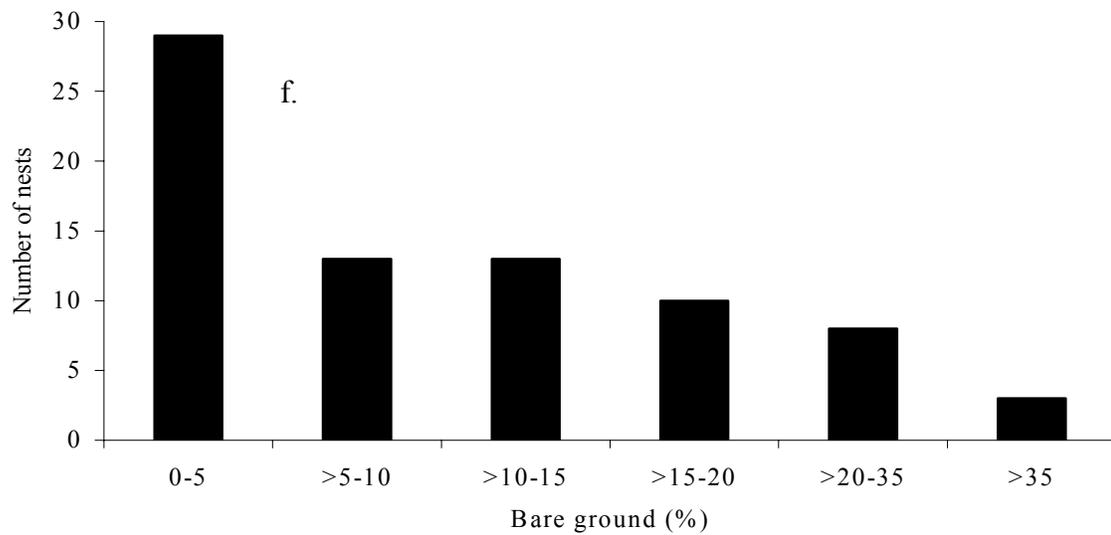
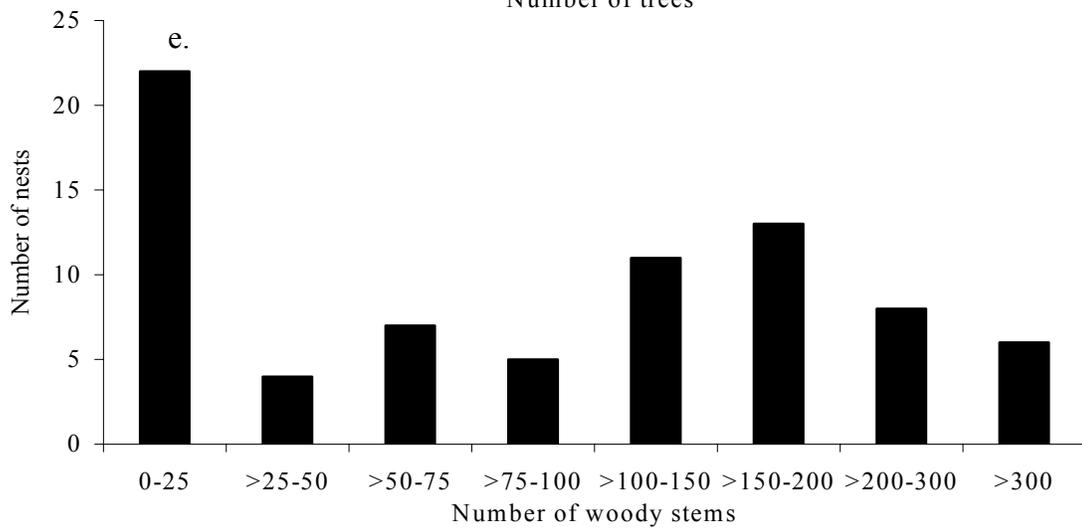
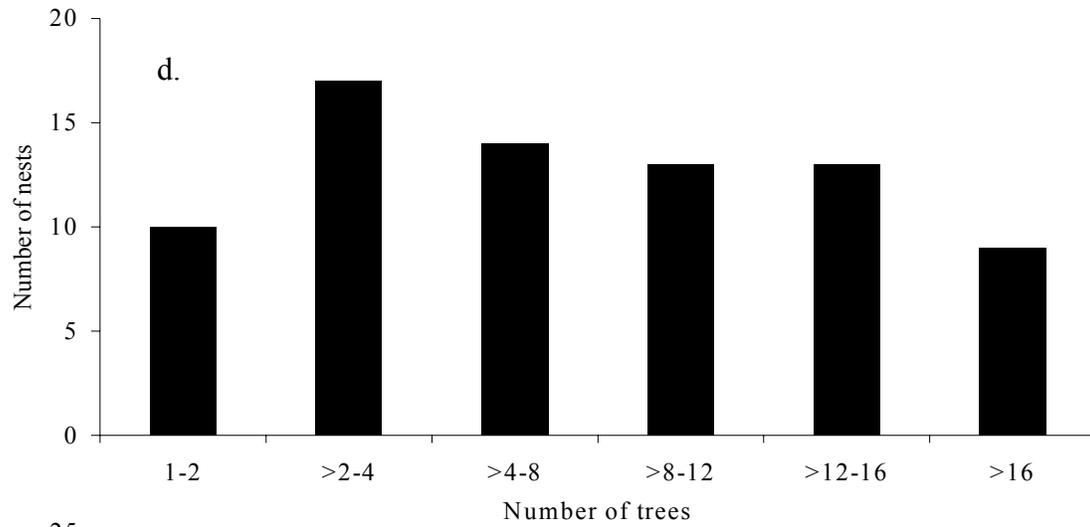


Table 2.6. Summary of habitat measurements taken at Lewis's Woodpecker nest sites and random plots. Values are mean followed by ± 1 SD (range). Effect size is the estimated difference in mean values between nest and random plots and corresponding 95% confidence interval.

Covariate	Nest (<i>n</i> = 71)	Random (<i>n</i> = 51)	Effect size	
			$\bar{x}_{\text{Nest}} - \bar{x}_{\text{Random}}$	95% CI
DBH	39.0 \pm 12.0 (21 - 70)	30.0 \pm 10.0 (21 - 62)	9.2	5.2 - 13.2
Tree height	15.0 \pm 5.0 (3.5 - 22)	14.0 \pm 5.0 (3 - 24)	1.4	-0.5 - 3.3
Number of trees	8 \pm 6 (1 - 19)	6 \pm 5 (1 - 18)	2.8	1.0 - 4.6
Number of stems	125 \pm 125 (0 - 571)	204 \pm 157 (10 - 732)	-79.7	-131.6 - -27.7
Bare ground (%)	12 \pm 12 (0 - 60)	19 \pm 15 (0 - 58)	-6.9	-11.8 - -2.0

Table 2.7. Summary of habitat measurements taken at vegetation plots (both nest and random) on cattle- and sheep-grazed sites. Values are mean followed by ± 1 SD (range). Effect size is the estimated difference in mean values for habitat covariates between cattle- and sheep-grazed sites and corresponding 95% confidence interval.

Covariate	Cattle-grazed (<i>n</i> = 83)	Sheep-grazed (<i>n</i> = 39)	Effect size	
			$\bar{x}_{\text{Cattle}} - \bar{x}_{\text{Sheep}}$	95% CI
DBH	35.0 \pm 11.6 (20.5 - 65.5)	36.0 \pm 13.3 (20.5 - 70.0)	-1.2	-6.1 - 3.7
Tree height	14.0 \pm 5.0 (3.0 - 22.0)	16.0 \pm 5.0 (3.5 - 23.5)	-1.9	-3.9 - 0.1
Number of trees	7.0 \pm 5.0 (1 - 19)	7.0 \pm 6.0 (1 - 18)	0.1	-1.9 - 2.2
Number of stems	160 \pm 151 (0 - 724)	154 \pm 131 (0 - 732)	6.1	-46.3 - 58.4
Bare ground (%)	16 \pm 13 (0 - 58)	12 \pm 14 (0 - 60)	3.9	-1.3 - 9.1

Nest-Site Selection

The global model adequately fit the data ($\chi^2_8 = 9.1$, $P = 0.33$) and received essentially all of the support (Table 2.8; Akaike weight = 0.99). We did not apply a quasi-likelihood correction to the model ranking criterion (AIC_c) because the overdispersion parameter estimate for the global model was close to one ($\hat{c} = 9.1/8 = 1.1$). Lewis's Woodpecker nest-site selection was positively influenced by dbh and tree density and negatively influenced by increasing amounts of bare ground and woody stems (Table 2.9). The odds of a tree containing a Lewis's Woodpecker nest doubled with every 5 cm increase in diameter, and the odds of a plot containing a Lewis's Woodpecker nest increased by 28% as the number of trees around the nest tree increased. As the number of woody stems increased by 50 stems, the odds of a plot containing a Lewis's Woodpecker nest were reduced by 27%. With every 5% increase in bare ground, the odds of a plot containing a Lewis's Woodpecker nest were reduced by 24%. Tree height was not a good predictor of whether or not a tree contained a nest as the confidence limits included one. Nests were 11.3 times more likely to occur on cattle-grazed sites than sheep-grazed sites.

Table 2.8. Model selection results based on logistic regression predicting nest-site selection of Lewis's Woodpeckers ($n = 122$ trials) nesting in aspen riparian woodlands of south-central Idaho, 2002-2004. Models are ranked from most supported ($\Delta AIC_c = 0$) to least supported; k is the number of parameters in each model. The Akaike weight (w_i) is the weight of the evidence for model i given the data. The model likelihood indicates the support of the model given the data.

Candidate model	k	AIC_c	ΔAIC_c	Akaike weight (w_i)	Model Likelihood
Dbh + Tree height + Tree + Stem + Bare ground + Treatment	7	109.51	0.00	0.99	1.00
Dbh + Tree + Treatment	4	119.86	10.35	0.01	0.01
Dbh + Tree height + Tree + Stem + Bare ground	6	125.30	15.79	0.00	0.00
Dbh + Tree	3	132.84	23.33	0.00	0.00
Tree + Stem + Bare ground + Treatment	5	134.59	25.09	0.00	0.00
Dbh + Tree height + Treatment	4	142.77	33.26	0.00	0.00
Tree + Stem + Treatment	4	143.84	34.33	0.00	0.00
Tree + Stem + Bare ground	4	147.38	37.88	0.00	0.00
Dbh + Tree height	3	151.97	42.46	0.00	0.00
Tree + Stem	3	152.56	43.06	0.00	0.00
Treatment	2	160.78	51.28	0.00	0.00

Table 2.9. Parameter estimates \pm SE, and adjusted odds ratios from the best model (Table 2.8) for predicting nest-site selection by Lewis's Woodpeckers nesting in aspen riparian woodlands in south-central Idaho, 2002-2004. Odds ratio for the categorical variable (treatment) indicates the odds of selecting a nest site in cattle-grazed vs. sheep-grazed treatments. Odds ratios for continuous variables indicate the odds of a site being a nest for every unit change (specified in "units" column) in the variable. Confidence limits that do not contain 1 represent a difference in the odds.

Parameter	Parameter estimate \pm 1 SE	Adjusted Odds Ratio		
		Unit	Estimate	95% Profile Likelihood Confidence Limits
Intercept	-4.00 \pm 1.32			
Dbh (cm)	0.14 \pm 0.04	5	2.06	1.49, 3.08
Tree height (m)	-0.07 \pm 0.07	1	0.93	0.81, 1.05
Number of trees	0.25 \pm 0.07	1	1.28	1.14, 1.48
Number of woody stems	-0.006 \pm 0.002	50	0.73	0.57, 0.90
Bare ground (%)	-0.05 \pm 0.02	5	0.76	0.62, 0.92
Treatment	1.21 \pm 0.32	1	11.25	3.47, 43.88

Nest Survival

Nest survival assuming a constant daily survival rate (i.e., our null model) was $0.9941^{51} = 0.74 \pm 0.06$. The estimate from this model is equivalent to that obtained via the Mayfield method (Mayfield 1975) as modified by Johnson (1979). However, the addition of covariates to this model better explained variation in DSR of Lewis's Woodpecker nests (Table 2.10). The model that received the most support given our data indicated that DSR was negatively related to nest initiation date ($\hat{\beta}_{\text{INITDIS}} = -0.16 \pm 0.04$; 95% CL = -0.23, -0.09) and viewing nest contents ($\hat{\beta}_{\text{OB}} = -2.08 \pm 0.59$; 95% CL = -3.23, -0.93) and positively related to daily average temperature ($\hat{\beta}_{\text{TEMP}} = 0.16 \pm 0.07$; 95% CL = 0.03, 0.30). The logistic regression equation for our best model was: $\text{logit(DSR)} = 5.53 - 0.16 (\text{Initiation Date}) + 0.16 (\text{Daily Average Temperature}) - 2.08 (\text{Observer Effect})$.

