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DO SAGEBRUSH DENSITY AND VEGETATION CONDITION AFFECT
DEMOGRAPHY OF BREWER'S SPARROWS NESTING IN THE
BLACKFOOT VALLEY?

By

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B.S., The University of Montana, Missoula, USA, 2000

Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
In Wildlife Biology

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Do sagebrush density and vegetation condition affect demography of Brewer's Sparrows nesting in the Blackfoot Valley? (78 pp.)

Chairperson: Jeffrey S. Marks

Vegetation condition can influence habitat quality by altering food abundance, predator abundance and species composition, and microclimate. In some habitats, livestock grazing alters vegetation condition in ways that affect the breeding success of passerines. Most sagebrush-dominated habitats have been heavily grazed by livestock, and the total area of sagebrush has declined substantially. Owing to this habitat loss and change, numbers of various sagebrush-obligate birds have declined, the Brewer's Sparrow among them. I examined the effects of cattle grazing on Brewer's Sparrow reproduction. Grazed plots, at the study-site scale, were characterized by higher potential nest-sagebrush density, and canopy cover, a higher number of exotic grass species, greater bare/rock ground cover, and lower grass/forb ground cover, compared with ungrazed plots. Trends in the characteristics of vegetation at the nest-patch scale were the same as those at the study-site scale. Reproductive performance was similar between grazed and ungrazed plots. Nestlings raised on ungrazed plots were larger than those on grazed plots in 2004, but not in other years. The numbers of breeding pairs were, however, higher in grazed plots than in ungrazed plots.

Vegetation condition also influences nest-site selection of organisms. Many studies assume that this selection is adaptive; however, it does not necessarily increase the fecundity of organisms. Vegetation condition becomes one of the important cues to select nest sites because organisms use vegetation as nest hiding cover, thermal cover, foraging sites, and display sites. I examined two questions, using model selection analysis: (1) does vegetation condition affect nest survival of Brewer's Sparrows?; and (2) does vegetation condition affect nestling size? There was no one best-approximating model to explain the correlation between vegetation features and nest survival, but all high-ranking models included nest-patch variables. In nestling-size models, nest-shrub size was positively correlated, and nest cover was negatively correlated, with nestling mass. Contrary to nest-survival models, nestling mass was strongly associated with nest-shrub variables rather than with nest-patch or understory-layer variables.

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Chapter 1

EVALUATING THE EFFECTS OF CATTLE GRAZING ON REPRODUCTION OF BREWER'S SPARROWS

ABSTRACT

Livestock grazing can influence wildlife by altering the structure and composition of vegetation communities. Changing habitat quality by livestock grazing can also affect food abundance, predator abundance and their species composition, and microclimate. Sagebrush-dominated habitats have been heavily grazed by livestock, and the total area of sagebrush lands in North America has been reducing substantially since the late 19th century. I examined the effects of cattle grazing on reproduction of Brewer's Sparrows (*Spizella breweri*) that are sagebrush obligates during the breeding season. Grazing changed vegetation structure and composition in my study area. Grazed plots were characterized by higher density of potential nest-sagebrush shrubs, higher sagebrush canopy cover, a higher number of exotic grass species, greater area of bare/rock ground cover, and lower density of grass/forb ground cover compared with ungrazed plots. Vegetation characteristics of nest sites at the nest-patch scale showed the same trend as those at the study-area scale. Vegetation variables at the nest-shrub scale (within 5-m radius around a nest) were similar by grazing status. Nest survival, predation rate, and season-long reproductive success were similar between grazed and ungrazed plots. However, yearly variation in daily nest survival rates were greater in grazed than ungrazed plots ($P = 0.035$). Nestlings raised on ungrazed plots were larger (11%) than those on grazed plots in 2004 ($P = 0.002$), when colder and rainier days were more common than in the other study years, but not in other years. The number of breeding

pairs was higher in grazed plots than in ungrazed plots in every year ($P = 0.043$). My study showed that grazing effects on Brewer's Sparrow's reproduction were little. Due to similar rates of nest survival between grazed and ungrazed plots, sparrows in grazed plots produced more fledglings each year. Grazing clearly changed vegetation structure and species composition, but did not seem to affect reproductive parameters of the sparrows.

INTRODUCTION

Historically, sagebrush habitats covered 60-100 million ha in western North America (Sturges 1973). For more than 100 years, immigrants developed wild sagebrush lands, and farmers and ranchers removed sagebrush to create agricultural fields and improve grazing opportunities for livestock (Braun et al. 1976; Reynolds 1981; Wiens and Rotenberry 1985). In addition, the arrival of livestock in the West in the late 19th century resulted in rapid overgrazing of remaining sagebrush lands (Yensen 1981). In the western United States, livestock grazing is the most common use of public lands, and livestock production is one of the most important economic resources (Sabb et al. 1995; Holechek et al. 1998). As a result, grazing has become controversial among land managers, ranchers, ecologists, and the public (Saab et al. 1995).

Livestock grazing has strongly influenced native wildlife by changing habitat structure (Logan 2001; Sutter and Ritchison 2005; Walsberg 2005); altering habitat quality that includes food abundance, predation rates, and nesting cover (Vander Haegen et al. 2002; Maron and Lill 2005; Sutter and Ritchison 2005); changing abundance of species (Page et al. 1978; Reynolds and Trost 1980; Dobkin et al. 1998; Vander Haegen et al. 2000); and reducing biodiversity (Reynolds and Trost 1980; Dobkin et al. 1998,

Scott et al. 2003). However, our knowledge of grazing effects on the reproduction of native wildlife is limited.

Owing to the loss and deterioration of sagebrush habitats, numbers of several species of sagebrush-inhabiting birds have declined over the past few decades (Reynolds and Trost 1981; Saab and Rich 1997; Paige and Ritter 1999; Knick et al. 2003). The nominate subspecies of Brewer's Sparrow (*Spizella breweri breweri*) is one such bird. "Sagebrush" Brewer's Sparrows are sagebrush obligates (Wiens and Rotenberry 1981; Petersen and Best 1985; Rotenberry et al. 1999). According to the most recent compilation of Breeding Bird Survey data (covering the period from 1966 to 2006), Brewer's Sparrow numbers have decreased by 2.3% per year across the species' entire range and by 1.9% per year in Montana (Sauer et al. 2007). Because most Brewer's Sparrows breed exclusively in sagebrush, alteration of this habitat can have serious effects on their population trends (Knick 1999; Paige and Ritter 1999).

The main reason thought to be responsible for negative trends in Brewer's Sparrow populations is alteration of sagebrush habitats for human benefits, which include livestock grazing. Outright loss of sagebrush habitat from urbanization and agriculture has an obvious and permanent negative effect on Brewer's Sparrows because the sparrows will not live where sagebrush does not occur. Less well understood is the influence that livestock grazing has on Brewer's Sparrow populations and reproduction. Overgrazing by livestock can radically change the species composition and condition of shrubsteppe vegetation. In general, long-term overgrazing by livestock leads to homogeneous vertical structure of vegetation, higher density of sagebrush, more bare ground, and lower density of native forbs and grasses (Holechek et al. 1998; Logan

2001). In contrast, rangeland that has received little or no grazing pressure tends to have more heterogeneous vertical structure of vegetation, lower density of sagebrush, less bare ground, and higher numbers and densities of native grass species (Holechek et al. 1998; Logan 2001). In the Intermountain West, sagebrush habitats evolved in the absence of large numbers of ungulates (Mack and Thompson 1982). As a result, bunchgrasses (e.g. *Agropyron* and *Festuca* spp.) and other components of native understory vegetation west of the continental divide are not resistant to overgrazing by livestock and are especially vulnerable to invasion by introduced grasses and forbs in response to heavy grazing (Mack and Thompson 1982).

Several studies have examined the effects of grazing on Brewer's Sparrows by comparing abundance among different grazing intensities, but results have been inconsistent. Logan (2001) found higher densities and higher nest survival in ungrazed habitats than in grazed habitats in central Montana. However, a study in Nevada found that sparrow abundance increased with heavy grazing at three sites and decreased at two others (Page et al. 1978). Other studies have claimed no effect of grazing on Brewer's Sparrow numbers (Reynolds and Trost 1980, 1981), or have shown a negative effect (Saab et al. 1995). In Washington, sparrow numbers were highest in areas with fair range condition, and there was no difference in numbers between sites with good and poor range condition (Vander Haegen et al. 2000). Because abundance can be a poor indicator of habitat quality (Van Horne 1983), it is important to consider reproductive success and productivity in addition to abundance when evaluating grazing effects.

Livestock grazing may affect reproduction of Brewer's Sparrows through changing (1) sagebrush density; (2) food abundance; (3) vulnerability of nests to

predation, brood parasites, and ectoparasites; and (4) nest microclimate. These four mechanisms can greatly influence passerine reproduction and population dynamics (Rotenberry and Wiens 1980; Murphy 1985; Martin 1987, 1992; Bosque and Bosque 1995; Kerley and Anderson 1995; Julliard et al. 1997; Reid et al. 1999, 2000).

(1) Sagebrush density and the numbers of breeding pairs.—Increases in sagebrush density as a result of grazing could lead to an increase in Brewer's Sparrow numbers by providing more nesting and foraging patches for sparrows (which nest and forage almost exclusively in sagebrush plants; Rotenberry and Wiens 1980; Petersen and Best 1985; Kerley and Anderson 1995; Rotenberry et al. 1999).

(2) Food abundance.—A higher density of sagebrush as a result of grazing might lead to increased food abundance if the insects sparrows eat live on sagebrush. Alternatively, changes in the species composition and amount of understory vegetation that result from grazing could decrease food availability for sparrows if the insects they eat rely on plant species other than sagebrush.

The effect on Brewer's Sparrows from grazing-induced changes in food abundance could be profound. Much empirical evidence shows that egg size/quality, clutch size, brood size, nestling growth, and nest survival increase in passerines when food abundance increases (Quinney et al. 1986; Martin 1987, 1995; Simons and Martin 1990; Siikamäki 1998; Neaf-Daenzer et al. 2000). In Brewer's Sparrows, these reproductive parameters increase in wet years, perhaps because of increased food abundance (Rotenberry and Wiens 1989, 1991).

Food shortage potentially affects avian reproduction in three ways (Martin 1987). First, food-stressed parents might reduce parental care and spend more time in self-

maintenance. Decreased provisioning rates that result from reduced parental care could affect nestling growth, nest-predation rate, and nest survival. Second, food shortage could decrease the condition of adults and therefore their future survival prospects. Third, higher reproductive costs owing to food limitation may adversely affect future reproductive success.

(3) Nest predation, brood parasitism, and ectoparasitism.—Nest predation is one of the most important factors that may influence nest survival for open-nesting songbirds (Martin 1992). A previous study has shown that vegetation cover largely influenced predation rates of Brewer's Sparrows in fragmented areas in Washington (Vander Haegen et al. 2002). The main nest predators in my study area are Columbian ground squirrels (*Spermophilus columbianus*), Common Ravens (*Corvus corax*), Black-billed Magpies (*Pica hudsonia*), and mice. Snakes can be major nest predators (Petersen and Best 1987; Rotenberry and Wiens 1991), but in my study area they do not seem to be common.

It is not immediately clear how grazing may influence nest predation in Brewer's Sparrows. On the one hand, because of the simpler vegetation structure that can result from grazing, nests in heavily grazed habitats may be more visible from the ground and have a higher risk of predation than those in less heavily grazed habitats with more complex vegetation structure. On the other hand, if vulnerability to nest predation is based largely on the total amount of shrub cover present, predation may be lower in heavily grazed habitats because of the higher density of sagebrush there. In addition, some studies have indicated that predator numbers are higher in grazed habitats (Reynolds and Trost 1980; Logan 2001).

In the same way that sagebrush density could influence detection of nests by predators, nests may also vary in their vulnerability to brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and to ectoparasitism by flesh flies (Sarcophagidae) and blowflies (*Protocalliphora braueri*). Brewer's Sparrows are uncommon hosts of Brown-headed Cowbirds (<5% of nests) rangewide (Rich 1978; Rotenberry et al. 1999; Vander Haegen and Walker 1999), and two studies in Montana have failed to find any cases of cowbird parasitism (B. Walker pers. comm.; Logan 2001). But, Brewer's Sparrow nestlings are commonly parasitized by flesh flies and blowflies (Petersen et al. 1986; Howe 1991; Rotenberry et al. 1999). In an Idaho study, flesh flies did not affect growth rates of Brewer's Sparrows; however, parasitized Sage Sparrow nestlings had shorter tarsi at fledging (Petersen et al. 1986). There are no data on how blowfly larvae affect growth rates and survival during the nestling period and after fledging in Brewer's Sparrows; however, parasitism can damage tissues of host nestlings (Rotenberry et al. 1999).

(4) Nest microclimate.—Grazing usually changes the composition and density of sagebrush and understory grasses, and these changes may affect microclimate at nests and foraging areas of Brewer's Sparrows. Increasing variation in temperatures at nesting and foraging patches may increase daily energy expenditure of sparrows if variation in temperature is large, because birds require more energy to maintain their body functions and adequate nest temperatures when ambient temperatures are outside the thermoneutral zone (Williams 1993; Weathers et al. 2002). Especially on cold mornings in sagebrush habitat, this effect can be large. As a result, adults may allocate more energy to raising their young and maintaining their own condition rather than to producing a larger number

of offspring. Several studies indicate that cold stress can result in decreased clutch size, egg size, and growth rates of birds (Murphy 1985; Nager and van Noordwijk 1992; Wiebe 2001). However, there are no data on how grazing affects temperature variation at nest locations.