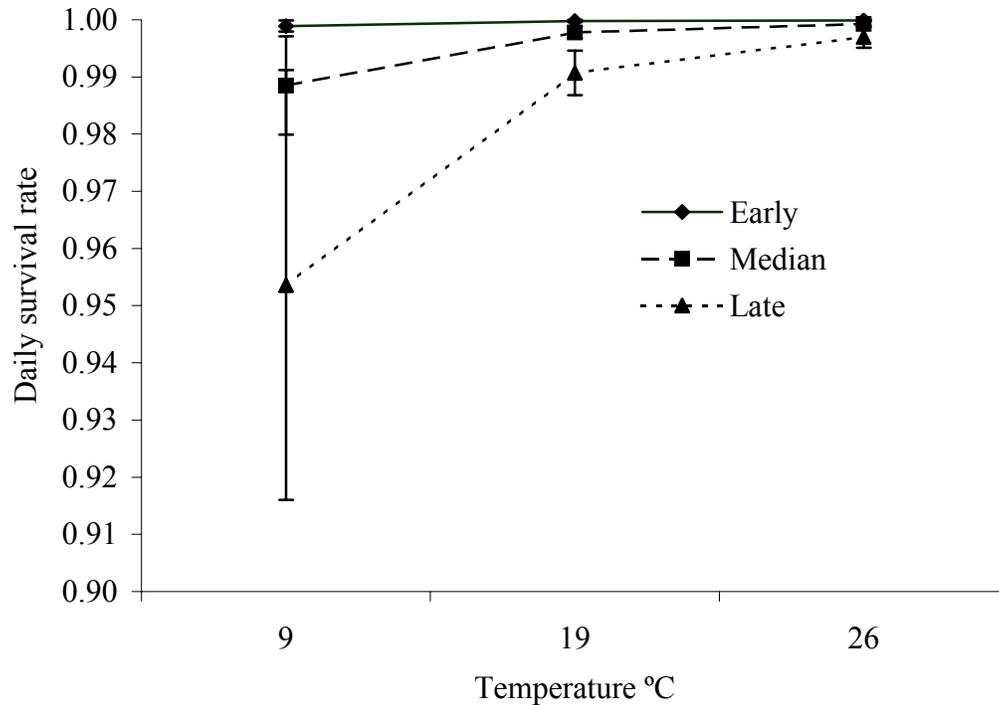
To evaluate the effects of initiation date and daily average temperature for days on which we did not view nest contents on the daily survival rate of Lewis's Woodpecker nests, we plotted DSR as a function of nest initiation date and daily average temperature for nests that initiated early (23 May), mid-season (7 June), and late (16 June) at low (9 °C), median (19 °C), and high (26 °C) values of daily average temperature (Figure 2.3). Nests that initiated earlier in the season had a consistently higher daily survival rate regardless of daily average temperature. Setting the values of initiation date and daily average temperature at their mean values (day 16; 19 °C), we estimated DSR for days with and without an observer effect. DSR was 0.9825 ± 0.009 for days that contents were viewed and 0.9978 ± 0.001 for days we did not view nest contents.

Although the model incorporating year as a covariate did not receive strong support (Table 2.10), the influence of both the 2002 and 2004 breeding seasons on DSR was negative ($\hat{\beta}_{2002} = -1.37 \pm 0.78$; 95% CL -2.87, 0.13, $\hat{\beta}_{2004} = -1.63 \pm 0.67$; 95% CL = -2.94, -0.32) relative to the 2003 breeding season. Models including nest-site characteristics and grazing treatment received no support, and all confidence intervals for the coefficients included zero.

Table 2.10. Daily survival rate (DSR) model ranking for the *a priori* candidate model list. Models are ranked from most supported ($\Delta AIC_c = 0$) to least supported; k is the number of parameters in each model. The Akaike weight (w_i) is the weight of the evidence for model i given the data. The model likelihood indicates the support of the model given the data.

Candidate Model	k	AIC_c	ΔAIC_c	Akaike weight (w_i)	Model likelihood
Initiation date + Daily average temperature + Observer effect	4	142.61	0.00	0.98	1.00
Initiation date + Daily average temperature	3	151.77	9.16	0.01	0.01
Initiation date + Daily average temperature + Precipitation	4	152.78	10.16	<0.01	<0.01
Initiation date + Nest age + Daily average temperature	4	153.78	11.16	0.00	0.00
Nest age + Initiation date	3	158.77	16.16	0.00	0.00
Initiation date	2	160.80	18.19	0.00	0.00
Nest age	2	171.40	28.79	0.00	0.00
Daily average temperature + Precipitation	3	175.29	32.68	0.00	0.00
Daily average temperature	2	175.80	33.19	0.00	0.00
2002 + 2004	3	176.59	33.98	0.00	0.00
Null model	1	180.27	37.66	0.00	0.00
Precipitation	2	180.30	37.69	0.00	0.00
Grazing treatment	2	180.99	38.38	0.00	0.00
Dbh + Nest height	3	181.87	39.26	0.00	0.00
Tree + (Tree x Tree)	3	182.36	39.75	0.00	0.00
Stem + Tree + Bare ground + Grazing treatment	5	184.71	42.10	0.00	0.00
Stem + Tree + Bare ground	4	184.75	42.14	0.00	0.00

Figure 2.3. Estimates of daily survival rate (± 1 SE) of Lewis's Woodpecker nests for days nest contents were not viewed as a function of initiation date and daily average temperature. Temperature values represent low, median, and high values of daily average temperatures. Values for nest initiation date represent early (23 May), median (7 June), and late initiation dates (16 June).



We developed a suite of five exploratory models based on results from our *a priori* models (Table 2.11). In general, results from our exploratory models were no better than our *a priori* models in explaining variation in nest survival, and the additive model including initiation date and daily average temperature remained the best supported model (Table 2.12). However, the model incorporating initiation date, daily average temperature, and an interaction between these two variables was also well supported ($\Delta AIC_c = 0.84$), suggesting that although DSR was always higher for nests initiating early, the strength of that positive effect depended on daily average temperature. The interaction between initiation date and daily average temperature was

weakly negative ($\beta_{\text{INITDIS*TEMP}} = -0.00517$) but highly imprecise (95% CL $-0.014, 0.004$), suggesting that the strength of the positive influence of nesting early on DSR was dampened by increasing daily average temperature.

Table 2.11. Exploratory models resulting from examination of *a priori* model selection results of covariates influencing the daily survival rate (DSR) of Lewis's Woodpecker nests in aspen riparian woodlands and the resulting model structure.

Prediction	Model Structure
Initiation date + Daily average temperature + 2003 + (Initiation date*2003)	$\beta_0 + \beta_1(\text{INITDIS}) + \beta_2(\text{TEMP}) + \beta_3(2003) + \beta_4(\text{InitDIS*2003})$
Initiation date + Daily average temperature + 2003 + (Daily average temperature*2003)	$\beta_0 + \beta_1(\text{InitDIS}) + \beta_2(\text{TEMP}) + \beta_3(2003) + \beta_4(\text{TEMP*2003})$
Initiation date + Daily average temperature + 2002 + 2004 + (Initiation date*2002) + (Initiation date*2004)	$\beta_0 + \beta_1(\text{INITDIS}) + \beta_2(\text{TEMP}) + \beta_3(2002) + \beta_4(2004) + \beta_5(\text{INITDIS*2002}) + \beta_6(\text{INITDIS*2004})$
Initiation date + Daily average temperature + 2002 + 2004 + (Daily average temperature*2002) + (Daily average temperature*2004)	$\beta_0 + \beta_1(\text{INITDIS}) + \beta_2(\text{TEMP}) + \beta_3(2002) + \beta_4(2004) + \beta_5(\text{TEMP*2002}) + \beta_6(\text{TEMP*2004})$
Initiation date + Daily average temperature + (Initiation date* Daily average temperature)	$\beta_0 + \beta_1(\text{InitDIS}) + \beta_2(\text{Avg}_t) + \beta_3(\text{InitDIS*Avg}_t)$

Table 2.12. Daily survival rate (DSR) model ranking for the combined *a priori* and exploratory candidate model lists. Models are ranked from most supported ($\Delta AIC_c = 0$) to least supported; k is the number of parameters in each model. The Akaike weight (w_i) is the weight of the evidence for model i given the data. The model likelihood indicates the support of the model given the data.

Candidate model	k	AIC_c	ΔAIC_c	Akaike weight (w_i)	Model likelihood
Initiation date + Daily average temperature + Observer effect	4	142.61	0.00	0.97	1.00
Initiation date + Daily average temperature	3	151.77	9.16	0.01	0.01
Initiation date + Daily average temperature + (Initiation date * Daily average temperature)	4	152.61	10.00	<0.01	<0.01
Initiation date + Daily average temperature + Precipitation	4	152.78	10.16	<0.01	<0.01
Initiation date + Daily average temperature + Nest age	4	153.78	11.16	0.00	0.00
Initiation date + Daily average temperature + 2003 + (Daily average temperature * 2003)	5	155.11	12.49	0.00	0.00
Initiation date + Average daily temperature + 2003 + (Initiation date * 2003)	5	155.11	12.50	0.00	0.00
Initiation date + Daily average temperature + 2002 + 2004 + (Initiation date * 2002) + (Initiation date * 2004)	7	157.13	14.52	0.00	0.00
Initiation date + Daily average temperature + 2002 + 2004 + (Daily average temperature * 2002) + (Daily average temperature * 2004)	7	158.08	15.46	0.00	0.00
Initiation date + Nest age	3	158.77	16.16	0.00	0.00
Initiation date	2	160.80	18.19	0.00	0.00
Nest age	2	171.40	28.79	0.00	0.00
Daily average temperature + Precipitation	3	175.29	32.68	0.00	0.00
Daily average temperature	2	175.80	33.19	0.00	0.00
2002 + 2004	3	176.59	33.98	0.00	0.00
Null model	1	180.27	37.66	0.00	0.00
Precipitation	2	180.30	37.69	0.00	0.00
Grazing treatment	2	180.99	38.38	0.00	0.00
Dbh + Nest height	3	181.87	39.26	0.00	0.00
Tree + Tree ²	3	182.36	39.75	0.00	0.00
Stem + Tree + Bare ground + Treatment	5	184.71	42.10	0.00	0.00
Stem + Tree + Bare ground	4	184.75	42.13	0.00	0.00

Discussion

Although several studies have examined Lewis's Woodpecker nest-site characteristics, no study has investigated the influence of these characteristics on nest survival. Nest-site selection may be adaptive if birds are selecting nest-site characteristics that increase their fitness (Martin 1993, Clark and Shutler 1999). We observed such adaptations in the pattern of nest-site selection (i.e., several nest site characteristics differed from random sites) but not in the process of how these characteristics influence fitness (i.e., none of the characteristics that we measured were important predictors of nest survival). Instead, nest survival was most influenced by temporal and seasonal trends associated with nest initiation date and daily average temperature.

Nest-Site Selection

Lewis's Woodpecker selected nest trees that were larger in diameter and nest sites with more trees, fewer woody stems, and less bare ground than random trees and plots, respectively. Our results are consistent with nest-site characteristics in burned pine and riparian cottonwood habitats (Raphael and White 1984, Block and Brennan 1987, Vierling 1997, Linder and Anderson 1998, Saab and Dudley 1998, Saab et al. 2002), suggesting that Lewis's Woodpecker selects similar nest-site attributes across habitats. The importance of a shrubby understory to this species is assumed to be an important attribute of breeding habitat due to the associated increase in arthropod prey (Bock 1970, Tobalske 1997, Saab and Vierling 2001), yet increased woody stem densities were not

associated with nest sites in our study. The abundance of woody stems at the nest tree may have less influence on foraging than woody stem abundance in the surrounding habitat. Our observations support this suggestion as we observed Lewis's Woodpecker regularly foraging up to 1 km from the nest. Thus, selection of characteristics associated with foraging and nesting habitat may occur at different spatial scales.

In burned pine and cottonwood riparian habitats, Lewis's Woodpecker nested almost exclusively in dead or dying trees (Bock 1970, Raphael and White 1984, Vierling 1997, Linder and Anderson 1998, Saab and Dudley 1998). Decayed trees provide the soft wood that many woodpecker species rely on to facilitate cavity excavation. In our study, the majority of Lewis's Woodpecker nests were located in live trees, suggesting that the majority of cavities are excavated in live trees. The importance of live aspen infected with heartrot fungus has been noted for many cavity nesters (Harestad and Keisker 1989, Daily 1993, Dobkin et al. 1995, Martin et al. 2004), and the susceptibility of aspen to heartrot fungus creates ideal conditions for cavity excavation (Hart and Hart 2001, Aitken et al. 2002). As a result, aspen habitats typically support high densities of woodpeckers (Dobkin et al. 1995, Martin et al. 2004). Aspen can apparently live for several years with infection, yet severity of infection increases with tree age (Basham 1958). High densities of excavators and the cavities they create in response to these conditions may provide abundant nest sites for Lewis's Woodpecker in aspen riparian woodlands.

We cannot explain why Lewis's Woodpecker placed nearly four times more nests in cattle-grazed sites than sheep-grazed sites, as vegetation characteristics that we

measured were similar between these two grazing treatments. Yet, other factors such as vegetation structure and plant species composition may have differed, subsequently influencing arthropod diversity and abundance (Dennis et al. 1998, Brose 2003).

Vegetation structure and composition are affected by not only the act of grazing, but they are also influenced by a complex relationship of stocking rates, rotation schedules, and timing (Knopf et al. 1988, Saab et al. 1995). The indirect effects of livestock grazing on arthropod numbers and their subsequent influence on food availability for birds merit further study. Moreover, examination of nest-site characteristics at additional spatial scales would provide further insight into the processes influencing Lewis's Woodpecker nest-site selection.

Nest Survival

The introduction of new analytical methodologies allowed us to model nest survival as a function of several biologically important variables (Dinsmore et al. 2002, Stephens 2003, Rotella et al. 2004) and provided valuable insight into the factors influencing nest survival of Lewis's Woodpecker in aspen riparian woodlands. We expected nest survival to be influenced by several nest-site characteristics, yet these characteristics were not strong predictors of nest survival. The high nest survival values we observed across a wide range of nest-site characteristics likely made it difficult to detect an effect of these variables on nest survival. Of the variables that we incorporated into our models, nest initiation date had the strongest influence on nest survival, and nests that initiated earlier were more likely to succeed. Although early nesters risked colder temperatures, this risk apparently did not exceed the overall benefits of nesting early.

The positive influence of early nest initiation on reproductive success has been reported for several bird species (Perrins 1970, Bryant 1988, Brown and Brown 1999, Wiktander et al. 2001, Blums et al. 2002), but the mechanism driving this relationship is still unclear.

One hypothesis is that differences in nest initiation dates reflect individual differences between birds. For example, birds in good condition can initiate nesting earlier and have higher reproductive output (i.e., lay more eggs), whereas birds in poorer condition must delay nesting until they reach adequate condition, typically laying fewer eggs (Perrins 1970). Differences in nest initiation dates may also be age-dependent, as older, more experienced birds tend to initiate nesting earlier (Saether 1990, Blums et al. 2002). A second hypothesis is that nest initiation is dictated by environmental variables such as temperature and precipitation. Specifically, birds will time their nesting to coincide with periods of high food abundance, which in turn are influenced by these seasonal trends (Lack 1966). Our results suggest that both of these mechanisms may be influencing nest initiation dates in Lewis's Woodpecker. In our study, early nesters had the largest clutch sizes, and clutch size declined with later initiation dates, suggesting that early nesters may have been in better condition. Although ages of individual birds in our study were unknown, nests located in cavities used during the previous breeding season were always the first to initiate nesting, suggesting that older birds may have been returning to these nest sites.

We also found evidence that temperature influenced nest initiation dates, suggesting that synchronization of nesting with periods of insect emergence may have

been critical to nest survival. Indeed, Bock (1970) observed annual variations in timing of breeding in relation to weather for Lewis's Woodpecker in California, and we observed a similar pattern. The earliest and mean initiation dates differed during the three breeding seasons of our study, suggesting birds varied the onset of breeding in response to environmental variables that in turn influenced prey availability. Lewis's Woodpecker concentrates its foraging efforts on temporarily abundant prey, exploiting abundant food resources when it matters most (e.g., nestling and early fledging periods; Bock 1970). Although we did not directly measure food abundance, we observed similar behavior. For example, we observed a nesting pair capture and cache at least 50 cicadas in 20 minutes, and adults returned to this cache throughout the nestling period.

Although temperature had a strong influence on nest survival, precipitation was not a good predictor in this study. South-central Idaho experienced extreme drought conditions throughout the duration of our study (National Climatic Data Center 2004), and very few days during the breeding season had measurable precipitation. In the absence of drought, rainfall may have a stronger influence on nest survival given the effect of precipitation on the activity and subsequent availability of aerial insects.

We expected nest age to have a strong, positive influence on nest survival given the increase in nest defense that we observed as the nesting cycle progressed. Given that we found 80% of nests before the nestling period, we should have had enough data to detect such an effect. However, parameter estimates for nest age in all models containing this covariate were effectively 0, indicating that this covariate had essentially no influence on nest survival.

Although we collected valuable demographic data via the use of a cavity viewer, incorporating an observer effect into our nest survival models (Rotella et al. 2000) indicated a substantial negative influence on nest survival for those days that we viewed nest contents. Exclusion of this covariate from our models would have resulted in negatively biased daily survival rate estimates, yet including this covariate allowed us to examine the survival rate of nests for days unaffected by viewing nest contents. For example, incorporating an observer effect into our null model increased our overall nest survival estimate from 0.74 ± 0.06 to 0.88 ± 0.05 . Because we viewed the nest contents of any one nest a limited number of times (typically fewer than four times), the effect on overall nest survival may have been minor. However, we cannot predict what influence viewing nest contents may have on nest survival in other studies. We encourage others to consider any potentially negative consequences and weigh these with the overall benefits this tool provides in answering their research questions.

Value of Aspen Riparian Woodlands as Breeding Habitat

We observed high overall nest survival and productivity values for Lewis's Woodpecker in aspen riparian woodlands. These values were similar to those reported for burned pine habitats and nearly twice those reported for cottonwood riparian habitats (Saab and Vierling 2001). Saab and Vierling (2001) hypothesized that the disparity in reproductive success between burned pine and cottonwood riparian habitats resulted from differences in predator assemblages and abundances. We frequently observed potential nest predators in our study area, yet overall nest survival rates for Lewis's Woodpecker remained quite high. Aspen habitats often have an abundance of cavities, resulting in

increased densities of suitable nest sites that could decrease the probability of a predator locating any one nest (Martin 1993). We propose that an abundance of cavities in aspen riparian woodlands may have decreased the chance that a predator “discovered” a Lewis’s Woodpecker nest. Moreover, the majority of Lewis’s Woodpecker nest trees contained multiple cavities, perhaps further reducing the risk of predation. A similar process may occur in recently burned forests, as these postfire habitats are known to attract high densities of primary cavity-nesting birds (Saab et al. 2004, 2005). High predation rates observed in cottonwood riparian habitats (Saab and Vierling 2001) may have been related to reduced cavity abundance as all Lewis’s Woodpecker nests in this study were located in natural cavities (Vierling 1997), suggesting cavities excavated by primary cavity nesters were limited or absent. If cavity abundance were in fact reduced, then predators would increase their likelihood of finding a cavity occupied by Lewis’s Woodpecker. Examining the relationship between primary cavity-nesting birds, cavity abundance, and predation rates of Lewis’s Woodpecker across habitats would provide valuable insight into the mechanisms driving nest predation.

The high nest survival and productivity values we observed suggest that aspen riparian woodlands provide high quality breeding habitat and may be a potential source habitat for this species in the Intermountain West. We encourage further study of Lewis’s Woodpecker in similar habitats throughout the Intermountain West. Moreover, increased monitoring efforts in aspen riparian woodlands may provide a better indication of the status of Lewis’s Woodpecker populations because of the stability of these habitats relative to ephemeral postfire forest habitats. Additionally, information is needed on

reproductive success in riparian woodlands that are not grazed by livestock. Although Breeding Bird Survey data indicate Lewis's Woodpecker populations are declining at a rate of 1.4% per year (Sauer et al. 2004), this species' sporadic distribution and known detection biases associated with this survey method increase the difficulty of assessing its population status and emphasize the need for habitat-specific studies. The loss of burned pine and riparian cottonwood habitats, the primary breeding habitats of this species, has been implicated in these population declines (Tobalske 1997). Fire suppression and loss of large trees due to logging have reduced the availability of burned pine habitats (Veblen et al. 2000), and the absence of regeneration and seedling establishment as a result of dams, water diversion, and livestock grazing have reduced cottonwood riparian habitats (Scott et al. 1997, Rumble and Gobeille 2004). Although aspen comprises a small proportion of the landscape in the West, it supports some of the highest diversity of flora and fauna (Hansen et al. 2000). Aspen habitat has declined by as much as 90% in some regions of the West due to heavy grazing by domestic and wild ungulates and fire suppression (Bartos and Campbell 1998, Bartos 2001). The dominant land use of aspen in the West is livestock grazing (West 1983), and heavy grazing can reduce or eliminate aspen recruitment (Sampson 1919, Fitzgerald and Bailey 1984, Bailey et al. 1990). Many aspen stands in the Intermountain West are composed of older trees in advanced states of decay, and many stands are beginning to decline (Mueggler 1989). Thus, the longevity of aspen stands in the Intermountain Region and the potential nest trees available to Lewis's Woodpeckers and other cavity-nesting species may be at risk.

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CHAPTER 3.

INFLUENCES OF LIVESTOCK GRAZING ON
BREEDING BIRD DENSITIES AND THEIR HABITATS IN
ASPEN RIPARIAN WOODLANDSIntroduction

Deciduous riparian woodlands are extremely limited in distribution throughout the arid western United States, comprising less than 1% of the total land area (Knopf et al. 1988), yet these habitats have a disproportionate value to breeding birds. Deciduous riparian woodlands support a higher density of breeding birds than any other habitat in the western United States (Carothers et al. 1974, Knopf et al. 1988, Dobkin 1994, Saab et al. 1995). Over 50% of western bird species breed primarily or exclusively in deciduous riparian habitats (Tewksbury et al. 2002). Several land use practices including dams, conversion of land near riparian areas to agricultural and urban complexes, and livestock grazing have caused degradation of riparian areas throughout the West, limiting the abundance and distribution of bird species dependent upon these habitats (Saab et al. 1995, Saab 1999, Tewksbury et al. 2002).

The impacts of livestock grazing on riparian areas have received considerable attention in recent decades, and livestock grazing is likely the most contentious issue confronting public land managers in the western U. S. Livestock grazing is the most common land use in portions of the West, particularly in the semiarid Intermountain sagebrush steppe (West 1983). In 2003 alone, nearly 219,000 cattle and over 457,000 sheep grazed National Forest land in the Intermountain Region (USDA Forest Service

Range Management 2004). Riparian areas are particularly important to livestock operations in semiarid regions because they are easily accessible and provide high quality forage and reliable sources of water and shade (Kauffman and Krueger 1984). Studies examining the effects of livestock grazing on riparian avian communities have focused on cattle grazing, while the influences of sheep grazing have been largely ignored. Yet, sheep and cattle can have very different impacts on riparian vegetation (Platts 1982, Ruyle and Bowns 1985). Sheep are typically herded and are grazed in upland areas more often than cattle. However, sheep spend considerable time grazing in riparian areas, particularly in late summer when temperatures are highest and much of the upland vegetation has dried (Platts 1982, Glimp and Swanson 1994). Sheep also generally forage upon woody plants and forbs more often than cattle (Platts 1982). Cattle prefer herbaceous vegetation, but as herbaceous vegetation dries or becomes too short for cattle to grasp, cattle begin to forage upon woody vegetation such as willows (*Salix* spp.) and tree seedlings (Hall and Bryant 1995). Although pastures are comprised of mainly upland areas, cattle spend a disproportionate amount of time in the riparian zone, particularly during warmer months (Roath and Krueger 1982, Goodman et al. 1989). Moderate slopes, shade, increased forage, and reliable water sources provided by riparian zones are features influencing increased riparian use by cattle during late summer (Marlow and Pogacnik 1986).