In order to evaluate effects of cattle-grazing on habitat quality of breeding Brewer's Sparrows, I compared each of the four mechanisms between grazed and ungrazed plots. Also, I compared vegetation features at three different scales (study-site, nest-patch, and nest-shrub) between treatments. Then, to understand the effects of grazing on Brewer's Sparrow reproductive performance and demographics, I examined reproductive variables such as nest survival, season-long reproductive success, clutch size, egg volume, and nestling mass, and demographic variables such as the number of breeding pairs and site fidelity between two treatments.

METHODS

Study Plots

I studied Brewer's Sparrows in the Blackfoot Valley near Ovando, Montana, during the breeding seasons of 2003-2005. I established four study plots (each 30-32 ha) in 2003, two of which were within ungrazed portions of Waterfowl Production Areas (H2-O and Kleinschmidt) managed by the U.S. Fish and Wildlife Service, and two of which were private lands that were heavily grazed by cattle. The Kleinschmidt plot was burned by wildfire in August 2003 after nesting activity of Brewer's Sparrows ended, but before I had collected vegetation data. In 2004 and 2005, I selected another Waterfowl Production Area, Blackfoot, to replace the burned site. The Blackfoot plot was classified

as ungrazed because livestock grazing had occurred only twice during short periods in summer over the last 20 years, and the vegetation condition and composition were very similar to those on the other ungrazed plots. All plots shared similar climate and elevation and were close to each other in order to control abiotic variation, but individual sparrows in one site did not use other sites for their daily activities. Each plot was at least 500 m from the next nearest one to avoid pseudoreplication. To make it easier to map the location of sparrow nests and pairs, I created a grid on each plot by marking points (with flagging tape or rebar) at 50-m intervals.

The dominant sagebrush species throughout the study area was big sagebrush (*Artemisia tridentata*). The main grass species on the ungrazed plots were rough fescue (*Festuca campestris*) and Idaho fescue (*Festuca idahoensis*); quackgrass (*Elymus repens*) was the dominant grass species on the grazed plots.

Nest Searching and Monitoring

To find nests, I systematically searched each territory to check every potential nest shrub and to flush incubating adults by shaking shrubs, or I observed adult behavior (e.g. carrying nest materials or food for young; Martin and Geupel 1993). I recorded nest locations with a GPS unit and marked each nest with flagging tape placed at least 10 m north of the nest. Nest searches occurred during morning.

I checked nests after 13:00 every day when I expected eggs were due to hatch (based on nest-initiation day); when I was not able to estimate nest-initiation day, I checked nests every day to determine the exact day of hatching. Otherwise, I monitored nests every two days. During each nest check, I recorded the number of eggs or nestlings and nest fate. To have as little influence as possible on the outcome of nesting attempts, I

approached each nest with special care to minimize disturbance to adults and nestlings and spent as little time as possible at nests while recording data (Martin and Geupel 1993; Vander Haegen et al. 2002). I considered that a nesting attempt had been completed if all nestlings fledged, if all nest contents disappeared before fledging, or if the adults abandoned the nest.

Capture, Banding, and Pair Density

I captured and marked adults to examine season-long reproductive success and evaluate site fidelity. I captured males in mist nets by broadcasting territorial songs. Because males were more responsive to territorial song playbacks during the beginning of the breeding season (pers. obs.), I focused trapping efforts on males first, then began trapping females. Brewer's Sparrows normally do not abandon nests in response to trapping (B. Walker pers. comm.); therefore, I set two mist nets in a vee near nests, and then flushed incubating or brooding sparrows into the nets.

I recorded sex (presence or absence of cloacal protuberance and incubation patch), body mass, wing chord, and tail length of all captured birds, and banded them with a U.S.G.S. aluminum band and a unique combination of three colored plastic bands. I attached the metal band on the lower left leg in 2003, the upper left leg in 2004, and the lower right leg in 2005 to identify year of capture. Additionally, I banded each nestling with a U.S.G.S aluminum band on its left leg if the chick was hatched in a grazed plot, or on the right leg if the chick was hatched in an ungrazed plot to help examine natal dispersal. I counted the number of pairs in each plot using spot-mapping (Verner 1985).

Nest Survival and Predation Rates

I calculated daily nest survival rates (DSR) at each site by the logistic-exposure

model (Shaffer 2004) using statistical software R. I defined a nest as successful if at least one nestling fledged. I accepted as evidence of success if I observed fledglings or parents' feeding behavior near the nest within two days after fledging. I assumed that predators had taken nests if eggs disappeared before hatching, if healthy nestlings suddenly disappeared before expected fledging dates, or if nests were damaged and emptied without catastrophic weather having occurred.

To determine season-long reproductive success, I intensively followed banded pairs throughout the breeding season and recorded number of nesting attempts and fate of each attempt. Brewer's Sparrow pair bonds generally persist throughout the breeding season, and sparrows renest soon after failure of first nests (Rotenberry et al. 1999). I calculated the average number of young fledged per pair per year throughout the breeding season at each site.

Nestling Feeding Rates

To assess food availability during the nestling period, I used a spotting scope to observe feeding frequency and amount of food that parents carried to nests. Because feeding rates of Brewer's Sparrows increase with increasing brood size and nestling age (Petersen and Best 1986; Rotenberry et al. 1999), I recorded data from nests with three or four nestlings that were six or seven days old. To control for weather effects, I observed a nest in a grazed plot and one in an ungrazed plot on each observation day (paired sampling) if appropriate nests were available. The first observation period started between 6:30 and 7:00 a.m., and the second observation started between 8:30 and 9:00 a.m., and each period lasted for one hour. Sampling intervals (first or second) alternated on every observation day between grazed and ungrazed treatments.

Nest Microclimate

I set thermal data loggers (thermochron i-buttons, Dallas Semiconductor, Dallas, Texas) in nests after all nesting activities were finished to measure nest-site temperatures at each study site throughout the breeding season. In 2004, I used two i-buttons at each study plot and put them in randomly chosen nests every other day between 12 June and 6 August. In 2005, I used three i-buttons per study plot, and recorded temperatures simultaneously at the three nests between 25 May and 10 August. In order to collect nest microclimate data during early breeding season of sparrows in 2005, I randomly selected a nest from available old nests while nests of 2005 were still active. I used three sets of i-buttons at each study plot. Thermal data from each nest were recorded once every hour in 2004 and once every 30 minutes in 2005 for at least 24 hours, and then moved to another nest. I used the average lowest temperatures and rates of temperature increase from 5 a.m. to 10 a.m., of each day at each study site for comparisons.

Clutch Size, Egg Volume, and Nestling Mass

I recorded the number of eggs per nest during each visit to determine clutch size. For each egg in nests found before hatching, I measured length and breadth using a caliper (± 0.1 mm) and determined egg volume by the formula $volume = \pi (length \cdot breadth^2)/6$ (Ricklefs 1993). To reduce variance, I used nests that had clutch sizes of three or four, and averaged clutch volumes for each nest for analysis, because differences within clutches are much smaller than those among clutches (Christians 2002).

I measured nestling mass (± 0.1 g) and tarsus length (± 0.1 mm) when nestlings were seven days old as an index of nestling size. Nestling measurements were taken after 13:00 to decrease daily variation in nestling mass. Brewer's Sparrow nestlings do not

achieve asymptotic growth during the nestling period (Petersen et al. 1986); therefore, I considered that the mass of a nestling at day seven, which is just before fledging, represented the condition of nestlings and potential survivability after fledging.

Site Fidelity

Forty-nine adult males and 33 adult females were banded at the one of the grazing plot in 2002, which was one year before my study began. I started resighting these sparrows during the 2003 breeding season to determine site fidelity (proportion of banded adults returning from one year to the next). During the 2004 and 2005 breeding seasons, I resighted banded adults from 2002, and also banded adults and young sparrows from 2003 and 2004 at all plots. I analyzed site fidelity of adults and young separately.

Brood Parasitic and Ectoparasitism Rates

I monitored the presence and number of Brown-headed Cowbird eggs in each nest during each nest visit. I visually checked the bodies of each nestling when I measured nestling size at day seven and observed whether nestlings contained blowfly larvae. Also, I recorded the number and physical location of parasitic larvae on nestlings.

Vegetation Survey

At the study-site scale, I systematically sampled 22 to 25 vegetation plots in each study site during 2003, 2004, and 2005 using an intersection of grids (grid point) as a center of a vegetation plot. Grid points on the borders of study sites were not available as the center of vegetation plots. The first point of the grid point was randomly selected. At the nest-patch scale, I collected vegetation data at 66 nests (48 grazed, 18 ungrazed) in 2003, 149 nests (85 grazed, 64 ungrazed) in 2004, and 150 nests (86 grazed, 64 ungrazed) in 2005 when nesting activity ended.

To collect vegetation data for both scales, I used a modified version of Breeding Biology Research and Monitoring Database (BBIRD) grassland vegetation sampling protocol (Martin et al. 1997). Vegetation plots were composed of a 5-m radius circle around a nest, grid point, or the nearest shrub from a grid point as a center. Within the circle, I established four quadrants with axes along the four cardinal directions. I delineated 1.0 m, 3.0 m, and 5.0 m points on each cardinal direction from the center. Then, I counted the number of potential nest-sagebrush shrubs (>50 cm tall) and estimated grass/forb ground cover and bare/rock ground cover in each quadrant. I also measured the height and vigor (the percentage of the nest-shrub canopy that was green at the time a nest was active) of the first four sagebrush shrubs at the center in each cardinal direction. Additionally, I recorded Robel pole measurements (Robel et al. 1970) and grass heights on the center and on the other three points of each cardinal direction. I used the line-intercept method to measure canopy cover of sagebrush (>30 cm tall). There were two transects in each vegetation plot, and each transect was 10 m long.

At the nest-shrub scale, I measured nest height, nest-shrub height, size, vigor, and nest cover. I classified nest shrubs into five size groups depending on height, length, and width (5 was the largest 1 the smallest). I estimated nest cover visually from directly above the nest and by looking at the nest from each cardinal compass direction, with my eyes at nest height while I stood 1 m away from the nest.

Comparison and Statistical Methods

I conducted statistical analyses to evaluate the effect of grazing on Brewer's Sparrow habitat quality and reproductive performance using statistical software R. I initially tested for differences in vegetation structure and characteristics at three different

scales, which were study-site, nest-patch, and nest-shrub scales, between grazed and ungrazed treatments. I used linear mixed models and likelihood ratio tests for all variables except size at the nest-shrub scale, which was a categorical variable. I treated a vegetation variable as a response variable, treatment as a fixed effect, and year and study site as random effects. To normalize the data, I transformed canopy cover by arc-sine, potential nest-shrub density by log, and grass/forb ground cover and bare/rock ground cover by square root. I used chi-square tests to analyze shrub size.

To test for differences in the numbers of feeding trips per hour between grazed and ungrazed plots, I used a generalized linear model with Poisson distribution. The correlation between feeding rates and seasons was weak in each year ($R^2 < 0.2$), so I eliminated seasonal effects from my feeding-rate model.

To determine whether DSRs differed between treatments, I used the logistic-exposure model (Shaffer 2004). In my nest-survival models, I initially considered treatment and year to be explanatory variables, and each nest check was a Bernoulli trial. Year effects were nearly significant in 2004 ($P = 0.08$), and significant in 2005 ($P = 0.005$). Therefore, I tested treatment effects on nest survival separately for each year. For assessment of season-long reproductive success, I used ANOVA and treated the number of young fledged per pair per year as the response variable, and treatment, year, and interaction as explanatory variables.

To evaluate differences in nest microclimate between grazed and ungrazed treatments, I compared daily differences of the lowest nest temperatures between treatments by *t*-tests. Also, I used *t*-tests to compare rates (slopes) of temperature increases from 5 a.m. to 10 a.m.

I used ANCOVA to examine the effects of treatment, year, and season on clutch size and ANOVA to examine the effects of treatment and year on egg volume. Seasonal effects were omitted because they were not important for egg volume ($R^2 = 0.03$). In the analysis of nestling mass, I used ANOVA and compared them separately by year because yearly differences within treatments were large (maximum 12.9%). I initially tested the correlation between the date when nestlings became seven days old and nestling mass (seasonal effects). Because the correlation was very weak ($R^2 = 0.09$), I eliminated the date from my model. However, variance in nestling mass between the early breeding season (through 180 Julian days) and the late breeding season (after 180 Julian days) was different ($P = 0.003$), so I added this categorical variable to my model.

To compare site fidelity at each study plot, I used a generalized linear model with binomial error distribution, and included study plot and year as explanatory variables. I treated each banded individual as one trial and compared rates of sparrows returning the following year. I treated as two independent trials in my model if sparrows returned two consecutive years after banding year, and treated them the same as newly banded sparrows, because site fidelity did not differ between newly banded sparrows and once-returned sparrows. The presence of parasites was compared using a generalized linear model with binomial distribution. I used a generalized linear model with Poisson distribution to test the differences in the number of pairs per site.

I checked violations of assumption such as normality of response variables, normality of error distribution, and heteroscedascity for models by the model check function of R. I also checked whether there was an overdispersion of errors by checking residual deviance when I used generalized linear models.

RESULTS

Most vegetation variables at the study-site scale (mean \pm SE) clearly differed between grazed and ungrazed treatments (Figure 1, Table 1). Robel readings and grass/forb ground cover were higher in ungrazed plots. Conversely, bare/rock ground cover, sagebrush canopy cover, potential nest-shrub density, and average shrub height were higher in grazed plots. Average grass height and average shrub vigor were similar between treatments.

Variables at the nest-patch scale showed the same trend as those at the study-site scale (Figure 2, Table 2). Robel readings and grass/forb ground cover were higher in ungrazed plots, and bare/rock ground cover, potential nest-shrub density, and shrub canopy cover were higher in grazed plots. Grass height, average shrub height, and average shrub vigor were similar between ungrazed and grazed plots. At the nest-shrub scale, no variable differed between grazed and ungrazed plots ($P > 0.378$; Figure 3).

Mean nestling feeding rates were similar between treatments (grazed 2004 = 15.35 ± 1.33 , grazed 2005 = 11.20 ± 0.85 , ungrazed 2004 = 15.95 ± 1.61 , ungrazed 2005 = 11.39 ± 0.70); however, yearly effects were large ($z = -4.037$, $P < 0.0001$; Figure 4).

Nest survival analysis showed that grazing did not affect DSR in each year (yearly range 0.986-0.973 on ungrazed plots, 0.990-0.967 on grazed plots, $P > 0.147$; Figure 5). Daily predation rates on nests also were similar ($P > 0.31$) between grazed (yearly range 0.010-0.026) and ungrazed plots (yearly range 0.010-0.020). However, yearly variations in DSR on grazed plots were much higher than those on ungrazed plots ($F_{2,6} = 6.21$, $P = 0.035$; Figure 5). In 2003 and 2004, mean season-long reproductive success (number of fledglings per pair) in grazed plots was slightly higher than in

ungrazed plots, although the differences were not statistically significant ($P = 0.44$, $P = 0.84$; Table 3). In 2005, mean season-long reproductive success was higher in ungrazed plots than in grazed plots ($P = 0.049$; Table 3). Season-long reproductive success was lower in 2004 than that in other years ($P = 0.053$).

Nest microclimate as measured by the lowest daily temperature was similar between treatments each year after accounting for study-site effects (2004: $P > 0.371$, 2005: $P > 0.140$). Lowest daily temperatures (mean \pm SE) early and late in the breeding season in 2004 were $4.21 \pm 0.75^\circ\text{C}$ and $6.09 \pm 0.55^\circ\text{C}$ in grazed plots and $4.03 \pm 0.84^\circ\text{C}$ and $6.35 \pm 0.62^\circ\text{C}$ in ungrazed plots, respectively. Those in 2005 were $2.79 \pm 0.69^\circ\text{C}$ and $5.79 \pm 0.66^\circ\text{C}$ in grazed plots and $2.41 \pm 0.69^\circ\text{C}$ and $5.55 \pm 0.66^\circ\text{C}$ in ungrazed plots, respectively. Because of lack of data early in the season in 2004, temperatures in 2005 were lower than those in 2004. Rates of temperature increase were also similar between grazed and ungrazed treatments in both years ($P > 0.70$; Figure 6).

Mean clutch size differed significantly by year (2003: 3.71 ± 0.09 , 2004: 3.46 ± 0.06 , 2005: 3.75 ± 0.05 ; $P < 0.001$) but not by grazing treatment ($P = 0.96$; Table 3). Also, clutch size decreased toward the end of the breeding season ($P < 0.001$). Egg initiation day ($R^2 = 0.03$) and year ($P = 0.63$) did not affect average egg volume, so I eliminated them from my models. However, I found no evidence that average egg volume differed by grazing treatment ($t = -0.615$, $P = 0.540$; Table 3). On the basis of nestling mass at day seven, nestlings early in the breeding season were smaller than those late in the breeding season (early = 8.58 ± 0.12 g, late = 9.31 ± 0.10 g, $t = -4.72$, $P < 0.001$). Year also had a great effect on nestling mass (Table 3, Figure 7). During the cool and wet year of 2004, nestlings were smaller than during other years in both

treatments ($t = -3.410$, $P < 0.001$); however, in each treatment, nestling sizes were similar between 2003 and 2005 ($P > 0.30$; Table 3). Nestling mass differed by treatment in 2004, when nestlings on ungrazed plots were larger than those on grazed plots ($F_{1,49} = 10.36$, $P = 0.002$; Table 3, Figure 7), but not in other years ($P > 0.23$).

Numbers of breeding pairs were higher on grazed plots than on ungrazed plots in every year ($z = 2.02$, $P = 0.043$; Table 3, Figure 8). Site fidelity of adults was very similar between treatments ($P > 0.45$; Table 3); however, more sparrows returned in 2004 than 2005 ($z = 2.513$, $P = 0.01$; Table 3). Of the 491 fledglings banded, I found seven (1.43%) that had returned to my study area one or two years later; in each case, they settled on their natal sites. Five returned to grazed plots (three males, one female, and one unknown) and two returned to ungrazed plots (one male and one female). The proportion of nests that were parasitized by blowfly larvae did not differ between grazed and ungrazed plots in 2003 ($z = -0.337$, $P = 0.74$) or 2005 ($z = 1.050$, $P = 0.29$; Table 3). In 2004, parasitic rates were lower on grazed plots than on ungrazed plots ($z = -2.273$, $P = 0.02$; Table 3). Brood parasitism by Brown-headed Cowbirds was rare in my study area. I detected no cases of parasitism in 2003, one in 2004 (0.6% of nests), and four in 2005 (2.4%). All cases of brood parasitism by Brown-headed Cowbirds occurred on the same grazed plot where cattle were regularly present during the breeding season.

DISCUSSION

My study showed that grazing effects on vegetation characteristics and species composition at the study-site and nest-patch scales were very strong. Grazed plots were characterized by higher sagebrush canopy cover, more bare/rock ground cover, higher

density of potential nest shrubs, and lower grass/forb ground cover. These results are similar to those from other studies (Holechek et al. 1998; Logan 2001; Sutter and Ritchison 2005; Walsberg 2005). Average sagebrush height differed between treatments at the study-site scale, but it was similar at the nest-patch scale, suggesting that Brewer's Sparrows select a nest patch with taller sagebrush shrubs. Average grass height was similar between treatments, but density and species composition clearly differed between treatments. In the Blackfoot Valley, rough fescue historically was the most dominant species (Montana Fish, Wildlife and Parks 2005), and I found it on all vegetation sampling plots on the two ungrazed plots. In contrast, I detected this species on only a few vegetation sampling plots on the two grazed plots. In addition, the number of native grass species was higher on ungrazed plots than on grazed plots. These differences suggested that the vertical vegetation structure was composed of two layers in grazed plots and three layers in ungrazed plots.

Nest-shrub characteristics were similar between ungrazed and grazed plots. One nest-shrub variable, average nest cover (which was a factor of the nest shrub itself and vegetation within 1 m around the nest), was also similar between grazing treatments, despite a higher density of sagebrush shrubs on grazed plots. One interpretation of this is that higher grass cover around nest shrubs in ungrazed plots compensated for loss of nest cover that usually is provided by greater density of sagebrush shrubs in grazed plots. Dense shrub cover in grazed habitats might work better for hiding a sparrow's flight path between feeding patches and the nest. This is especially beneficial when frequent nest visits are required, such as during the nestling period, because some predators locate nests by observing flights to the nest (Martin and Ghalambor 1999; Ghalambor and

Martin 2000). Higher grass cover on ungrazed plots might increase postfledging survival probability because dense grass cover could hide fledglings from predators as the fledglings moved among shrubs.

Nestling feeding rates differed between years, being higher in 2004 than in 2005 in both treatments, even though nestlings were smaller in 2004 than in 2005. Feeding rates indicate the abundance of potential prey, not nutrient conditions, which more likely depend on the sizes and types of prey. However, I was not able to record the size and species of prey owing to dense cover near nests. Accordingly, I could not determine why yearly differences occurred; was it because prey abundances were different or the sizes and types of prey, which are more likely related to nutritional values, were different? Larger nestling mass in 2005 may indicate that more large prey species and/or prey of higher nutritional value were available in 2005, or that nestlings used less energy for self-maintenance in 2005.

The difference in yearly variation in DSR between grazing treatments might be explained by differences in the incidence chicks dying in nests, in nest abandonment, and in hatching failure. More nestlings were dead in nests, more nests were abandoned, and more eggs failed to hatch on grazed plots when the annual nest survival was lower than on ungrazed plots. In contrast, the rates of these incidents were similar during the study periods on ungrazed plots. As a result, nest survival generally was similar among years. This suggests that nests in grazed plots were more vulnerable to mechanisms that I did not study, such as weather conditions. The number of nests taken by predators on grazed plots was lower in 2003 than in other years and also was lower than that on ungrazed plots in 2003. In 2004, when rainy and cold days were more common at the beginning of

breeding season than they were during the other study years, the incidence of dead nestlings with no external damage, and of partial mortality of broods (i.e. losses to factors other than nest predation), were higher on grazed plots than on ungrazed plots. In contrast, nest-predation rates on ungrazed plots were very similar for the three study years, and the incidence of dead nestlings that did not appear to be killed by predators was very low. I also observed yearly variation in nest-predation rates; however, the trend in variation was similar between treatments; in other words, when predation on grazed plots was relatively high, it was also high on ungrazed plots.

Season-long reproductive success differed between treatments only in 2005, when nest-predation rates in both treatments were the highest; sparrows on ungrazed plots had higher season-long reproductive success than those in grazed plots. In 2005, higher numbers of adults on grazed plots terminated their reproductive attempts or disappeared from the plots after their first nest attempts were completed or failed, than did those on ungrazed plots. This suggests that if reproductive conditions were not optimal, breeding pairs on ungrazed plots would have higher reproductive output than those on grazed plots. In 2003 and 2004, there were no statistical differences in season-long reproductive success between grazed and ungrazed plots, although the number of nestlings fledged per nest was slightly higher on ungrazed plots than on grazed plots. However, yearly differences were clearly detected; season-long reproductive success in 2003 was higher than in 2004 in both treatments. The difference between 2003 and 2004 can be explained by higher numbers of nestlings fledged per nest in 2003 with the similar probabilities of re-nesting. In other words, wetter and colder weather in the beginning of the 2004 breeding season increased nestling mortality, which was not observed in 2003.

Generally, grazing effects on reproductive parameters of Brewer's Sparrows were small, but yearly differences were relatively large. In addition, when the reproductive condition of a year is harsher than normal, these differences potentially become substantial, and grazing may affect reproduction of sparrows. Average clutch sizes were very similar in 2003 and 2005, but average clutch sizes were approximately 10% lower in 2004, when more rain and colder days were common. However, grazing did not affect clutch size each year. Nestling mass at day seven differed between early and late nests, and among years. These results also occurred in another study of Brewer's Sparrows that documented that nestling growth rates varied significantly among years and between periods of the breeding season (Petersen et al. 1986). In addition, nestling mass differed between grazing treatments in 2004, but not in 2003 and 2005. Nestlings raised on ungrazed plots were larger than those on grazed plots. Petersen et al. (1986) suggested that seasonal and yearly variation results from different food availability among years and timing (early or late) of nesting attempts. However, I found no differences in food delivery rates between treatments. A potential reason for this phenomenon is differences in nest-site conditions, which were influenced by weather conditions. In 2003 and 2005, differences in nestling mass between treatments were very low, but in 2004, there was a clear difference. Owing to the colder and rainier weather in 2004, nestlings from nests that were in lower-quality sites may have allocated more energy to thermoregulation than to growth than those in higher-quality sites.

Higher density of sagebrush on grazed plots provided more nesting and feeding sites for sparrows; as a result, the number of breeding pairs was higher on grazed plots in all three years. This explanation is supported by many studies that have documented

negative effects of complete or partial sagebrush removal on abundance of Brewer's Sparrows (Best 1972; Schroeder and Sturges 1975; Reynolds and Trost 1980, 1981; Bock and Bock 1987; Petersen and Best 1987; Kerley and Anderson 1995). All banded adults and fledglings that were detected in later years returned to the same study plots where they were captured (adults) or hatched (fledglings). Site fidelity of adults ranged from 10.7-50%; the highest return rate of adults occurred on one of the grazed plots in 2003, and the lowest occurred on one of the grazed plots in 2005. More sparrows returned in 2004 than in 2005. Return rates of adults were similar to those reported in previous studies (Oregon and Idaho: approximately 25%, Petersen and Best 1987, Rotenberry et al. 1999; Washington: approximately 50%, Walker 2000).

In each year, blowfly parasitism rates were higher than those reported in a previous study in central Idaho (6%; Howe 1991), indicating that blowfly parasites are relatively common in western Montana. The maximum parasite load per brood was 40 larvae on three nestlings at an ungrazed plot; these loads were much higher than in other broods. The average number of parasites per infected brood was 5.73 on grazed plots and 4.95 on ungrazed plots, which is much higher than the average load reported in central Idaho (2.5/infected brood; Howe 1991). In 2004, blowfly parasitism was higher on ungrazed plots than on grazed plots, but they were similar in 2003 and 2005. Brood parasitism by Brown-headed Cowbirds on Brewer's Sparrows is rare compared with many other passerines (Rotenberry et al. 1999). Cowbird parasitism varied from 0-13% of nests except in Alberta, where it was 52% (Rich 1978; Biermann et al. 1987, Rotenberry and Wiens 1989; Vander Haegen and Walker 1999; Logan 2001). Cowbird parasitism rates in my study area also were low; I only found 5 cases out of 428 (1.2%)

observed nests during three breeding seasons. All five of these nests occurred on one of the grazed plots where cattle grazed throughout the breeding season.