In the Intermountain Region, aspen riparian woodlands are considered prime livestock summer range (Sampson 1919). Aspen is the predominant deciduous tree species in riparian areas, occurring in small stands along streams and meadows and in

snowmelt drainages on mountain slopes (Mueggler 1985). These woodlands have diverse and complex plant communities (Mueggler 1988, Campbell and Bartos 2001) with aboveground biomass considerably higher than other habitats (Hansen et al. 2000). The understory of healthy aspen stands are multilayered, consisting of medium-height shrubs and tall forbs, but intensive grazing can reduce plant species diversity and stand complexity, leading to an understory of unpalatable species composed of weedy annuals (Mueggler 1985). Isolated aspen patches in shrubsteppe regions and riparian aspen are highly impacted by grazing because livestock concentrate in these areas for shade and bedding sites (Debyle 1985), potentially reducing or eliminating aspen regeneration (Sampson 1919, Fitzgerald and Bailey 1984, Bailey et al. 1990). Indeed, grazing by both livestock and wild ungulates has been implicated in the decline of aspen woodlands throughout the West (Schier 1975, Mueggler 1988, Kay 1997, Bartos and Campbell 1998).

In general, birds respond to the impacts of livestock on vegetation rather than directly to the presence of livestock (Bock and Webb 1984). Because of their reliance on riparian habitats, many western landbirds are particularly susceptible to population declines due to habitat degradation (Saab et al. 1995, Tewksbury et al. 2002), and many riparian bird species in the West are experiencing regional declines (Sauer et al. 2004). Open-cup nesting birds are the most affected because nesting substrates used by these species often consist of the lower vegetation layers that are directly impacted by grazing (Taylor and Littlefield 1986, Saab et al. 1995, Tewksbury et al. 2002, Krueper et al. 2003). Canopy and cavity-nesting birds may escape the short-term effects of grazing, yet

over the long term reduced regeneration rates and canopy recruitment may affect tree stand longevity and subsequent nest-site availability (Dobkin et al. 1995, Saab et al. 1995, Tewksbury et al. 2002). Influences of livestock grazing on vegetation structure and plant species composition not only alters the availability of nesting substrate but can also influence the abundance and composition of arthropod prey (Dennis et al. 1998). Additionally, many riparian bird species, particularly open-cup nesting long-distance migrants, are vulnerable to brood parasitism by the Brown-headed Cowbird (*Molothrus ater*), a species that tends to increase in the presence of livestock (Saab et al. 1995, Goguen and Mathews 1999).

In May 2003, we initiated a study to assess the effects of sheep and cattle grazing on populations and habitats of breeding birds in aspen riparian woodlands of south-central Idaho. We set out to answer four questions: 1) How does riparian vegetation differ between sheep- and cattle-grazed areas? 2) Do current levels of sheep and cattle grazing allow successful aspen stand regeneration? 3) Does the distribution of aspen diameter size classes differ between sheep- and cattle-grazed aspen riparian woodlands? 4) Do breeding bird densities and species composition differ between sheep- and cattle-grazed aspen riparian woodlands? Here, we present breeding bird densities and vegetation measurements in aspen riparian woodlands in the context of current and historic grazing regimes. We expected that bird species composition and densities would differ between sheep- and cattle-grazed areas, depending upon their nesting and foraging guild. Specifically, we predicted cattle-grazed areas would have reduced ground cover vegetation and riparian shrub densities, resulting in lower densities of ground- and shrub-

nesting bird species. Conversely, we expected sheep-grazed areas would have reduced aspen regeneration and subsequently lower densities of large diameter aspen, resulting in lower densities of canopy and cavity-nesting bird species.

Methods

Study Area

The study occurred on the Pioneer Mountain Ranch in Butte and Blaine Counties, Idaho in the foothills of the Pioneer Mountains, north of the Snake River Plain. This portion of the state is a mix of private and public lands used primarily for cattle and sheep grazing. Elevation of the study area varies from 1,600 – 2,000 m, and vegetation is characteristic of the Intermountain sagebrush steppe ecosystem (West 1983). The landscape is composed of narrow riparian zones ($\leq 50 - 100$ m in width) dominated by aspen, thinleaf alder (*Alnus incana*), willow (*Salix* spp.), mountain snowberry (*Symphoricarpos oreophilus*), and rose (*Rosa* spp.), surrounded by a matrix of sagebrush steppe (*Artemisia* spp.). Black cottonwood (*P. trichocarpa*) also occurs along some streams. Small stands of aspen also occur on sideslopes and in snowmelt pockets at higher elevations of some drainages. Riparian aspen habitat is very limited, comprising < 7% (900 ha) of the study area (14,000 ha). Aspen communities in these areas are considered “stable” due to the absence of conifers and natural disturbance such as fire (Mueggler and Campbell 1982, Mueggler 1988).

We chose four study sites; two of the sites were grazed by cattle, and two were grazed by sheep. Each study site was comprised of approximately 5 km of linear riparian

habitat. Livestock grazing has occurred on each study site for at least 100 years. From at least 1994 until 2002, each cattle-grazed site had approximately 200 animal units (AUs) in the form of cow/calf pairs. This number was reduced to approximately 100 AUs per site in 2002 and remained at this number throughout the study. Each cattle-grazed site was composed of two to three pastures ranging from 214 – 1,245 ha. Each pasture consisted primarily of upland shrubsteppe vegetation with relatively steep (30 - 40°) slopes. The riparian portion of each pasture was relatively flat and comprised < 2 – 6% of the total area of each pasture. Cattle were moved onto these pastures in late April or early May and remained until late September when they were moved onto irrigated pastures. All cattle were rotated from pasture to pasture on each site, and some pastures were not grazed during each growing season. Cattle grazed individual pastures continuously (i.e., they were unrestricted within the pasture), but the length of the grazing period as well as the timing of grazing on each pasture varied annually (Table 3.1). The two sheep-grazed sites were located on one large (1,500 ha) allotment, of which approximately 8% was aspen riparian woodlands. Annual sheep stocking densities have been similar for at least the past 10 years. Each sheep-grazed site had approximately 900 ewe/lamb pairs (270 AUs) from early June to early July, at which point the lambs were shipped. After shipping, two or more bands were merged resulting in a total band size of approximately 1,200 ewes (240 AUs), and these ewes grazed the study sites from early July until August. These bands were intensively herded, and the exact number of days sheep spent in any one area was unknown. We were unable to find nearby study sites

with comparable habitat characteristics in ungrazed aspen riparian woodlands, thus we were only able to compare cattle- and sheep-grazed sites.

Table 3.1. Percent riparian habitat, grazing period, and stocking rates for cattle-grazed pastures on the Pioneer Mountain Ranch, Idaho, 2003-2004. An animal unit month (AUM) represents the amount of dry forage consumed by one cow/calf pair in one month.

Pasture	Riparian habitat (%)	2003			2004		
		Grazing period	# of cow/calf pairs	AUMs	Grazing period	# of cow/calf pairs	AUMs
1	2.3	27 May - 11 June	92	48.4	30 Apr - 16 May	127	71.0
					6 July - 16 July	127	45.9
2	1.6	10 Sep -22 Sep	63	26.9	17 May - 23 May	127	29.2
3	4.4	rested	0	0.0	1 June - 13 June	127	45.9
4	3.5	25 July - 25 Aug	89	23.4	rested	0	0.0
5	6.2	26 Aug - 2 Sep	89	93.6	rested	0	0.0

Vegetation Measurements

We established 30 points per grazing treatment (15 per study site) within riparian vegetation to conduct point transect surveys for breeding birds. We recorded all bird species detected within a 50-m radius of each point (see Point Transect Surveys, below). We placed survey points ≥ 200 m apart to reduce the likelihood that the same bird was detected at different points. We determined the beginning of each transect based on pasture or allotment boundaries and placed subsequent points randomly within the riparian zone. We measured vegetation characteristics at all 60 points once during the study from mid-July through August. Measurements and plot design were based on BBIRD protocol (Martin et al. 1997) with some modifications (Table 3.2). We established three vegetation plots within each 50-m radius survey area (Figure 3.1). We

centered the first plot on the point and established two satellite vegetation plots in opposite directions 30 m from the point along the riparian zone. Each plot consisted of an 11.3-m radius circular plot with a nested 5-m radius circular subplot centered on the point.

Table 3.2. Description of habitat variables measured at each vegetation point.

Variable	Measurement/Characteristic	Description
Ground cover	% Grass	Mean of 40 point-intercept estimates taken in four cardinal directions every 0.5 m within 5-m radius subplot.
	% Native forb	
	% Bare ground	
	% Weed cover	
Litter depth	Litter depth (cm)	Mean of 12 litter depth (cm) measurements taken in four cardinal directions every 2 m within 5-m radius subplot.
Shrubs	Total number of woody stems ≥ 50 cm in height by species and size class	Live stems <2.5 , >2.5 -5, >5 -8 cm within 5-m radius subplot.
Aspen suckers	Live aspen suckers	Live stems < 2 m in height within 11.3-m radius plot.
Aspen (live trees and snags)	Total number ≥ 1.37 m	Within 11.3 m radius plot.
	Diameter at breast height (DBH)	Diameter tape; Size categories 2.5–5 cm dbh; > 5 –8 cm dbh; > 8 –12 cm dbh; > 12 –20 cm dbh; > 20 –30 cm dbh; > 30 cm dbh.
	Height	Clinometer estimate.

Within each 5-m radius subplot, we measured shrub densities by counting all woody stems between 0.5 and < 1.37 m in height. All shrubs were recorded to species. We used a point-intercept method to estimate ground cover by placing a sharpened dowel every 0.5 m from the center of the plot in four perpendicular directions for a total of 40 measurements. All cover types touching the dowel ≤ 1.0 m in height were recorded. We estimated percent cover of each cover type by totaling the number of times the dowel hit

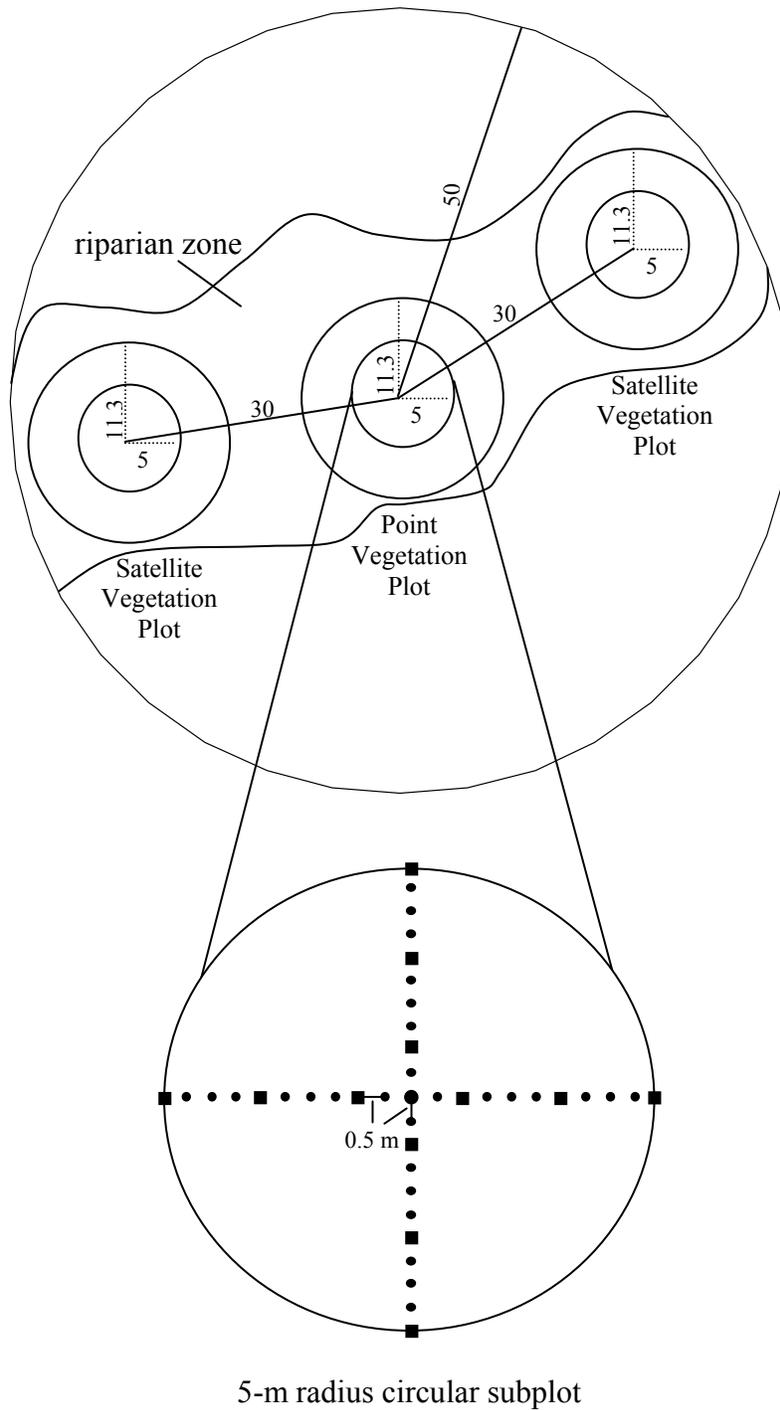
a cover type out of 40 measurements. We also measured litter depth (cm) using this same method at 2 m intervals. Within the entire 11.3-m plot, we tallied live and dead aspen ≥ 1.37 m in height and ≥ 2.5 cm in diameter and measured diameter at breast height (dbh) and tree height. Values of all vegetation measurements were averaged over the three plots to obtain a single value for each point.