Conclusions and Management Implications

Grazing clearly altered vegetation structure and plant species composition of Brewer's Sparrow breeding habitat at the study-site and nest-patch scales, but there was no effect at the nest-shrub scale. Grazing had no clear negative effect on nest survival, season-long reproductive success, predation rate, nestling feeding rate, nest microclimate, site fidelity, and other reproductive parameters, such as clutch size and egg volume. However, I found a small difference in mass of seven-day-old nestlings, and a clear difference in the numbers of breeding pairs, between grazed and ungrazed plots. Especially in the year that was colder and rainier than normal, the difference in nestling mass between grazed and ungrazed plots was large.

Conservation of lands that support a high density of sagebrush plants, independent of grazing intensity, should be a high priority to managers concerned with sustaining healthy populations of Brewer's Sparrows (although not necessarily for other species such, as Greater Sage-Grouse [*Centrocercus urophasianus*]). Owing to declining trends in Brewer's Sparrow numbers, conservation of their limited breeding habitat will become increasingly important as more sagebrush lands are lost to development. Many ranchers want to reduce sagebrush density to improve grazing conditions on their lands and on public grazing allotments, making it difficult to manage for sagebrush-obligate birds like Brewer's Sparrows. I observed a positive correlation between sagebrush density and numbers of breeding sparrows. Breeding density by itself does not always indicate a habitat's quality (Van Horne 1983), but as long as nest survival and season-long

reproductive success are similar between grazed and ungrazed sites, as in my study, I conclude that higher densities of sagebrush that can result from grazing will result in more pairs of Brewer's Sparrows that produce more offspring. Although I was not able to test the effect of sagebrush removal on nest survival and reproductive performance on grazed plots, I can infer from previous studies that sagebrush removal negatively affects the abundance of Brewer's Sparrows (Best 1972; Schroeder and Sturges 1975; Reynolds and Trost 1980, 1981; Bock and Bock 1987; Petersen and Best 1987; Kerley and Anderson 1995). Also, we still do not know how much sagebrush density can be reduced without reducing pair density and reproductive output. Generally, grazing results in a higher density of sagebrush, more bare ground, and less grass cover. Therefore, a critical question remains: what will happen to Brewer's Sparrow reproduction if we reduce sagebrush density without increasing grass cover, given that grasses may have an important role for Brewer's Sparrows by providing cover in ungrazed habitats? Answering this question will be necessary before deciding whether sagebrush reduction is an appropriate management regime for multiple species that are using the same habitats.

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Table 1. Summary of vegetation analysis between grazed and ungrazed treatments. Mean \pm SE, χ^2 , and *P*-values of all vegetation variables at study-site scale.

Variables	Grazed	Ungrazed	χ^2	<i>P</i> -values
	Mean \pm SE	Mean \pm SE		
Robel readings (dm)	3.48 \pm 0.15	5.18 \pm 0.33	4.39	0.036
Grass/forb ground cover (%)	33.92 \pm 1.34	50.29 \pm 1.43	4.78	0.029
Bare/rock ground cover (%)	21.70 \pm 1.12	10.50 \pm 0.98	4.68	0.031
Sagebrush canopy cover (%)	36.93 \pm 1.17	25.70 \pm 0.88	5.28	0.021
Potential nest-shrub density (no./m ²)	0.61 \pm 0.02	0.38 \pm 0.02	4.97	0.026
Average shrub height (cm)	64.54 \pm 1.01	58.56 \pm 1.01	5.49	0.019
Average grass height (cm)	23.34 \pm 0.82	26.69 \pm 0.84	0.97	0.033
Average shrub vigor (%)	62.26 \pm 0.89	63.53 \pm 1.08	0.03	0.856

Table 2. Summary of vegetation analysis between grazed and ungrazed treatments. Mean \pm SE, χ^2 , and *P*-values of all vegetation variables at nest-patch scale.

Variables	Grazed	Ungrazed	χ^2	<i>P</i> -values
	Mean \pm SE	Mean \pm SE		
Robel readings (dm)	3.96 \pm 0.12	5.33 \pm 0.25	5.49	0.019
Grass/forb ground cover (%)	28.42 \pm 0.94	50.18 \pm 1.33	7.46	0.006
Bare/rock ground cover (%)	22.37 \pm 0.85	6.76 \pm 0.54	11.90	<0.001
Sagebrush canopy cover (%)	42.45 \pm 0.81	32.10 \pm 0.84	6.12	0.013
Potential nest-shrub density (no./m ²)	0.69 \pm 0.02	0.44 \pm 0.01	5.60	0.018
Average shrub height (cm)	72.36 \pm 0.80	70.98 \pm 0.83	0.20	0.655
Average grass height (cm)	26.61 \pm 0.75	30.20 \pm 0.74	0.88	0.346
Average shrub vigor (%)	65.70 \pm 0.55	66.09 \pm 0.71	0.09	0.764

Table 3. Summary of Brewer's Sparrow's reproductive performance and demographic rates of each year.

Variable	Year	<i>n</i>		Grazed	Ungrazed
		Grazed	Ungrazed	Mean ± SE	Mean ± SE
Season-long reproductive success (fledglings/pair)	2003	23	23	4.87 ± 0.40	4.39 ± 0.38
	2004	31	29	3.97 ± 0.35	3.66 ± 0.44
	2005	32	28	3.44 ± 0.43	4.61 ± 0.37
Clutch Size	2003	30	22	3.63 ± 0.13	3.82 ± 0.11
	2004	59	47	3.49 ± 0.07	3.43 ± 0.10
	2005	58	39	3.76 ± 0.57	3.74 ± 0.10
Egg Volume (mm ³)	2003	22	20	1447.6 ± 23.1	1454.1 ± 20.4
	2004	51	40	1468.2 ± 19.5	1432.5 ± 20.7
	2005	46	32	1463.5 ± 14.8	1476.4 ± 19.3
Nestling Size (g)	2003	18	14	9.06 ± 0.18	9.21 ± 0.24
	2004	31	21	8.03 ± 0.17	8.94 ± 0.26
	2005	27	25	9.06 ± 0.15	9.31 ± 0.19
Pair Density (no./10 ha)	2003	2	2	12.17 ± 2.17	9.56 ± 1.12
	2004	2	2	13.50 ± 1.17	11.78 ± 0.11
	2005	2	2	13.67 ± 1.67	10.01 ± 0.32
Site Fidelity (%)	2004	2	1	0.381 ± 0.118	0.286 ± NA
	2005	2	2	0.204 ± 0.096	0.219 ± 0.081
Parasitic Rates (%) (Blowfly)	2003	2	2	0.49 ± 0.12	0.54 ± 0.08
	2004	2	2	0.19 ± 0.02	0.40 ± 0.08
	2005	2	2	0.32 ± 0.07	0.21 ± 0.10

FIGURE LEGENDS

Figure 1. Mean values for vegetation variables on ungrazed and grazed plots at the study-site scale, 2003-2005. Error bars are standard errors. Rows represented mean of Robel pole reading, bare/rock ground cover, potential nest shrub density, grass/forb ground cover, sagebrush canopy cover, and average sagebrush height, respectively, from top to bottom, and left to right.

Figure 2. Mean values for vegetation variables on ungrazed and grazed plots at the nest-patch scale, 2003-2005. Error bars are standard errors.

Figure 3. Mean values for vegetation variables on ungrazed and grazed plots at the nest-shrub scale, 2003-2005. Error bars are standard errors.

Figure 4. Mean feeding rates of Brewer's Sparrow nestlings on ungrazed and grazed plots in 2004 and 2005. Error bars are standard errors.

Figure 5. Median daily survival rates of Brewer's Sparrows on grazed and ungrazed plots with interquartile range.

Figure 6. Mean rates (slope/day) of temperature increase from 5 to 10 am at grazed and ungrazed plots in 2004 and 2005.

Figure 7. Mean nestling mass of Brewer's Sparrows on grazed and ungrazed plots, 2003-2005. Error bars are standard errors.

Figure 8. Brewer's Sparrows pair densities on grazed and ungrazed plots, 2003-2005. Error bars are standard errors.