To assess aspen regeneration, we counted the number of aspen suckers (aspen < 2 m in height and < 2.5 cm in diameter) within each 11.3-m radius plot. The number of aspen suckers in an aging stand may be an index to the longevity of that stand (Mueggler 1989). Sheep and cattle can graze to a height of 1.2 and 1.8 m respectively, and aspen > 2 m in height are generally beyond the reach of domestic livestock (Sampson 1919). Within the 5-m radius subplot at point vegetation plots only, we tallied both live and dead suckers and measured height and total number of stems (live and dead) at the base of each sucker (Hessl and Graumlich 2002). Suckers do not produce lateral branches until their second year of growth (Jones and Schier 1985), so suckers with multiple stems are typically the result of browsing. Suckers send up a new shoot directly below any browsed terminal (Debyle 1985); however, we only counted stems that occurred ≤ 10 cm above ground to differentiate them from lateral branches.

Point Transect Surveys

Field techniques were based on Reynolds et al. (1980), Ralph et al. (1993), and Saab (1999) with some modifications. We conducted three visits at each point between 1 June and 10 July during the breeding seasons of 2003 – 2004. We began surveys within 30 minutes of sunrise and completed all surveys by 10:00. Each visit totaled eight minutes in length, but we recorded detections in three separate time periods (3, 2, and 3 minutes) to correspond with other data taken concurrently in the area. For the initial visit at each study site, we randomly selected the point at which to begin the survey. Successive counts during the season were conducted in reverse order (e.g., points initially visited in order of #1 – #15 were revisited in order #15 – #1) to reduce detection biases associated with time of day (e.g., dawn vs. mid-morning). We maintained this order throughout the study and visited each point on the same day each season. We did not conduct surveys during periods of inclement weather (e.g., rain and high winds). We recorded all bird species seen and heard and estimated their distance within 50 m of the point based on their location when first detected. Because most birds were detected aurally, estimating precise distances was difficult. Consequently, we recorded detections in five distance categories: 0–10 m; > 10–20 m; > 20–30 m; > 30–40 m; and > 40–50 m from the point. To assure accurate distance estimations, the observer (K. R. Newlon) practiced estimating the distance to flags placed at varying distances at the beginning of each breeding season before point surveys were initiated. Birds detected > 50 m from the point or detected while flying over the point were not used to estimate densities but were

Figure 3.1. Schematic diagram of point vegetation plot (with distances in meters) and corresponding satellite vegetation plots along the riparian zone with expanded view of 5-m radius subplot. Demarcations on 5-m radius subplot represent ground cover (●) and litter depth (■) sampling locations.



recorded and noted for a complete species list (Appendix A). We recorded the following for each individual detected: distance from point, sex, method of identification (V=visual, S=song, C=call, T=territorial, VC=visual/call, VS=visual song), number detected, and vegetation type associated with each detection (aspen, sagebrush, riparian). We also recorded air temperature, Beaufort wind score, and cloud cover before the start of each point survey and noted bird species observed before and after each survey as well as during travel between points.

Data Analysis

Vegetation measurements. We used multiple analysis of variance (MANOVA) with Hotelling's T^2 to assess overall differences in vegetation characteristics between grazing treatments and separate *a posteriori* univariate *F* tests to assess the effect of grazing treatment (cattle or sheep) on individual vegetation variables using PROC GLM in Program SAS (SAS Institute, Inc. 2000). Our dependent variables were bare ground (%), grass cover (%), forb cover (%), nonnative weed cover (%), litter depth (cm), number of woody stems (shrubs), number of aspen suckers, and number of live aspen (≥ 2.5 cm dbh, ≥ 1.37 m in height) with grazing treatment (cattle-grazed vs. sheep-grazed) as a factor. To test for multicollinearity among vegetation variables, we calculated Pearson correlation coefficients (Table 3.3). To compare shrub species composition between grazing treatments, we estimated the differences in mean shrub density (i.e., the effect size) and corresponding 95% confidence intervals for the most common shrubs: sagebrush, thinleaf alder, chokecherry (*Prunus virginiana*), currant (*Ribes* spp.), rose, willow, and mountain snowberry. We provide effect sizes because they allow us to

estimate the magnitude of the difference between nest-site and random plot habitat covariates (Anderson et al. 2001).

We compared indices of aspen regeneration between grazing treatments by estimating differences in mean live aspen sucker density, mean live sucker height, and mean number of stems per live sucker and their corresponding 95% confidence intervals. We used a χ^2 test of independence to investigate whether or not grazing treatment influenced the distribution of aspen diameter size classes.

Table 3.3. Pearson correlation coefficients among vegetation variables measured at point transects in cattle- and sheep-grazed aspen riparian woodlands, Pioneer Mountain Ranch, Idaho.

	Bare ground	Grass (%)	Forb (%)	Weed (%)	Litter depth (cm)	Number of woody stems	Number of aspen suckers	Number of aspen
Bare ground	1.00	-0.34	-0.35	-0.06	-0.53	-0.11	0.07	-0.05
Grass (%)		1.00	0.37	0.43	-0.04	-0.22	0.20	0.03
Forb (%)			1.00	0.05	-0.01	0.16	-0.06	-0.19
Weed (%)				1.00	0.00	-0.23	0.10	-0.26
Litter depth (cm)					1.00	0.30	-0.15	-0.03
Number of woody stems						1.00	-0.51	-0.37
Number of aspen suckers							1.00	0.54
Number of aspen								1.00

Point transect surveys. To assure adequate sample sizes in each grazing treatment, we pooled data from 2003 and 2004. Because the same observer conducted all point transect surveys, we assumed that detection probability did not differ between years. We averaged the number of detections at each point over the three survey visits because we assumed the detections during one visit were not independent from detections during another visit. For example, if a point were located within the territory of a male

Lazuli Bunting (*Passerina amoena*), then the same individual would likely be detected during all three visits (assuming nothing prevented the bird from maintaining that territory throughout the breeding season). Although we recorded females in the field, we did not include them in the analysis because their detection probability is much less than that of males. We also did not include any detection for which the bird could not be sexed reliably.

Conducting surveys in riparian habitats can be problematic due to their linear nature and potential edge effects that can result in biased density estimates (Buckland et al. 2001). In other words, the probability of detecting some species will differ dramatically within riparian vegetation versus at the edge of the riparian zone or in adjacent habitat. The very narrow character of the riparian zones in our study area and subsequent abrupt habitat edge are problematic in that species that occur in both habitats may have different habitat-specific detection probabilities. We attempted to alleviate this problem by only including individuals that we detected within riparian habitat into our analyses.

We estimated breeding bird densities for species with ≥ 60 detections in each grazing treatment using Program Distance 4.1 Release 2 (Thomas et al. 2004). To obtain reasonable density estimates, ≥ 60 observations are recommended (Buckland et al. 2001). Program Distance models the probability of detecting a bird as a function of the distance between the bird and the observer. This method accounts for a decrease in the probability of detecting a bird with increasing distance from the point. This approach has several key assumptions: 1) all birds located at the point are detected with certainty; 2) all birds are

detected at their initial location; and 3) distance estimates are correct (Buckland et al. 2001). A violation of assumption 2 can occur with increasing length of the survey period. As the length of the survey period increases, birds may move closer to the observer and in turn are more easily observed, or new birds may move into the survey area. Both events would result in an overestimation of density estimates (Buckland et al. 2001). To alleviate this problem, we used a “snapshot” approach (Buckland et al. 2001) and included only male birds detected during the first three-minute period of the survey to estimate densities. Thus, we estimated densities of males per hectare of aspen riparian woodland.

We modeled the probability of detection for species with ≥ 60 detections separately by grazing treatment using the multiple covariates distance sampling (MCDS) engine of Program Distance (Thomas et al. 2004). This engine allows the probability of detection to vary not only with distance from the point but also as a function of different covariates that may influence the probability of detection. MCDS allows detection probability to be modeled using two “key functions”, half-normal and hazard rate, which model the shape of the detection function (Buckland et al. 2001). Additional covariates are assumed to influence the rate at which detectability decreases with distance but not the shape of the detection function (Marques and Buckland 2003). We hypothesized that several habitat covariates (bare ground, grass cover, forb cover, number of aspen suckers, number of shrub stems, and number of live trees) might influence the detectability of bird species in the riparian zone. For each species, we developed several models of the detection function that included: 1) the key function only (half-normal or hazard rate), or

2) the key function with the addition of a single habitat covariate. Program Distance provides multiple methods (AIC, likelihood ratio tests, etc.) to select the most appropriate model of the detection function. We used AIC corrected for small sample size (AIC_c ; Burnham and Anderson 2002) and selected the model with the lowest AIC_c value to obtain density estimates for each species separately by grazing treatment. We compared density estimates between grazing treatments for species with ≥ 60 detections by estimating the differences in mean densities and corresponding 95% confidence intervals.

We were most interested in examining the effects of habitat covariates not only on the detection probabilities of bird species but also on their densities. However, standard methods such as generalized linear models do not take into account differences in detectability among species (Royle et al. 2004). Distance sampling techniques provide a way to examine the influence of covariates on detection probabilities; however, little research has focused on modeling covariates that affect density. A few analytical methods have been recently proposed (Hedley et al. 2004, Royle et al. 2004), but these methods have yet to be developed into easily tractable techniques.

Predictions

Increased use of the riparian zone by cattle can result in increased areas of bare ground and reduced herbaceous and litter cover due to trampling and soil compaction (Schulz and Leininger 1990, Popolizio et al. 1994). Season-long cattle grazing can also result in a shift in diet from herbaceous to woody vegetation (Hall and Bryant 1995, DelCurto et al. 2005). Thus, we predicted that cattle grazing would have a greater influence on the riparian zone (e.g., reduced herbaceous cover, shrub densities, and litter

depths, and increased bare ground). Conversely, we predicted sheep would have a weaker influence on these vegetation characteristics because they are intensively herded. However, sheep in our study area are often herded into aspen woodlands for short periods during the summer months because these areas provide the only available shade and bedding sites. This concentrated use results in periods of grazing that are short in duration but high intensity (Glimp and Swanson 1994). We predicted that this use coupled with their preference for aspen would result in short, multi-stemmed aspen suckers that occurred in low densities and few small diameter aspen (i.e., young trees) on sheep-grazed sites. We also predicted that historic sheep grazing would have reduced canopy recruitment, resulting in fewer live aspen of larger diameter size classes.

Differences in bird densities should reflect differences in habitat variables between the grazing treatments. We predicted that ground- and low-nesting bird species would have reduced densities in cattle-grazed sites in response to the influence of cattle on herbaceous ground cover and shrub densities. In contrast, canopy- and cavity-nesting bird species should have reduced densities in sheep-grazed sites due to lack of aspen regeneration and reduced canopy recruitment.

Results

Vegetation Measurements

Vegetation characteristics differed between grazing treatments (Hotelling's $T^2_{8,51} = 29.18$, approximate $F = 3.21$, $P = 0.005$). In particular, cattle-grazed sites had more bare ground ($F_{1,58} = 12.29$, $P < 0.001$) and less forb cover ($F_{1,58} = 5.57$, $P = 0.02$) than

sheep-grazed sites. Values of grass cover, weed cover, litter depth, shrub stem densities, and aspen densities were similar between grazing treatments but highly variable (Table 3.4). Although overall shrub stem densities were similar between grazing treatments, the species composition of shrubs differed (Table 3.5). Cattle-grazed sites averaged 90 (95% CI, 21.6 – 158.2) more snowberry stems per point, whereas sheep-grazed sites averaged 34 (95% CI, -1.9 – 69.9) more stems of willow species per point. In particular, the number of yellow willow (*S. lucida*) and coyote willow (*S. exigua*) stems was three times higher on sheep-grazed sites than cattle-grazed sites (1,632 and 545 stems, respectively).