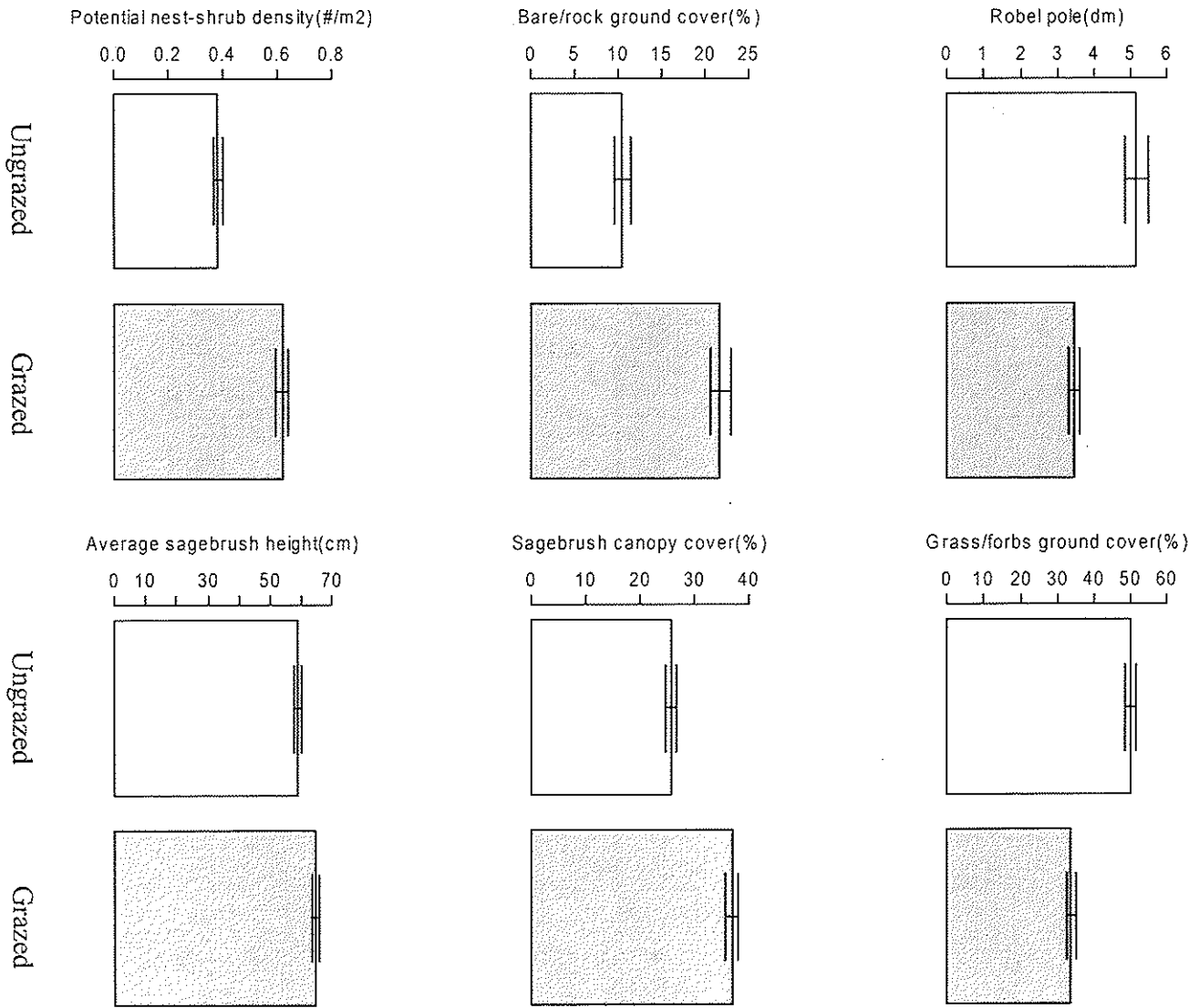


Figure 1

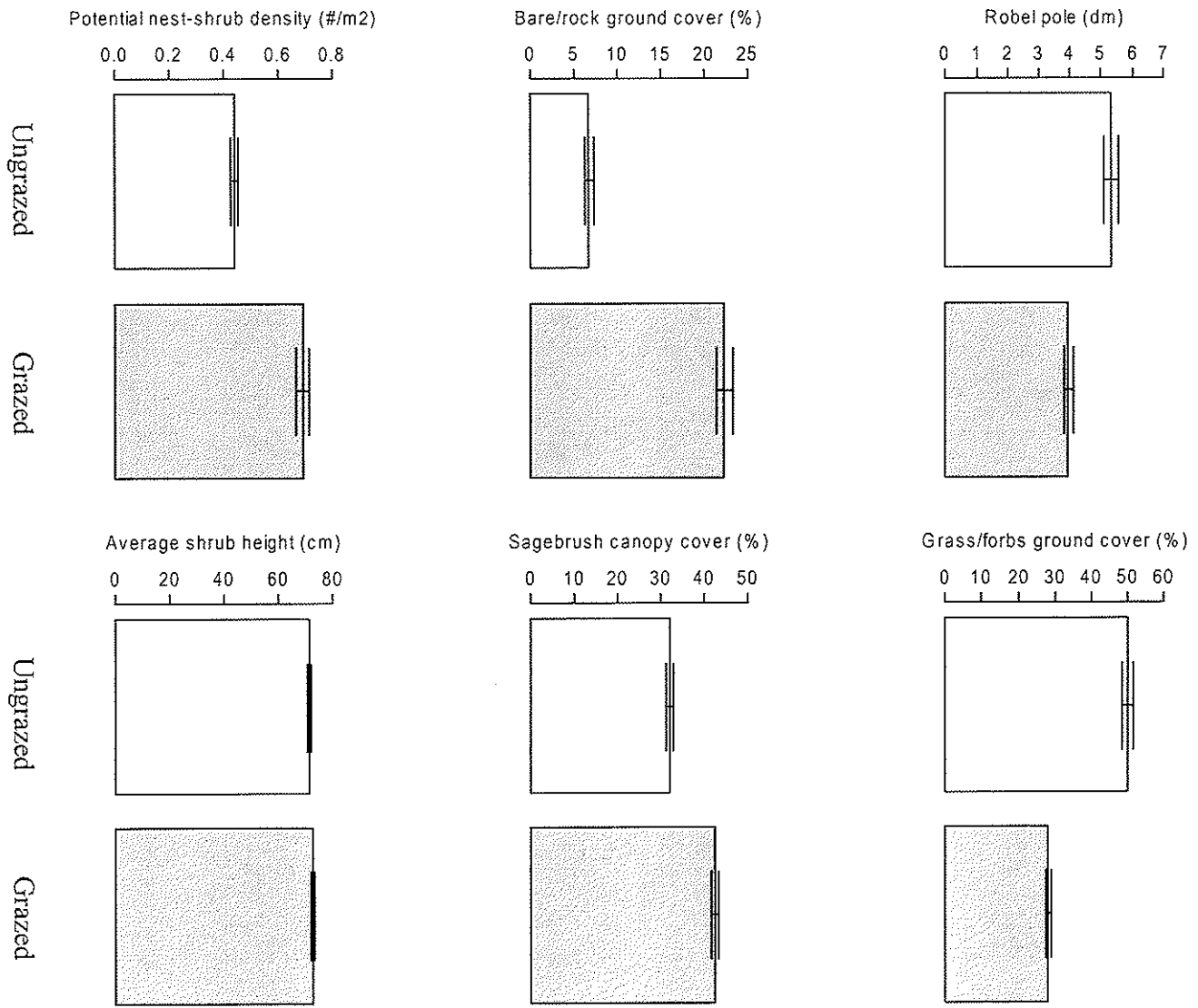


Figure 2

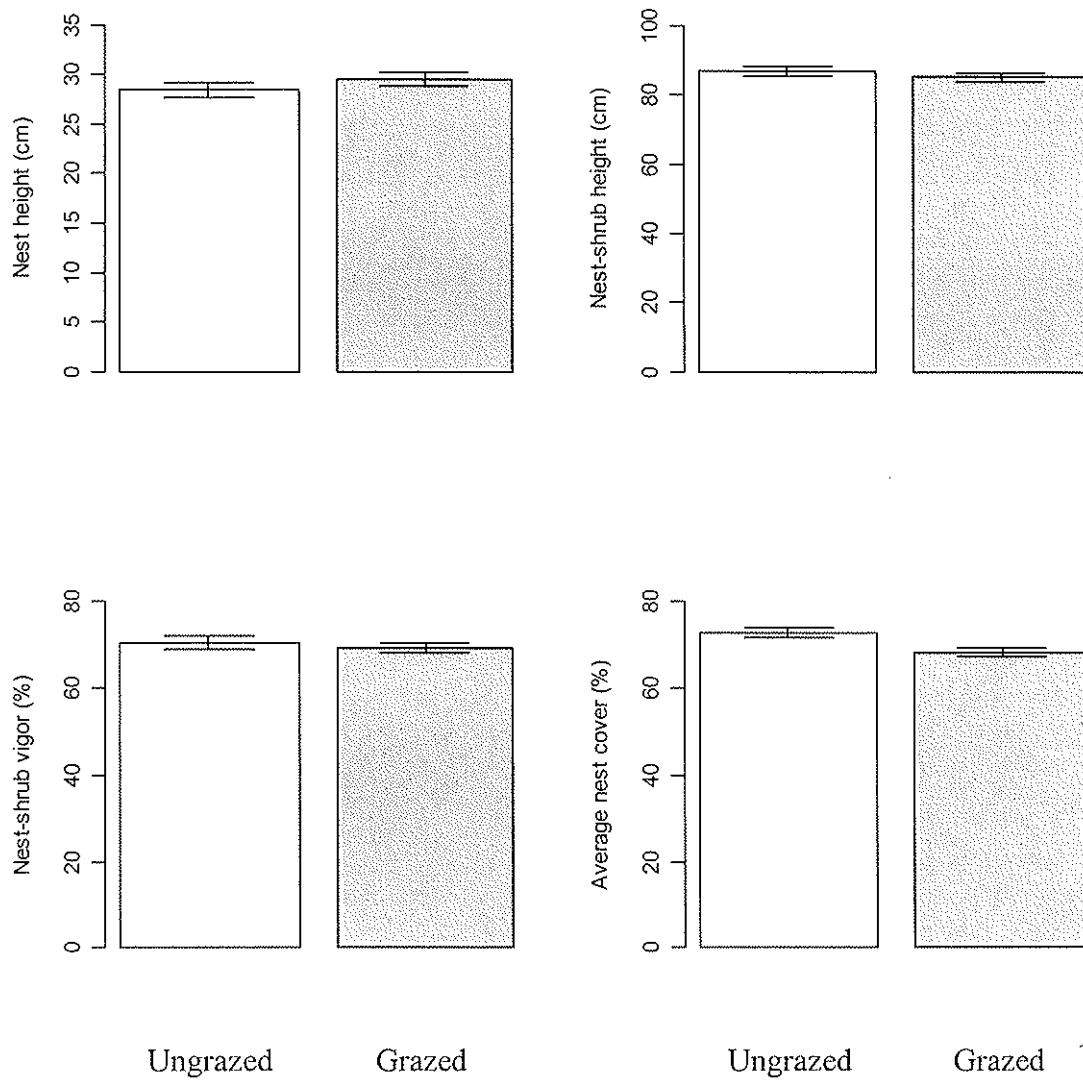


Figure 3

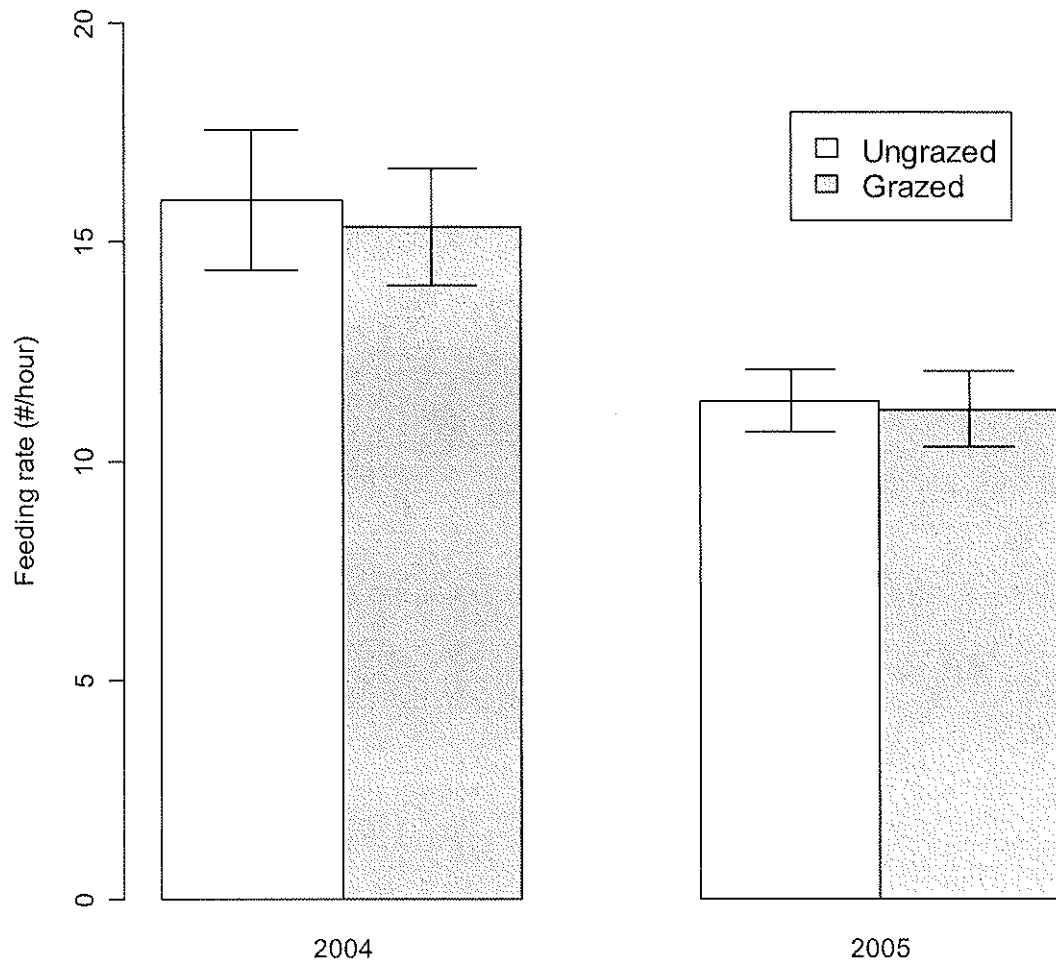


Figure 4

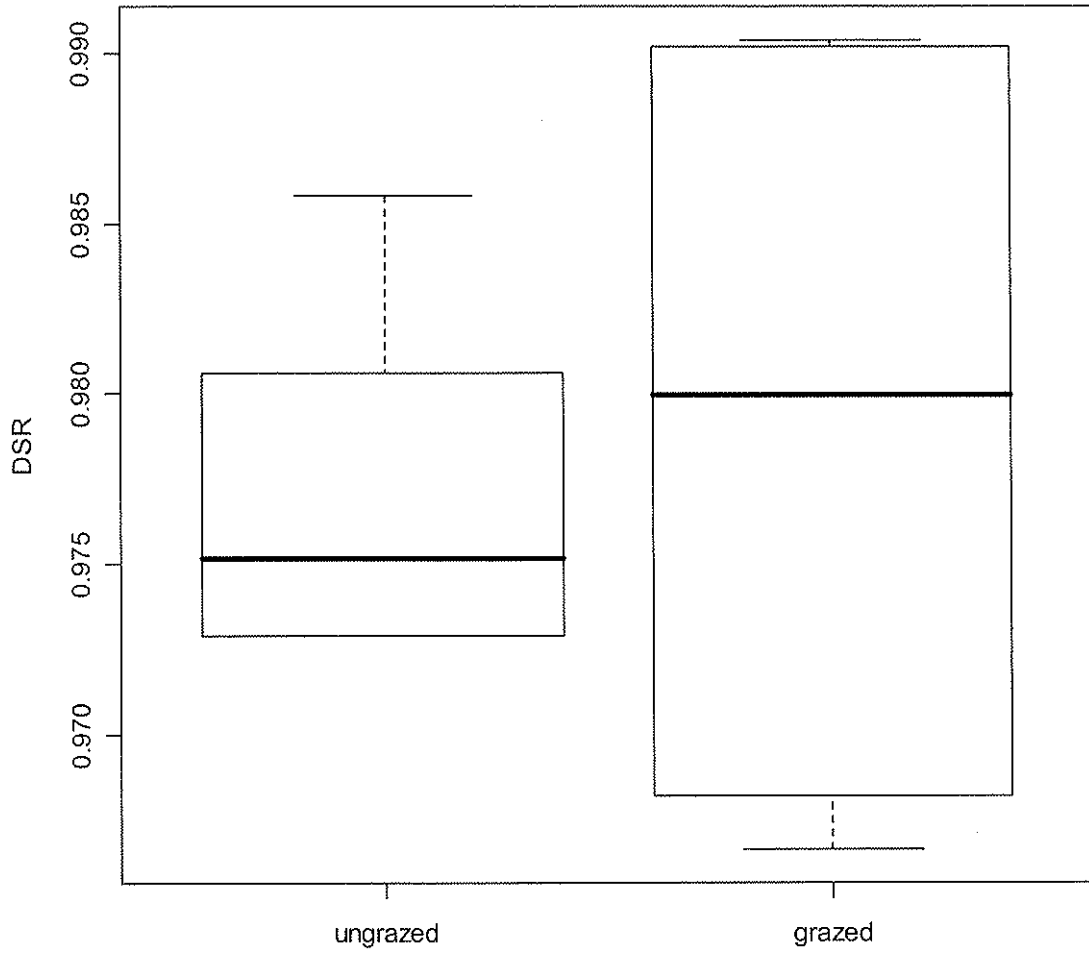


Figure 5

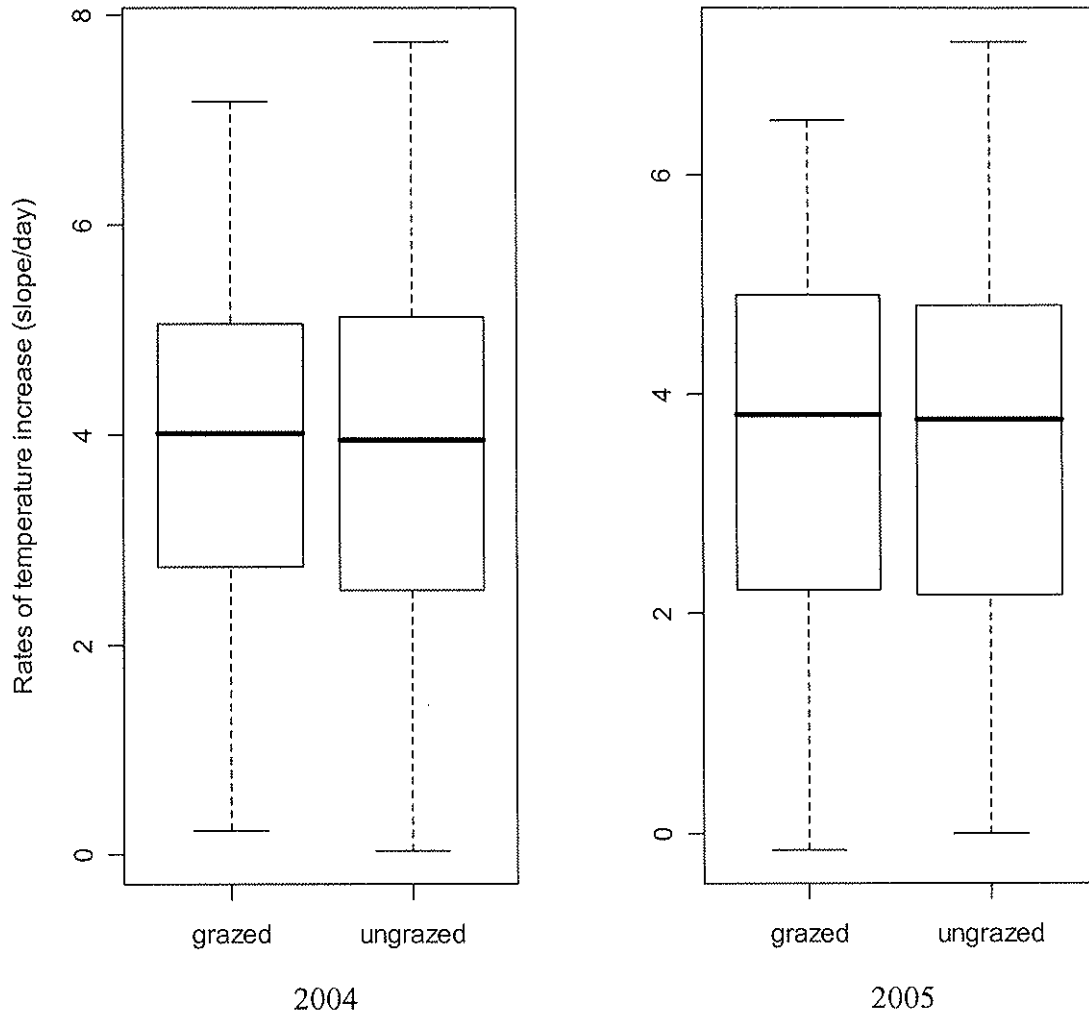


Figure 6

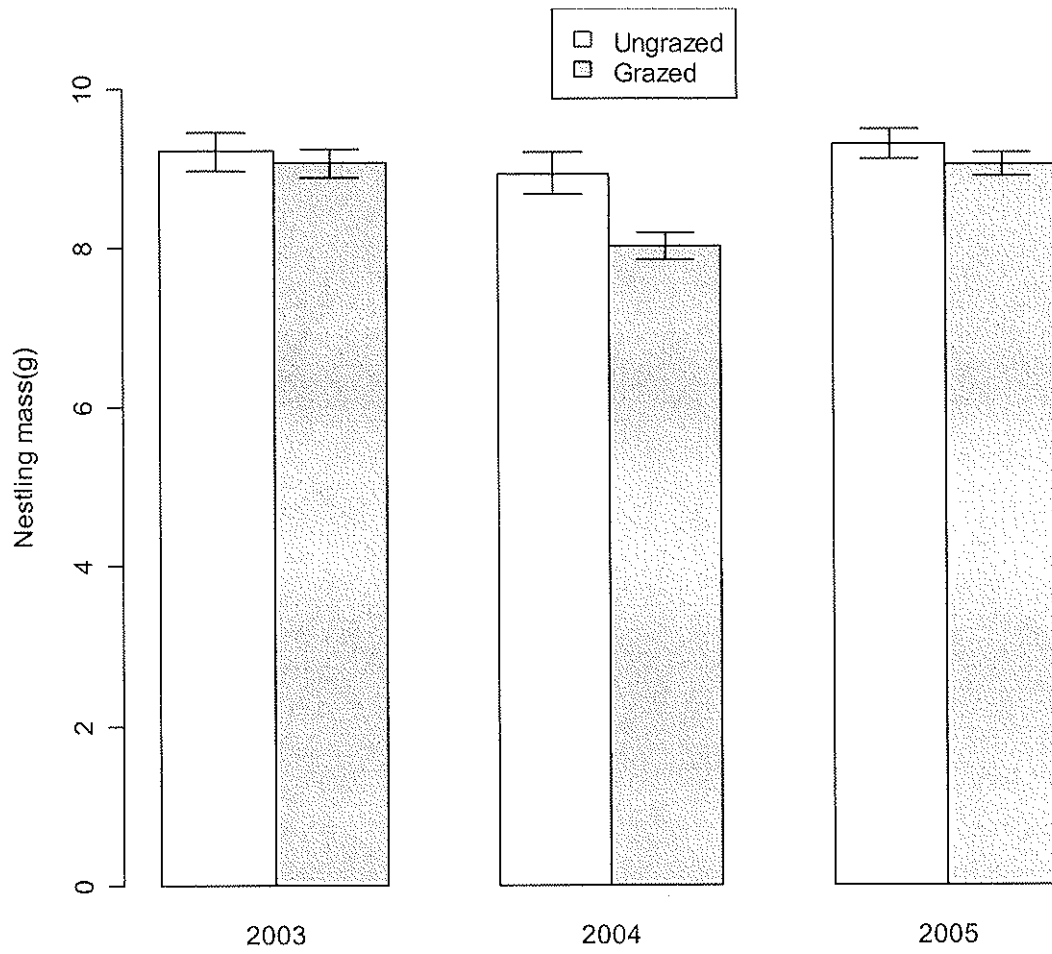


Figure 7

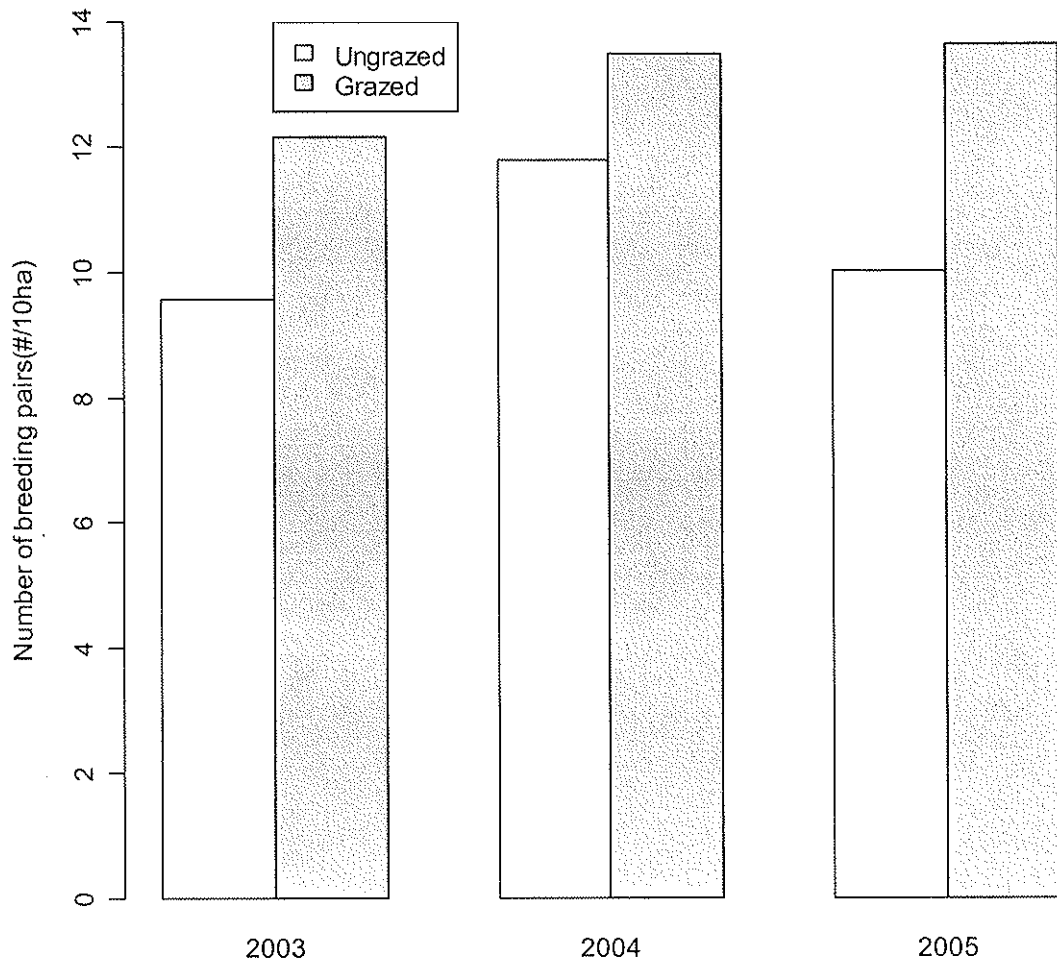


Figure 8

Chapter 2

EFFECTS OF MICROHABITAT SELECTION ON NEST SURVIVAL AND NESTLING MASS IN BREWER'S SPARROWS

ABSTRACT

I examined how nest-site selection as influenced by vegetation condition at the nest-shrub scale, nest-patch scale, and understory layer affects nest survival and nestling mass of Brewer's Sparrows in a sagebrush-dominated habitat. Models that included nest-patch variables, such as average shrub height, shrub canopy cover, and potential nest-shrub density, received the strongest support in the set of candidate models. However, there were five models, from the best-approximating model to the fifth-ranked model, within $2 \Delta AIC$; all five of these models included variables that represented characteristics of shrubs at the nest-patch scale. This indicates that nest-patch variables, rather than nest-shrub or understory-layer variables, were more strongly associated with nest survival. Potential nest-shrub density was positively, and average shrub height and shrub canopy cover were negatively, associated with nest-survival rates of Brewer's Sparrows. The positive correlation between potential nest-shrub density and nest survival can be explained by the predation hypothesis, which indicates that risk of predation decreases with increasing density of shrubs. However, negative correlations between canopy cover or average shrub height, and nest survival are more likely explained by association with nest microclimate or abundance of different types of predators. The best-approximating models for nestling mass included nest-shrub size and average nest cover. Shrub size was positively, and nest cover was negatively, associated with nestling mass. Contrary to the nest-survival model, nestling mass was strongly associated with nest-shrub variables