Aspen sucker density varied widely from 0 – 8,500 suckers per hectare on both grazing treatments, but sheep-grazed sites averaged nearly 400 more aspen suckers per hectare than cattle-grazed sites (Table 3.6). The number of stems per sucker also varied widely (range 1 – 19 suckers), but suckers on both grazing treatments averaged 1.5 stems per sucker (Table 3.6). The proportion of suckers > 150 cm in height was low on both cattle- and sheep-grazed sites (19% and 13%, respectively), indicating that the proportion of suckers beyond the reach of livestock was low on both grazing treatments.

Suckers on cattle-grazed sites averaged 10.5 cm taller than suckers on sheep-grazed sites (Table 3.6). The distribution of aspen in each size class differed between grazing treatments ($\chi^2_5 = 114.94, P < 0.001$). Most aspen on cattle-grazed sites were in the smallest diameter size class (2.5 – 5 cm), and trees in the larger diameter size classes were distributed evenly (Figure 3.2). Although cattle-grazed site had more small aspen, sheep-grazed sites had more aspen in all other size classes and nearly two to four times more aspen in the medium diameter size classes (> 5 – 20 cm).

Table 3.4. Mean values (± 1 SD) per 50-m radius point transect survey for vegetation variables in cattle- and sheep-grazed aspen riparian woodlands, Pioneer Mountain Ranch, Idaho. Effect sizes and corresponding 95% confidence intervals represent estimated differences in mean values between grazing treatments. *P*-values are from *a posteriori* univariate *F*-tests.

Variable	Cattle-grazed	Sheep-grazed	<i>F</i>	<i>P</i>	Effect size	
					$\bar{x}_{\text{Cattle}} - \bar{x}_{\text{Sheep}}$	95% CI
Bare ground (%)	25.4 \pm 10.5	15.7 \pm 11.1	12.29	<0.001	9.8	4.3 - 15.2
Forb cover (%)	8.1 \pm 6.1	14.3 \pm 12.8	5.57	0.02	-6.1	-11.2 - -1.0
Grass cover (%)	35.1 \pm 13.3	39.4 \pm 23.8	0.77	0.38	-4.4	-14.1 - 5.4
Weed cover (%)	7.1 \pm 8.5	4.4 \pm 7.0	1.72	0.19	2.6	-1.3 - 6.6
Litter depth (cm)	3.7 \pm 1.2	3.7 \pm 1.1	0.01	0.91	0.0	-0.5 - 0.6
Aspen suckers	229 \pm 234	275 \pm 283	0.47	0.50	-46.0	-177.1 - 85.3
Shrubs (# stems)	317.6 \pm 219.7	276.7 \pm 184.2	0.61	0.44	41.0	-61.6 - 143.6
Aspen (# trees)	27.8 \pm 28.4	38.5 \pm 40.8	1.40	0.24	-10.7	-28.5 - 7.1

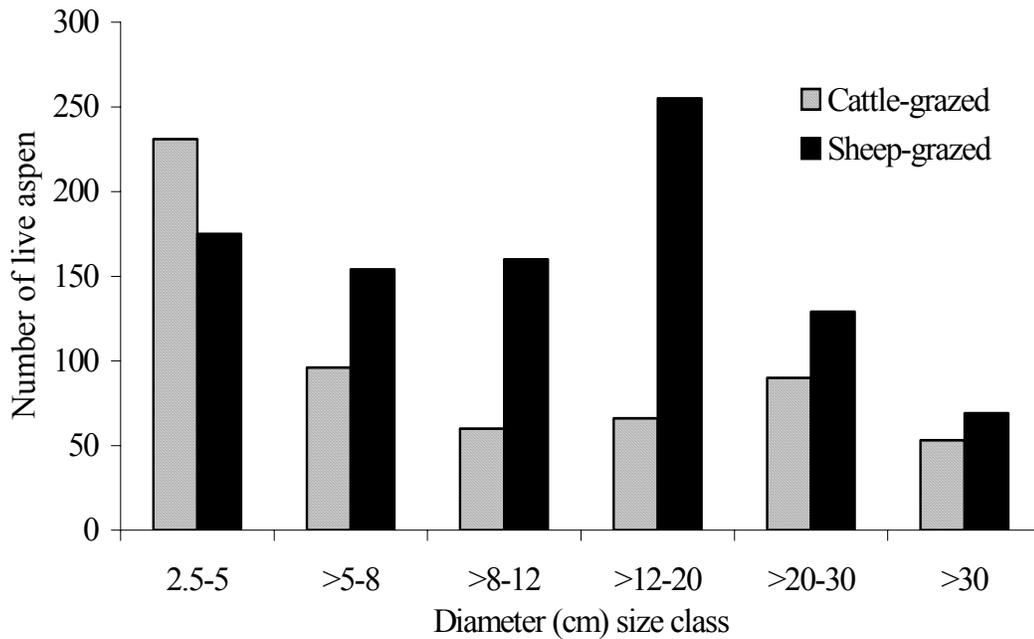
Table 3.5. Mean number of stems (± 1 SD) per 50-m radius point transect survey in cattle- and sheep-grazed aspen riparian woodlands, Pioneer Mountain Ranch, Idaho. Effect sizes and corresponding 95% confidence intervals represent estimated differences in mean values between grazing treatments.

	Cattle-grazed	Sheep-grazed	Effect size	
			$\bar{x}_{\text{Cattle}} - \bar{x}_{\text{Sheep}}$	95% CI
Thinleaf alder	36 \pm 39	43 \pm 56	-6.9	-31.4 - 17.5
Sagebrush spp.	71 \pm 79	82 \pm 106	-11.8	-59.0 - 35.4
Chokecherry	21 \pm 62	17 \pm 31	4.1	-20.8 - 29.1
Currant spp.	26 \pm 31	24 \pm 26	1.9	-12.5 - 16.3
Rose spp.	16 \pm 22	16 \pm 29	0.3	-12.9 - 13.4
Willow spp.	29 \pm 35	63 \pm 94	-34.0	-69.9 - 1.9
Mountain Snowberry	113 \pm 186	23 \pm 43	89.9	21.6 - 158.2

Table 3.6. Mean values (± 1 SD) for aspen regeneration indices, effect sizes, and corresponding 95% confidence intervals measured in cattle- and sheep-grazed aspen riparian woodlands, Pioneer Mountain Ranch, Idaho.

	Cattle-grazed	Sheep-grazed	Effect size	
			$\bar{x}_{\text{Cattle}} - \bar{x}_{\text{Sheep}}$	95% CI
Sucker density (#/ha)	1909 \pm 1948	2292 \pm 2355	-383	-1476 - 711
Number of stems per sucker	1.5 \pm 1.2	1.5 \pm 1.3	0.03	-0.1 - 0.1
Sucker height (cm)	80.2 \pm 49.4	69.7 \pm 44.7	10.5	5.5 - 15.5

Figure 3.2. Frequency distribution of aspen diameter size classes in cattle- and sheep-grazed aspen riparian woodlands, Pioneer Mountain Ranch, Idaho.



Point Transect Surveys

We recorded 2,397 detections in riparian habitat comprising 68 bird species during point transect surveys conducted from 1 June – 9 July of 2003 – 2004, 49 of which were observed on both grazing treatments (Appendix A). Over 90% of detections were aural, and 70% of these detections occurred during the first three minutes of the survey. We used 1,420 detections of 35 species to estimate breeding bird densities. Cattle-grazed sites had 180 more detections than sheep-grazed sites, yet five species (Warbling Vireo, Yellow Warbler, Song Sparrow, House Wren, and Lazuli Bunting) comprised 66 - 78% of the total detections on cattle- and sheep-grazed, respectively (Table 3.7). These species represent a range of nesting guilds from open-cup, ground and canopy nesters to cavity-nesting species (Table 3.8). Of these five species, all but the House Wren had \geq 60 detections per grazing treatment. Although House Wren had only 41 detections in the sheep-grazed treatment, we estimated density for this species because of the high number of detections ($n = 175$) in the cattle-grazed treatment.

Initial examination of histograms of our detection probabilities showed a spiked distribution for Lazuli Bunting, Warbling Vireo, and Yellow Warbler (i.e., most of the detections of these species occurred close to the point). Modeling the detection function for these three species using the hazard rate function resulted in unreasonable density estimates that were positively biased (Buckland et al. 2001). Thus, we modeled detection probability for these three species using only the half-normal function and both the hazard rate and half-normal functions for the other two species. Models incorporating a

habitat covariate received more support than models including the key function only for all species except Lazuli Bunting, although most models had a poor fit (Table 3.9).

Both House Wren and Song Sparrow had lower detection probabilities within the 50-m radius survey area on sheep-grazed sites, while the detection probabilities of the other species were similar between grazing treatments (Table 3.10). These two species also had the largest differences in mean density per hectare between treatments (Table 3.11). Song Sparrow, a ground nester, had higher densities in the sheep-grazed treatment, whereas House Wren, a cavity-nesting species, had much higher densities in the cattle-grazed treatment. Warbling Vireo, a mid- to high-canopy nester, and Yellow Warbler, a mid-shrub nester, each had higher densities in the sheep-grazed treatment, but the 95% confidence intervals around the estimated differences in their mean densities included 0. Densities of Lazuli Buntings, a low shrub nester, were similar between treatments.

Table 3.7. Number of detections for all male bird species detected within the first three minutes of point transect surveys conducted in cattle- and sheep-grazed aspen riparian woodlands, Pioneer Mountain Ranch, Idaho, 2003-2004.

Common Name	Scientific Name	Grazing treatment	
		Cattle-grazed	Sheep-grazed
House Wren	<i>Troglodytes aedon</i>	175	41
Yellow Warbler	<i>Dendroica petecha</i>	108	153
Warbling Vireo	<i>Vireo gilvus</i>	95	123
Lazuli Bunting	<i>Passerina amoena</i>	84	74
Song Sparrow	<i>Melospiza melodia</i>	65	91
Spotted Towhee	<i>Pipilo maculates</i>	49	0
Orange-crowned Warbler	<i>Vermivora celata</i>	31	5
Dusky Flycatcher	<i>Empidonax oberholseri</i>	30	19
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	28	5
American Robin	<i>Turdus migratorius</i>	27	13

Table 3.7. continued

Common name	Scientific name	Cattle-grazed	Sheep-grazed
MacGillivray's Warbler	<i>Oporornis tolmiei</i>	18	24
Western Wood-Pewee	<i>Contopus sordidulus</i>	15	5
Brown-headed Cowbird	<i>Molothrus ater</i>	15	2
Western Tanager	<i>Piranga ludoviciana</i>	9	8
Bullock's Oriole	<i>Icterus bullockii</i>	8	1
Black-capped Chickadee	<i>Poecile atricapilla</i>	7	0
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	6	12
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	6	1
American Goldfinch	<i>Carduelis tristis</i>	5	3
Willow Flycatcher	<i>Empidonax traillii</i>	3	13
Plumbeous Vireo	<i>Vireo plumbeus</i>	3	0
Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	2	14
Fox Sparrow	<i>Passerelia iliaca</i>	2	3
Western Meadowlark	<i>Sturnella neglecta</i>	2	1
Calliope's Hummingbird	<i>Stellula calliope</i>	2	0
Northern Flicker	<i>Colaptes auratus</i>	2	0
Blue Grouse	<i>Dendragapus obscurus</i>	1	2
Common Snipe	<i>Gallinago gallinago</i>	1	1
Hairy Woodpecker	<i>Picoides villosus</i>	1	0
Chipping Sparrow	<i>Spizella passerina</i>	0	3
Audubon's Warbler	<i>Dendroica coronata</i>	0	1
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	0	1
Vesper Sparrow	<i>Pooecetes gramineus</i>	0	1
Total Detections		800	620

Table 3.8. Nest vegetation layer and nest type for the five most commonly detected bird species in cattle- and sheep-grazed aspen riparian woodlands, Pioneer Mountain Ranch, Idaho, 2003-2004.

Species	Nest layer	Nest type	Foraging layer	Source
House Wren	Mid/upper canopy	Cavity	Ground/sub canopy	Johnson 1998
Lazuli Bunting	Low shrub	Open	Ground/low shrub	Greene et al. 1996
Song Sparrow	Ground/near ground	Open	Ground	Arcese et al. 2002
Warbling Vireo	Mid/upper canopy	Open	Canopy	Gardali and Ballard 2000
Yellow Warbler	Mid shrub	Open	Mid/upper canopy	Lowther et al. 1999

Table 3.9. Model selection results of detection functions for the five most commonly detected species in cattle- and sheep-grazed aspen riparian woodlands, Pioneer Mountain Ranch, Idaho, 2003–2004.

Species	Model selected	Goodness of fit		
		χ^2	df	<i>P</i>
House Wren	Half-normal + Live trees	4.72	2	0.09
Lazuli Bunting	Half-normal	25.35	1	<0.01
Song Sparrow	Half-normal + Forb cover	8.06	2	0.02
Warbling Vireo	Half-normal + Live trees	18.00	2	<0.01
Yellow Warbler	Half-normal + Live trees	24.65	2	0.00

Table 3.10. Probability (p) of detecting a male within a 50-m radius survey area and the effective detection radius (EDR) \pm 1 SE (95% CI) for males of the five most commonly detected bird species in cattle- and sheep-grazed aspen riparian woodlands, Idaho, 2003-2004. EDR is the radius within which the probability of detecting a given species is 100%.

Species	Cattle-grazed				Sheep-grazed			
	p	95% CI	EDR	95% CI	p	95% CI	EDR	95% CI
House Wren	0.43 \pm 0.03	0.38-0.49	32.83 \pm 0.99	30.94-34.84	0.35 \pm 0.05	0.26-0.46	29.49 \pm 2.03	25.66-33.90
Lazuli Bunting	0.42 \pm 0.04	0.33-0.51	32.08 \pm 1.70	28.87-35.64	0.41 \pm 0.04	0.33-0.51	32.08 \pm 1.70	28.89-35.64
Song Sparrow	0.43 \pm 0.04	0.36-0.52	32.94 \pm 1.57	29.96-36.22	0.32 \pm 0.03	0.26-0.39	28.15 \pm 1.42	25.48-31.11
Warbling Vireo	0.37 \pm 0.03	0.31-0.43	30.37 \pm 1.26	27.97-32.97	0.33 \pm 0.03	0.29-0.39	28.92 \pm 1.11	26.80-31.21
Yellow Warbler	0.33 \pm 0.03	0.28-0.39	28.69 \pm 1.16	26.48-31.07	0.33 \pm 0.02	0.29-0.37	28.58 \pm 0.99	26.69-30.60

Table 3.11. Mean density estimate (\hat{D}) of males per hectare of aspen riparian woodland (\pm 1 SE), effect sizes, and corresponding 95% confidence intervals for the five most commonly detected bird species in cattle- and sheep-grazed aspen riparian woodlands, Idaho, 2003-2004.

Species	\hat{D}		Effect size	
	Cattle-grazed	Sheep-grazed	$\hat{D}_{\text{Cattle}} - \hat{D}_{\text{Sheep}}$	95% CI
House Wren	2.87 \pm 0.36	0.83 \pm 0.22	2.04	1.21 - 2.87
Lazuli Bunting	1.44 \pm 0.24	1.27 \pm 0.23	0.17	-0.48 - 0.82
Song Sparrow	1.06 \pm 0.20	2.03 \pm 0.42	-0.97	-1.88 - -0.06
Warbling Vireo	1.82 \pm 0.32	2.60 \pm 0.37	-0.78	-1.74 - 0.18
Yellow Warbler	2.32 \pm 0.34	3.31 \pm 0.42	-0.99	-2.05 - 0.07

Discussion

Vegetation on cattle- and sheep-grazed sites differed most in terms of the amount bare ground, native forb cover, shrub species composition, and aspen tree densities. Supporting our predictions, cattle-grazed sites had more bare ground and reduced herbaceous cover. Cattle that graze into late summer often spend a disproportionate amount of time in the riparian zone (Roath and Krueger 1982, Gillen et al. 1985, Marlow and Pogacnik 1986), and use of this area is particularly high if the surrounding habitat is composed of steep slopes and xeric vegetation (Skovlin 1984, Clary and Medin 1990). Increased bare ground as a result of trampling and hoof action by cattle is commonly observed in riparian areas (Chaney et al. 1990). The decrease in native forbs on cattle-grazed sites and greater percent weed cover may indicate a conversion from native perennial species to nonnative annual species such as field pennycress (*Thlapsi arvense*) and dandelion (*Taraxecum officinale*). Such a conversion to weedy annual plant species is typical in riparian areas influenced by long-term cattle grazing (Mueggler 1985, Popolizio et al. 1994). We also expected to observe lower amounts of grass and litter on cattle-grazed sites as several other studies have noted a decrease in these characteristics in cattle-grazed riparian areas (Schulz and Leininger 1990, Popolizio et al. 1994, Kay and Bartos 2000). However, values of grass and litter were similar between grazing treatments. Similarities in grass cover were surprising given the preferential grazing of grasses by cattle. Although we did not quantify the presence of individual grass species, exotic grass species such as cheatgrass (*Bromus tectorum*) and Kentucky bluegrass (*Poa pratensis*) were prevalent. These and other exotic grass species are highly competitive

and have replaced native caespitose grasses such as Idaho fescue (*Festuca idahoensis*), and the increased bare ground on cattle-grazed sites creates ideal conditions for their establishment (Roath and Krueger 1982, Kauffman et al. 1983, Schulz and Leininger 1990).

Although we expected cattle-grazed sites to have lower shrub stem densities, we observed similar densities in both grazing treatments. We did, however, observe differences in the composition of shrub species between grazing treatments. Mountain snowberry comprised more than 35% of total stem densities on cattle-grazed sites while willow species made up less than 10%. The differences in densities of mountain snowberry and willow species may reflect historic season-long cattle grazing. Snowberry tends to increase with cattle grazing and is unpalatable to cattle (Fitzgerald and Bailey 1984, Fitzgerald et al. 1986, Bailey et al. 1990). Conversely, several studies have observed a decline in willow densities in the presence of season-long or late-season cattle grazing (Kauffman et al. 1983, Schulz and Leininger 1990, Sedgwick and Knopf 1991, DelCurto et al. 2005). We found that willow densities, particularly densities of coyote (*S. exigua*) and yellow willow (*S. lutea*), were three to four times higher on sheep-grazed sites. The potential influence of recent reductions in cattle stocking densities on the riparian shrub community is unknown. One recent study found willow canopy cover, height, and stem densities increased with a reduction in cattle numbers, but values were always higher in areas where cattle were excluded (Holland et al. 2005).

We expected to find lower aspen sucker and tree densities on sheep-grazed sites because sheep preferentially browse aspen, yet we observed higher densities of both

aspen suckers and trees on these sites. Reduced aspen regeneration and subsequent canopy recruitment may have been reduced on cattle-grazed sites due to historic season-long cattle grazing, and mid- to late-season cattle grazing has been used to control aspen regeneration in some regions (Fitzgerald and Bailey 1984, Fitzgerald et al. 1986). We also expected to find a higher incidence of aspen sucker browsing on sheep-grazed sites. In general, the majority of aspen suckers were single-stemmed on both grazing treatments, indicating most suckers had not been browsed. We observed most multi-stemmed aspen suckers in areas of concentrated use such as creek crossings and sheep trailing sites. Aspen sucker densities on both grazing treatments are within the range of densities reported for healthy aspen stands elsewhere in the western U.S. (Schier 1975, Bartos and Mueggler 1982), suggesting that aspen riparian woodlands in our study area have the potential to successfully replace themselves. However, aspen suckers often arise in clumps, and aspen sucker density may give an inflated estimate of sucker production because sucker clumps are not uniformly distributed across the landscape. Instead, these clumps arise in the vicinity of residual trees where root density is highest (Schier 1975). We counted all suckers within a clump, so sucker density may also give an inflated estimate of potential canopy recruitment because only one of these suckers will develop into a mature tree (Schier 1975, Frey et al. 2003).

Aspen diameter is moderately correlated with age ($R^2 = 0.42 - 0.72$) throughout our study area (Newlon, unpublished), thus the distribution of aspen diameter size classes suggests aspen in these woodlands are multi-aged. Such multi-aged stands indicate successful recruitment of trees into the canopy, even in the presence of historic livestock

grazing. Contrary to our predictions, sheep-grazed sites had more aspen in all but the smallest diameter (2.5 – 5 cm) size class, suggesting canopy recruitment may be greater on these sites. In multi-aged stands, gaps in the canopy produced by the death of older trees allow for increased sucker production, maintaining the multi-aged nature of the stand (Mueggler 1989).

We attempted to make grazing treatments as comparable as possible by choosing study sites with similar vegetation, elevation, stocking rates, and timing of grazing. However, we almost certainly detected differences in vegetation characteristics that may not be directly attributable to livestock grazing. In particular, aspen regeneration and tree density is also a product of several microsite characteristics, such as soil type, slope, stand integrity and vigor, and genetic differences (Frey et al. 2003). We also cannot overlook the drought conditions throughout our study area. We measured vegetation during the fifth and sixth year of an extreme drought (National Climatic Data Center 2004), and this drought has certainly had an influence on herbaceous and woody plant growth as well as aspen regeneration. Additionally, the lack of available ungrazed control sites further complicates our ability to relate observed differences in vegetation characteristics solely to differences in grazing regimes.

In general, estimated breeding bird densities in these aspen riparian woodlands corresponded with observed differences in vegetation between the grazing treatments. The species that breed primarily or exclusively in riparian habitats (Song Sparrow, Yellow Warbler, and Warbling Vireo) all had higher densities in sheep-grazed sites. As we expected, density of the ground-nesting and ground-foraging Song Sparrow on sheep-

grazed sites was nearly twice that of cattle-grazed sites. This species requires areas of streamside vegetation, particularly dense herbaceous cover, for concealment during nesting and foraging (Arcese et al. 2002). Song Sparrow generally decreases with cattle grazing (Saab et al. 1995, Tewksbury et al. 2002, Krueper et al. 2003), and some local populations of this species have been eliminated altogether in grazed riparian areas (Arcese et al. 2002). Conversely, the cavity-nesting House Wren occurred on cattle-grazed sites at densities twice that of sheep-grazed sites. Although this species is a specialist in the sense that it requires cavities for nesting, the House Wren breeds in a wide variety of habitats with a deciduous overstory component, selecting nest sites with an open understory (Johnson 1998), and often increases in the presence of cattle grazing (Saab et al. 1995, Tewksbury et al. 2002). Yellow Warbler, a mid-shrub nesting species, relies on dense willows for nesting and foraging, and densities of this species can increase dramatically with the exclusion of cattle (Taylor and Littlefield 1986, Ohmart 1994, Krueper et al. 2003). Warbling Vireo, a canopy-nesting species, requires a dense deciduous canopy, although it appears to be less selective in terms of understory structure and composition (Gardali and Ballard 2000). Densities of the Lazuli Bunting, a low-shrub nesting species, were similar in both grazing treatments. This species breeds in a wide variety of brushy habitats from riparian areas to arid, shrubby slopes (Greene et al. 1996), and we frequently heard Lazuli Buntings singing from shrubsteppe habitat.

Clearly there will be tradeoffs when attempting to manage for multiple species. Of the species we examined, those most closely associated with riparian habitats had higher densities on sheep-grazed sites, yet other riparian associated species we detected

during point transect surveys (Bullock's Oriole, Dusky Flycatcher, Western Tanager, Lewis's Woodpecker) have been found to increase in riparian woodlands grazed by cattle (Saab et al. 1995, Tewksbury et al. 2002, Earnst et al. 2004, Newlon 2005, Chapter 2). Conversely, other species commonly observed in riparian habitats of the western U.S. were absent from our study area. Most of these species are ground- and low-shrub nesters such as Veery (*Catharus fuscescens*), Yellow-breasted Chat, and Gray Catbird (*Dumetella carolinensis*). These species are known to occur in nearby ungrazed riparian areas near our study area (Newlon, unpublished report) and are associated with areas of dense willow shrub cover (Gray Catbird and Veery) or high herbaceous cover (Yellow-breasted Chat) (Saab 1999).