rather than with nest-patch or understory-layer variables. Nest-site selection of Brewer's Sparrows was a function of two different scales and there were tradeoffs on fitness consequences between nest-site selection based on risk of predation and that based on nest microclimate.

INTRODUCTION

Nest-site selection and habitat selection during reproduction are among the most common behavioral decisions that affect the fitness of animals (Alcock 1997; Clark and Shutler 1999), and this process generally is hierarchical from large scale to small scale (Hutto 1985). Animals select their breeding habitats first, and then select specific nest sites within habitats (i.e. a nonrandom portion of their habitat use) to maximize reproductive performance and survival (Fretwell 1972; Pulliam and Danielson 1991; Block and Brennan 1993; Holmes et al. 1996; Clark and Shutler 1999; Morris 2003). If reproductive success differs in response to the selection of breeding habitats and nest sites, natural selection should favor outcomes that result in higher numbers of surviving offspring and a higher probability of parental survival (Jaenike and Holt 1991). However, the relationship between these decisions and fitness is not always positive, because the most preferred habitats and nest sites do not always result in the highest reproductive success or adult survival (e.g. Thompson 1988; Holway 1991; Filliater et al. 1994; Mayhew 1997; Hoover and Brittingham 1998; Misenhelter and Rotenberry 2000; Willson and Gende 2000; Kolbe and Janzen 2002; Lloyd and Martin 2004). There are several factors to consider when evaluating habitat selection, including resources (Holmes et al. 1996; Morris and Knight 1996; Rotenberry and Wiens 1998; Morris and

Davidson 2000), conspecific and interspecific interactions (Fretwell 1972; Pulliam and Danielson 1991), microclimate and thermoregulation (With and Webb 1993; Wiebe and Martin 1998; Martin 2001; Kolbe and Janzen 2002), and predation risk (Martin 1992, 1993, 1998; Clark and Shutler 1999). If the combination of these factors increases fitness, we refer to the habitats as good habitats.

Two hypotheses that have been developed to explain the evolution of nest-site selection in birds stress the importance of reducing predation risk (Martin 1993), and increasing stability of thermal effects (With and Webb 1993; Wolf and Walsberg 1996; Lloyd and Martin 2004). Because these hypotheses are tightly associated with each other, it is very difficult to test them individually. However, each of these hypotheses reinforces the concept that nest-site selection is tightly connected with reproductive performance.

Among these hypotheses, predation potentially plays the most critical role in habitat selection in birds (Martin 1993). Parents at nests, and the nestlings themselves, face a high risk of predation, and parental movements around nests potentially attract predators (Martin and Ghalambor 1999; Ghalambor and Martin 2000). Predation risk is especially high for open-cup nesting birds given that predation is the most common cause of nest failure for these species (Martin 1988, 1992; Martin and Ghalambor 1999; Ghalambor and Martin 2000). However, other hypotheses still can be useful in explaining the evolution of nest-site selection in birds. Nest temperatures outside the thermoneutral zone may result in reduced clutch size, slower nestling growth, and increased energy expenditure by adults during the breeding season (Murphy 1985; Nager and van Noordwijk 1992; Williams 1993; Wolf et al. 2000; Wiebe 2001; Weathers et al.

2002). Food abundance also affects reproductive performance (Quinney et al. 1986; see Martin 1987, 1995; Simons and Martin 1990; Siikamäki 1998; Naef-Daenzer et al. 2000). All of these types of stress and/or extra energy use by adults and nestlings might reduce future reproductive output.

One of the most important keys to represent habitat conditions and describe nest-site selection in birds is vegetation features at breeding sites. Vegetation cover around nests can reduce potential predation risk (Martin 1993, 1998) and change nest microclimate (Martin 1998; Kim and Monaghan 2005; Suedkamp Wells and Fuhlendorf 2005). Vertical vegetation structure could influence the type (avian versus mammalian) and abundance of predators in breeding habitats, and the different type of predators could attack nests or adults at different rates (Liebezeit and George 2002). Vegetation features around nests also affect nest microclimate by blocking or accepting direct solar radiation or wind (Wolf and Walsberg 1996). Moreover, birds use vegetation features as cues to select breeding habitats. As a result, vegetation features can strongly influence nest survival and other reproductive parameters.

“Sagebrush” Brewer’s Sparrows breed exclusively in sagebrush (sagebrush obligates); therefore, alteration of this habitat can have serious effects on their population trends and nest-site selection (Wiens and Rotenberry 1981; Knick 1999; Paige and Ritter 1999; Rotenberry et al. 1999). Owing to loss and degradation of sagebrush lands from agriculture, livestock grazing, fire, and invasion of exotic plants, the amount of breeding habitat for Brewer’s Sparrows has declined rapidly. Only about 39 million ha of sagebrush remain out of the 60-100 million ha that originally occurred in the West (Sturges 1973; Wiens and Rotenberry 1985; Holechek et al. 1998; Paige and Ritter 1999),

and much of these lands are in poor to fair condition according to Bureau of Land Management assessments (J. Marks pers. comm.).

As a result of habitat alteration, numbers of several species of sagebrush-inhabiting birds have declined over the past few decades (Reynolds and Trost 1981; Saab and Rich 1997; Paige and Ritter 1999). The nominate subspecies of Brewer's Sparrow is one such bird. According to the most recent compilation of Breeding Bird Survey data (covering the period from 1966 to 2006), Brewer's Sparrow numbers have decreased by an estimated 2.3% per year across the species' entire geographic range and by 1.9% per year in Montana (Sauer et al. 2007). Many researches have reported on habitat selection by nesting Brewer's Sparrows and on how their preferred habitats affect abundance (Best 1972; Schroeder and Sturges 1975; Bock and Bock 1987; Kerley and Anderson 1995). However, the abundance or density of birds in a particular habitat type does not necessarily equate with habitat quality (Van Horne 1983). Therefore, estimating the strength of the link between vegetation characteristics at nest sites and reproductive output is very important in assessing habitat quality and predicting future population trends of the species.

The goal of my study was to evaluate which habitat conditions are linked to higher reproductive success rates and provide these results to land managers to improve habitat conditions and sustain Brewer's Sparrow populations. I examined how vegetation conditions and structures from two different scales and one layer, nest-patch scale, nest-shrub scale, and understory layer, affect nest survival and nestling mass of Brewer's Sparrows. In addition, I examined which particular vegetation variable or combinations of variables were most strongly related to nest survival and reproductive performance. In

order to evaluate these questions, I developed two sets of candidate models; each of those models described how vegetation features of two different scales and one vegetation layer influenced nest survival and nestling size of Brewer's Sparrows, and used Akaike's Information Criterion (AIC) to select the best model.

METHODS

Study Plots

I studied Brewer's Sparrows in the Blackfoot Valley near Ovando, Montana, during the breeding seasons of 2003-2005. I established four study plots (each 30-32 ha) in 2003, two of which were within ungrazed portions of Waterfowl Production Areas (H2-O and Kleinschmidt) managed by the U.S. Fish and Wildlife Service, and two of which were private lands that were grazed by cattle. The Kleinschmidt plot was burned by wildfire in August 2003 after nesting activity of Brewer's Sparrows ended, but before I had collected vegetation data. In 2004 and 2005, I selected another Waterfowl Production Area, Blackfoot, for the replacement of the burned site. The Blackfoot plot was classified as ungrazed because livestock grazing had occurred only twice during short periods in summer, the last 20 years, and the vegetation condition and composition were very similar to those on the other ungrazed plots. All plots shared similar climate and elevation and were close to each other in order to control abiotic variation, but individual sparrows in one site did not use other sites for their daily activities. Each plot was at least 500 m from the next nearest one to avoid pseudoreplication. To make it easier to map the location of sparrow nests and pairs, I created a grid on each plot by marking points (with flagging tape or rebar) at 50-m intervals.

The dominant sagebrush species throughout the study area was big sagebrush (*Artemisia tridentata*). The main grass species on the ungrazed plots were rough fescue (*Festuca campestris*) and Idaho fescue (*Festuca idahoensis*); quackgrass (*Elymus repens*) was the dominant grass species on the grazed plots.

Nest Searching and Monitoring

To find nests, I systematically searched each territory to check every potential nest shrub and to flush incubating adults by shaking shrubs, or I observed adult behavior (e.g. carrying nest materials or food for young; Martin and Geupel 1993). I recorded nest locations with a GPS unit and marked each nest with flagging tape placed at least 10 m north of the nest. Nest searches occurred during morning.

I checked nests after 13:00 every day when I expected eggs were due to hatch (based on nest-initiation day); when I was not able to estimate nest-initiation day, I checked nests every day to determine the exact day of hatching. Otherwise, I monitored nests every two days. During each nest check, I recorded the number of eggs or nestlings and nest fate. To have as little influence as possible on the outcome of nesting attempts, I approached each nest with special care to minimize disturbance to adults and nestlings and spent as little time as possible at nests while recording data (Martin and Geupel 1993; Vander Haegen et al. 2002). I considered that a nesting attempt had been completed if all nestlings fledged, if all nest contents disappeared before fledging, or if the adults abandoned the nest.

Nest Survival and Predation Rates

I calculated daily nest survival rates (DSR) at each nest by the logistic-exposure model (Shaffer 2004) using statistical software R. I defined a nest as successful if at least

one nestling fledged. I accepted as evidence of success if I observed fledglings or parents' feeding behavior near the nest within two days after fledging. I assumed that predators had taken nests if eggs disappeared before hatching, if healthy nestlings suddenly disappeared before expected fledging dates, or if nests were damaged and empty without catastrophic weather having occurred.

Nestling Mass and Ectoparasitism Rates

I measured nestling mass (± 0.1 g) and tarsus length (± 0.1 mm) when nestlings were seven days old as an index of nestling size. Nestling measurements were taken after 13:00 to decrease daily variation in mass. Because Brewer's Sparrow nestlings do not achieve asymptotic growth during the nestling period (Petersen et al. 1986), I considered mass of the nestling at day seven, which is just before fledging, to reflect the condition of nestlings and potential survivability after fledging. Also on day seven I visually checked the bodies of each nestling to record the number and location of parasitic larvae.

Vegetation Survey

At nest-patch scale and understory layer, I collected vegetation data at 66 nests (48 grazed, 18 ungrazed) in 2003, 149 nests (85 grazed, 64 ungrazed) in 2004, and 150 nests (86 grazed, 64 ungrazed) in 2005 when nesting activity ended. I used a modified version of Breeding Biology Research and Monitoring Database (BBIRD) grassland vegetation sampling protocol (Martin et al. 1997). Vegetation plots of both nest-patch scale and understory layer were composed of a 5-m radius circle around a nest. Within the circle, I established four quadrants with axes along the four cardinal directions. I delineated 1.0 m, 3.0 m, and 5.0 m points on each cardinal direction from the center.

At nest-patch scale, I counted the number of potential nest-sagebrush shrubs (>50

cm tall) and measured the heights of the first four sagebrush shrubs from the center. I used the line-intercept method to measure canopy cover of sagebrush (>30 cm tall). There were two transects in each vegetation plot, and each transect was 10 m long. At understory layer, I estimated grass/forb and bare/rock ground cover in each quadrant and measured grass height at the center and three other points in each cardinal direction. At nest-shrub scale, I measured nesting sagebrush characteristics such as nest height, nesting sagebrush height, size, and nest cover. I classified nest shrubs into five size groups depending on height, length, and width (5 was the largest 1 the smallest). I estimated nest cover visually from directly above the nest and by looking at the nest from each cardinal compass direction, with my eyes at nest height while I stood 1 m away from the nest. Abbreviations of vegetation variables that I used in my models are explained in Table 1.

A priori Hypotheses

Nest-patch scale.—I hypothesized that sagebrush canopy cover, average sagebrush height, and potential nest-sagebrush density may associate with nest survival or nestling mass. Previous studies have documented that Brewer's Sparrows prefer greater sagebrush canopy cover and higher density of sagebrush shrubs compared to average levels of those variables, for their nest sites (Best 1972; Petersen and Best 1985; Chalfoun 2006). My study also showed the same trends as those studies (Chapter 1). Canopy cover and shrub density would seem to be positively associated with each other; however, in reality, the relationship between these two variables was not strong ($R^2 = 0.19$). Large sagebrush shrubs can create a large area of canopy cover with a small number of plants in a nest patch, but a large number of smaller sagebrush shrubs is

necessary to create the same area of canopy cover as the large shrubs create. Nest patches with a preponderance of large shrubs can have the same average canopy cover as nest patches with a much higher density of smaller shrubs. Therefore, I included these two variables in a model. Each variable and combination of these three variables in my models indicated the complexities and volume of habitat vegetation features. If sparrow's preferences (i.e. positive correlation) match the best approximating model that are selected by AIC, and if the model shows positive correlation with nest survival rates or nestling mass, I conclude that Brewer's Sparrow's preferences are adaptive. Furthermore, I conclude that they select nest sites that are characterized by greater vegetation complexity and volume and suggest that these relationships are closely related to risk of nest predation. In this case, the models at nest-patch scales should receive stronger support than those at nest-shrub scales. This is because a clump of sagebrush shrubs works better to hide parents' activities and a nest from predators than a single sagebrush shrub. But, I predicted the opposite selection if nest-microclimate condition is a main factor of nest-site selection, because dense and tall sagebrush shrubs around nests can block direct solar radiation at nests during cold mornings.

Understory layer.—I selected average grass height, grass/forb ground cover, bare/rock ground cover as understory-layer variables; additionally I added a nest-height variable in some a priori models. A single variable or combinations of these variables represented the status (i.e. presence or absence) and volume of understory layer in nest patches. If predation is an important factor in nest-site selection, grass/forb should be positively correlated with nest survival or nestling mass. The variation in sagebrush canopy cover and grass/forb ground cover was large within each study plot, so grass/forb

ground cover must be important where sagebrush canopy cover is low. Nest height with understory-layer variables may affect nest survival and nestling mass. This is because if these are important variables to reduce risk of predation, low nests must be at an advantage compared with high nests. In contrast, if nest microclimate is a leading factor, higher nests may have an advantage because they are exposed to solar radiation earlier than are lower nests.

Nest-shrub scale.—Nest-shrub height, nest-shrub size, average nest cover, and nest cover from above, east, and south may affect nest survival rates and nestling mass of Brewer's Sparrows. Nest-shrub height and nest-shrub size were correlated with each other; therefore, I did not use these variables together in one model. Nest-shrub size was calculated depending on the height, length, and width of nest shrubs, and was classified into five groups (five was the largest group, and one was the smallest). Nest cover may positively correlate with nest survival if predation is a primary factor, but negatively correlate with nest survival if nest microclimate is a primary factor. The same trends are expected between nest cover and nestling mass.

Statistical Methods

Nest survival.—I used logistic-exposure models to evaluate the effects of vegetation on nest survival (Shaffer 2004). I included year in all candidate models because yearly fluctuations in nest survival are a common phenomenon, especially for open-cup nesting passerines (Rotenberry and Wiens 1989). Moreover, fluctuations in predation rates and temperature regimes, which largely affect nest survival rates (Rotenberry and Wiens 1989, 1991; Rodenhouse and Holmes 1992; Schmidt and Whelan 1999; Franklin et al. 2000), were common in my study area (see Chapter 1). Because

grazing affects vegetation structure and condition, I added grazing variable to the best-approximating models to understand how grazing affects nest survival through altering vegetation features. However, the effects of the grazing variable were very small (nest survival: 1.7 AIC unit worse), so I did not include it in my models. Candidate models are listed in Table 2.