Of course, densities of these species are not necessarily indicators of suitable breeding habitat (Van Horne 1983, Brawn and Robinson 1996), particularly if those habitats are influenced by anthropogenic disturbances (Bock and Jones 2004). This disparity can be even more pronounced if those disturbances have happened relatively recently, and species have not had sufficient time to adapt (e.g., Knick and Rotenberry 2000, Misenhelter and Rotenberry 2000). One such alteration brought about by forest clearing for agriculture and livestock grazing is the relatively recent (early 1900s) dispersal of the Brown-headed Cowbird into the western U.S. (Lowther 1993). All five species for which we estimated densities are known hosts of this brood parasite (Friedmann and Kiff 1985); however, the four open-cup nesting species are the most frequent hosts. Declines of these species have been attributed, in part, to reduced

reproductive success due to increased rates of parasitism (Greene et al. 1996, Lowther et al. 1998, Gardali and Ballard 2000, Arcese et al. 2002).

Management Implications

Our results indicate that cattle- and sheep-grazed aspen riparian woodlands differed most in terms of ground cover (bare ground and forb cover), shrub species composition, and distribution of aspen diameter size classes. Cattle grazing during the summer months, particularly mid- and late-season grazing (July – September), may be most detrimental to the integrity of riparian areas, particularly when implemented year after year (Kinch 1989). In the absence of complete exclusion, reducing the amount of days grazed during this period may lessen the influence on woody vegetation. Actively herding cattle away from riparian areas, particularly during the hottest part of the day, may also help balance the distribution of livestock throughout the pasture (DelCurto et al. 2005). Grazing management strategies have typically been developed to maintain upland vegetation in order to maximize forage production (Platts 1982, DelCurto et al. 2005), yet upland and riparian areas require different management approaches in terms of stocking densities and timing. Although herding reduces the overall influence of sheep on riparian vegetation, sheep trails and bedding sites as well as herder campsites are often located in sensitive riparian areas. In our study area, the same trails and campsites have been used for over a decade. Herder campsites may be considered “sacrifice” areas, whereas sheep trails could be moved to nearby upland areas. Herders could also limit the distribution of

bedding sites to reduce their overall impact on the riparian zone (Glimp and Swanson 1994).

The disproportionate value of riparian areas in the semiarid West to multiple interests has resulted in increased awareness of the need to conserve these areas for wildlife as well as to develop sustainable management strategies. Although much work has been devoted to documenting the effects of livestock on riparian vegetation, few studies have examined the long-term dynamics of these systems (see Dobkin et al. 1998, Krueper et al. 2003, Earnst et al. 2004). Our work provides a basis for the establishment of a long-term monitoring program, and continued surveys would provide data on breeding bird responses to changing livestock grazing regimes and offer insights into which regimes are most compatible with the native bird community. Nearly 40% of the 35 species used in our analysis are listed as high priority breeding bird species by Idaho Partners in Flight (Ritter 2000), signifying the need for continued monitoring of breeding bird populations in this habitat. Information on the abundance and composition of the breeding bird community may also provide a useful measure of the ecological integrity of aspen riparian woodlands in south-central Idaho (cf. Bryce et al. 2002, Rich 2002).

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CHAPTER 4.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

The limited distribution of aspen woodlands, as well as their precipitous decline, has been the focus of several studies (e.g., Schier 1975, Mueggler 1989, Kay 1997, Bartos and Campbell 1998), and the value of this habitat to breeding birds is well known (Finch and Reynolds 1987, Dobkin et al. 1995, Martin and Eadie 1999, Griffis-Kyle and Beier 2003, Martin et al. 2004). The decline of aspen has, in part, been attributed to livestock grazing (DeByle 1985, Mueggler 1989, Kay 1997). Thus, we examined the response of several breeding bird species to aspen riparian woodlands influenced by sheep and cattle grazing.

Over the three years of our study, we found that several microhabitat features influenced Lewis's Woodpecker nest-site selection (Chapter 2). In particular, Lewis's Woodpecker selected trees that were larger in diameter than random non-nest trees, and nest sites that were surrounded by more trees, fewer woody stems, and less bare ground than random non-nest plots. Additionally, Lewis's Woodpecker placed nearly four times more nests in cattle-grazed sites than sheep-grazed sites. Factors that we did not measure such as vegetation structure and plant species composition may have differed between these two grazing treatments, influencing arthropod diversity and abundance (Dennis et al. 1998, Brose 2003), and subsequently, the selection of nest sites by Lewis's Woodpecker. Further study of the indirect effects of livestock grazing on arthropod numbers and subsequent prey availability for birds is needed. Moreover, studies

conducted at multiple spatial scales will provide additional insight into the mechanisms influencing nest-site selection in this species.

We expected nest survival to be influenced by several nest-site characteristics, yet these characteristics were not strong predictors of nest survival. We observed high nest survival values across a wide range of nest-site characteristics that likely made it difficult to detect an effect of these variables on nest survival. Instead, we found that nest survival was strongly influenced by the temporal and seasonal variables of nest initiation date and temperature. Nest survival was highest for nests initiating early in the breeding season and increased with increasing temperature. Our results suggest that the timing of nesting to coincide with periods of greatest arthropod abundance is critical for nest survival in this species. We urge future studies to incorporate measures of arthropod abundance to further investigate this hypothesis. Additionally, Lewis's Woodpecker nests in aspen riparian woodlands suffered much lower predation rates relative to cottonwood riparian habitats (Saab and Vierling 2001). This difference may be related to differences in the abundance and diversity of primary cavity-nesting birds, which in turn influence the abundance and availability of nest cavities. Examination of the complex interactions of primary cavity-nesting bird densities, cavity availability, and nest predation would answer several important ecological questions. Moreover, we encourage additional study of Lewis's Woodpecker in aspen riparian woodlands throughout the Intermountain West to determine if results from our study hold at a regional scale. Increased monitoring efforts in aspen riparian woodlands may provide a better indication of the status of Lewis's Woodpecker populations because of the stability of these habitats relative to

ephemeral postfire forest habitats. Additionally, information is needed on reproductive success in riparian woodlands that are not influenced by livestock grazing.

In Chapter 3, we took a broader approach and examined the influence of sheep and cattle grazing on aspen riparian woodlands and the associated breeding bird community. Sites grazed by cattle had more bare ground, less forb cover, and lower willow and aspen tree densities than sheep-grazed sites. Results from our point transect surveys revealed that differences in breeding bird densities of the species we examined (House Wren, Lazuli Bunting, Song Sparrow, Warbling Vireo, and Yellow Warbler) corresponded with differences in vegetation characteristics between cattle- and sheep-grazed sites, although bird species composition was similar in both grazing treatments. Song Sparrow, a ground-nesting riparian obligate species that requires dense herbaceous cover, had nearly twice the density in sheep-grazed sites. House Wren, a generalist species that often selects nest sites with an open understory, had over three times higher densities on cattle-grazed sites. Yellow Warbler and Warbling Vireo, species that rely on high willow densities and dense herbaceous canopy cover respectively, each had higher densities in sheep-grazed sites. Lazuli Bunting, a habitat generalist, had similar densities in the two grazing treatments.

Results from our study indicate there are tradeoffs when attempting to manage for multiple species with different responses to grazing regimes. In other words, some species can coexist and even increase under certain grazing regimes while other species tend to decrease or are excluded completely. Unfortunately, we could not find representative ungrazed sites, so we were unable to investigate how our results compare

to similar habitats in the absence of grazing. Examining habitats and their associated breeding bird communities under various grazing regimes, including no grazing, is critical to gaining a complete understanding of these complex interactions.

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APPENDIX A

BIRD SPECIES DETECTED DURING POINT TRANSECT
SURVEYS CONDUCTED ON THE PIONEER MOUNTAIN RANCH,
IDAHO, 2003-2004.

Appendix A. All bird species detected during 8-minute point transect surveys on the Pioneer Mountain Ranch, Idaho, 2003 – 2004. Species without an “X” were not detected during surveys in that grazing treatment.

Common name	Scientific name	Treatment	
		Cattle-grazed	Sheep-grazed
American Crow	<i>Corvus brachyrhynchos</i>	16	20
American Goldfinch	<i>Carduelis tristis</i>	22	20
American Kestrel	<i>Falco sparverius</i>	14	7
American Robin	<i>Turdus migratorius</i>	24	20
Audubon's Warbler	<i>Dendroica coronata</i>	0	3
Belted Kingfisher	<i>Ceryle alcyon</i>	1	2
Black-billed Magpie	<i>Pica hudsonia</i>	8	4
Black-capped Chickadee	<i>Poecile atricapilla</i>	12	14
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	23	9
Blue Grouse	<i>Dendragapus obscurus</i>	8	2
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	4	3
Brewer's Sparrow	<i>Spizella breweri</i>	17	7
Brown-headed Cowbird	<i>Molothrus ater</i>	27	17
Bullock's Oriole	<i>Icterus bullockii</i>	19	12
Calliope's Hummingbird	<i>Stellula calliope</i>	3	0
Cedar Waxwing	<i>Bombycilla cedrorum</i>	2	1
Chipping Sparrow	<i>Spizella passerina</i>	5	6
Clark's Nutcracker	<i>Nucifraga columbiana</i>	0	1
Common Nighthawk	<i>Chordeiles minor</i>	0	1
Common Poorwill	<i>Phalaenoptilus nuttallii</i>	1	0
Common Raven	<i>Corvus corax</i>	1	0
Common Snipe	<i>Gallinago gallinago</i>	6	7
Cooper's Hawk	<i>Accipiter cooperii</i>	2	1
Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	2	12
Downy Woodpecker	<i>Picoides pubescens</i>	4	4
Dusky Flycatcher	<i>Empidonax oberholseri</i>	22	16
Eastern Kingbird	<i>Tyrannus tyrannus</i>	1	0
European Starling	<i>Sturnus vulgaris</i>	16	4
Fox Sparrow	<i>Passerelia iliaca</i>	2	7
Golden Eagle	<i>Aquila chrysaetos</i>	0	1
Great Horned Owl	<i>Bubo virginianus</i>	2	0

Appendix A. continued.

Common name	Scientific name	Treatment	
		Cattle-grazed	Sheep-grazed
Great Blue Heron	<i>Ardea herodias</i>	0	1
Green-tailed Towhee	<i>Pipilo chlorurus</i>	7	4
Hairy Woodpecker	<i>Picoides villosus</i>	9	7
House Wren	<i>Troglodytes aedon</i>	29	23
Lazuli Bunting	<i>Passerina amoena</i>	29	28
Lewis's Woodpecker	<i>Melanerpes lewis</i>	12	5
MacGillivray's Warbler	<i>Oporornis tolmiei</i>	18	20
Mallard	<i>Anas platyrhynchos</i>	1	1
Mourning Dove	<i>Zenaida macroura</i>	19	11
Northern Flicker	<i>Colaptes auratus</i>	25	24
Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>	2	1
Orange-crowned Warbler	<i>Vermivora celata</i>	22	12
Pine Siskin	<i>Carduelis pinus</i>	2	2
Plumbeous Vireo	<i>Vireo plumbeus</i>	3	0
Red-breasted Nuthatch	<i>Sitta canadensis</i>	1	2
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	16	13
Red-tailed Hawk	<i>Buteo jamaicensis</i>	4	0
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	7	10
Rock Wren	<i>Salpinctes obsoletus</i>	7	3
Ruby-crowned Kinglet	<i>Regulus calendula</i>	0	1
Rufous Hummingbird	<i>Selasphorus rufus</i>	0	1
Sandhill Crane	<i>Grus canadensis</i>	0	6
Song Sparrow	<i>Melospiza melodia</i>	27	24
Sora	<i>Porzana carolina</i>	1	X
Spotted Towhee	<i>Pipilo maculatus</i>	28	0
Swainson's Thrush	<i>Catharus ustulatus</i>	1	0
Tree Swallow	<i>Tachycineta bicolor</i>	7	5
Vesper Sparrow	<i>Pooecetes gramineus</i>	20	9
Violet-green Swallow	<i>Tachycineta thalassina</i>	1	0
Warbling Vireo	<i>Vireo gilvus</i>	27	29
Western Meadowlark	<i>Sturnella neglecta</i>	18	11
Western Tanager	<i>Piranga ludoviciana</i>	22	13
Western Wood-Pewee	<i>Contopus sordidulus</i>	16	5

 Appendix A. continued.

Common name	Scientific name	Treatment	
		Cattle-grazed	Sheep-grazed
Willow Flycatcher	<i>Empidonax traillii</i>	3	4
Wilson's Warbler	<i>Wilsonia pusilla</i>	4	1
Yellow Warbler	<i>Dendroica petecha</i>	30	30
Yellow-breasted Chat	<i>Ictera virens</i>	1	0