I used AIC to select the best model from a set of candidate models (Burnham and Anderson 2002). AIC is an index used to identify which competing models best fit the information in the data set. I used AIC rather than AICc for model selection regarding the effect of vegetation on nest survival because sample size was large ($n = 2,655$). I ranked candidate models from AIC best model to poorest using Δ AIC and Akaike weights (Burnham and Anderson 2002). Model(s) with lowest AIC values refer to the best-approximating model. Because AIC is a relative scale, I used Δ AIC for evidence of support of the AIC best model. I considered that if Δ AIC was within <2 points from the best AIC model, then both models received the same magnitude of support (Burnham and Anderson 2002). If Δ AIC was 2-10 from the AIC best model, these models received less support. Lastly if Δ AIC was >10 , these models received no support (Burnham and Anderson 2002). Akaike weights, which are normalized for the models (i.e. summing to 1), were calculated to evaluate strength of support for each model. Models with larger weights received stronger support than those with smaller values.

Nestling mass.—I used multiple-regression models to evaluate effects of vegetation on nestling mass. I included year, parasite loads in nestlings, and grazing variables in all of the candidate models to account for these effects from my models to evaluate vegetation effects on nestling mass. I used AICc for this model selection

because sample size was 123, which was smaller than $n/k < 40$ (where k = the number of estimated parameters; Burnham and Anderson 2002). Other methods I used for understanding AIC effects were the same as the nest-survival analysis above. Candidate models I used for analyzing vegetation effects on nestling mass are listed in Table 5.

RESULTS

Nest Survival

I found 425 Brewer's Sparrow nests during the breeding seasons of 2003, 2004, and 2005. I used data from 335 of these nests to evaluate the effects of nest microhabitat on nest survival. The other nests were excluded from analyses because vegetation data were missing (owing to fire destroying a study plot), or nest fates were unknown.

Models that included nest-patch variables, such as average shrub height, shrub canopy cover, and potential nest-shrub density, received stronger support than models that included nest-shrub variables, such as nest-shrub height, nest-shrub size, nest cover and nest height (Table 3). In addition, models that included variables that explained the characteristics of understory layer such as average grass height, grass/forb ground cover, bare/rock ground cover, and nest height received the poorest support (Table 3). The best-approximating model (AIC = 749.70) included average shrub height, shrub density, and shrub canopy cover. However, the difference between the best model and other models was very small; there were five models within 2 AIC units of one another (Table 3). Akaike weights indicated a high degree of uncertainty among models (Table 3).

The best-approximating model included shrub canopy cover (slope \pm S.E., -0.024 ± 0.012), which was negatively associated with nest survival (Figure 1a); average shrub

height (slope \pm S.E., -0.015 ± 0.010), which also was negatively associated with nest survival (Figure 1c); and shrub density (slope \pm S.E., 0.891 ± 0.596), which was positively associated with nest survival (Figure 1c). I listed five models from the best-approximating model to the fifth ranked model in Table 4. Parameters were transformed by a logistic-exposure-link function (Shaffer 2004), so it was necessary to back transform them to understand the effects. For example, if nest habitat changed from 40% canopy cover, 1.0 shrub per m², and 100 cm shrub height to 20% canopy cover, 0.5 shrubs per m², and 60 cm shrub height, the daily nest survival changed from 0.986 to 0.993, and nest survival during incubation and nestling periods changed from 73.9 to 85.2%.

Nestling Mass

I used vegetation data from 123 nests that were found before hatching (i.e. nestlings were of known age) for my model selection. Moreover, I selected nests that included three or four nestlings to decrease the effects of brood size on nestling mass. I averaged nestling mass per nest and used it for the response variable of multiple regressions for model selection.

The best-approximating model included nest-shrub size and average nest cover (Table 6). Nest-shrub size was positively associated with nestling mass; as nest-shrub classes increased from one to two, to three, to five, the average nestling mass increased 0.502 (SE = 0.217), 0.553 (SE = 0.211), and 0.971 (SE = 0.306) grams, respectively. Class four was not applicable to estimate the association between nestling mass and shrub size class because of higher standard error (-0.313 ± 0.298). Average nest cover was negatively associated with nestling mass (slope \pm S.E., -0.012 ± 0.0057). The value of AICc was 313.83, and the second-ranked model had an AICc value, 316.23, which were

more than 2 Δ AICc larger than the best-approximating model (Table 6); therefore, I concluded that the model that included shrub size and average nest cover strongly represented the relationship between nestling mass and vegetation structure. Akaike weight, 0.753, also indicated strong support of this model (Table 6). I listed a number of parameters, AICc, Δ AICc, and Akaike weights of all candidate models in Table 6. The best-approximating model (values and names in parentheses explain a standard error for each β and the name of variables) was:

Nestling mass = 9.702 + 0.498 (0.215, shrub-size 2) + 0.539 (0.208, shrub-size 3) - 0.318 (0.296, shrub-size 4) + 0.953 (0.302, shrub-size 5) - 0.012 (0.0055, average nest cover) - 0.601 (0.220, year2004) + 0.242 (0.232, year2005) + 0.253 (0.168, parasite) - 0.513 (0.155 grazing). For example, if a nestling lived in nest-shrub class 1 (smallest) with 90% average nest cover, estimated size of the nestling is 8.622 grams after accounting for the effects of parasitized status, plots, and year. However, if a nestling lived in nest-shrub class 5 (largest) with 60% average nest cover, estimated size of the nestling is 9.935 grams, which is 15.2% heavier than the first example.

The first through fifth ranked models included only nest-shrub variables. None of the models with nest-patch and understory-layer variables received support by AIC model selection.

DISCUSSION

Nest Survival

Models including variables at nest-patch scale received the strongest support by AIC compared with models at other scales and vegetation layers, which suggests that nest

survival of Brewer's Sparrows is closely related to nest-patch quality and conditions. Other models that represented the characteristics of understory layer at nest patches and the nest shrub did not receive support by AIC model selection. The best-approximating model included canopy cover, potential nest-shrub density, and average shrub height. Although, there were five models within two AIC units of the best-approximating model (Table 4), all of these models included variables that represented the characteristics of shrubs in nest patches. Variables at the nest-shrub scale may not be important in the sagebrush system even if predation is a main factor in Brewer's Sparrow nest-site selection. This is because sagebrush shrubs in the largest group are still relatively small compared with the nest substrates of other species of passerines (i.e. trees or other shrub species), and they are not large and dense enough to hide a nest from predators when parental activities around a nest are high. Therefore, the size of clumps of sagebrush shrubs around a nest may be a more important variable than the size of single nest shrub.

Nest-site selection of Brewer's Sparrows (i.e. their preferred nest sites) did not exactly match the nest sites where sparrows had the highest rates of success. Sagebrush canopy cover and average shrub height were negatively correlated with nest survival (Figure 1a, c). However, number of breeding pairs was positively correlated with sagebrush canopy cover in my study area, as found in previous studies (Larson and Bock 1986; Rotenberry et al. 1999; Chalfoun 2006). If nest sites preferred by sparrows had matched higher rates of nest survival, I would have observed higher nest survival at more dense and structurally complicated sites, but my results were opposite of this. It is important to keep in mind that this result does not mean that the lower the sagebrush canopy cover, the better the conditions for reproduction in Brewer's Sparrows. Mean,

range, and interquartile range of canopy cover were 0.381, 0.738, and 0.165, and those of average shrub height were 86.2, 115.0, and 19.0 cm, respectively. Therefore, excluding some extreme cases, lower values of canopy cover and average shrub height still provide fairly dense cover and tall shrubs for Brewer's Sparrows. Within these conditions, nest survival increases as canopy cover and average shrub height decrease. Without question, sagebrush canopy cover is important for Brewer's Sparrows, but canopy coverage at the high end of the range seems to have a negative effect on their reproduction. Additionally, the Brewer's Sparrows I studied almost always built nests in shrubs that exceeded 50 cm in height: nest-shrub height in only 3 of 335 nests was below 50 cm, but in all three cases shrub height was just under 50 cm (45, 47, and 47 cm).

There are two potential explanations for these negative effects. One is the association with thermal conditions at the nest, and the other is abundance of different types of predator species that use different search strategies. In my study area, the lowest nest temperatures in the morning remain low from the beginning of the breeding season in mid-May to the nestling period of the first nest attempt in mid-June, (mean \pm 95% CI: $0.95 \pm 1.49^\circ\text{C}$). If vegetation cover at nests is low, Brewer's Sparrow nests might gain a thermal advantage from direct sunlight heating the nests sooner than at nests placed in denser shrub cover. Twenty percent canopy coverage by shrubs in a nest patch is probably dense enough to hide a nest from predators, and canopy coverage greater than 20% may not provide any extra advantages (e.g. decrease nest-predation rates for sparrows). Conversely, too high a density of nest cover might be thermally disadvantageous to nest survival. Researches have shown that in cold environments, warmer nests produce larger nestlings and have higher nest survival (Webb 1987;

Dawson et al. 2005). Alternatively, different predators use different cues or strategies when searching for nests (Liebezeit and George 2002). Avian predators use visual cues to locate nests, whereas mammalian predators tend to use olfaction or auditory cues to locate nests. These differences may be altered by density of shrub canopy cover. For example, dense shrub canopy cover may hold smells produced by nests with nestlings longer than does sparse shrub canopy cover.

Paradoxically, shrub density was positively associated with nest survival. This selection matched the preferred nest sites of Brewer's Sparrows. This trend was explained by the potential-prey-site hypothesis. This hypothesis predicts that as the number of potential nest sites increase (in my case, sagebrush density), the number of nest failures by predation decreases. Chalfoun's (2006) study of Brewer's Sparrows in central Montana supported the potential-prey-site hypothesis. I did not conduct experiments to verify this hypothesis; however, my observational result clearly supported this hypothesis.

Nestling Mass

Models at the nest-shrub scale received stronger support by AICc than models at understory layer or nest-patch scale, which suggests that nestling mass was closely related with nest-shrub variables, but not with nest-patch variables, as was nest survival. Variables that represented conditions of the understory layer at nest patches were ranked in the middle and were also weakly supported by AICc. The best-approximating model included nest-shrub size and average nest cover. The second-ranked model, which included nest-shrub size, was 2.40 Δ AICc units larger than the best-approximating model (Table 6); therefore, I concluded that the best-approximating model received strong

support compared with other candidate models. The grazing variable improved AICc value a little, but it did not affect ranking of models.

Risk of predation may not be an important factor in explaining the relationship between nestling mass and vegetation features. Nest-patch models should have been received stronger supports if predation would be a leading factor of nestling mass, but this was not happened in my study area. Moreover, the negative correlation between average nest cover and nestling mass also supported this phenomenon. However, why nestlings raised in the smallest group of shrubs were the smallest, and those in the largest group of shrubs were the largest, remains unclear.

Differences in nest microclimate may explain the effects of vegetation on nestling mass in my study area. Nestlings require a certain period to develop thermoregulatory abilities (Visser 1998; Pereyra and Morton 2001). During this period, parents must brood the young to keep their body temperature optimal. This behavior can be costly to parents because of increased energy expenditure, increased predation risk, and decreased time for self maintenance (Martin 1988, 1992; Bosque and Bosque 1995; Düttmann et al. 1998). Therefore, there might be an advantage for sparrows to placing nests in location that receive direct solar radiation during periods when nest temperatures are still cold. Wolf et al. (2000) demonstrated that heat gain from direct solar radiation is very efficient for small birds. Moreover, Dawson et al. (2005) reported that nestlings in warmer nests were larger than those in colder nests. These results matched my results in that average nest cover was negatively associated with nestling mass. Mean, range, and interquartile range of average nest cover were 69.6, 73.0, and 22.0%, respectively. This does not mean that the minimum nest cover provides an advantage for nestlings. Because sagebrush

generally provides good cover for nests of Brewer's Sparrows, the minimum nest cover that Brewer's Sparrows selected still can hide nests from predators. Moreover, nest-predation rates in my study system were relatively low (Chapter 1). There are probably some advantages in using larger sagebrush for nest shrubs. For example, large shrubs may provide protection from strong winds with minimum loss of the advantages of direct solar radiation on the nest. As a result of these effects, nests in large shrubs maintain more moderate temperature than nests in small shrubs.

Effects of food abundance and quality on nestling mass remain unclear. Nestling growth rates and mass primarily are a function of predation risk, nest microclimate, and food abundance (Bosque and Bosque 1995; Gebhardt-Henrich and Richner 1998; Martin 2002). However, food abundance as estimated by feeding rates did not differ among plots or between grazing treatment (Chapter 1). Food was probably abundant everywhere in my study area; however, I could not observe how prey species composition and prey size were different depending on vegetation features and gradients. Therefore, this is a potential explanation to describe the relationship between nestling and vegetation features over nest-microclimate conditions.

Conclusions

Nest-site selection of Brewer's Sparrows was a function of two different sales. Nest survival was closely related with nest-patch variables, whereas nestling mass was closely related with nest-shrub variables. The fitness consequences for sparrows did not match their preferred nest-site features except for potential nest-shrub density in nest survival models. Predation risk appears to play an important role in nest-site selection in that Brewer's Sparrows selected nest patches with a high number of potential nest shrubs,

and these sites had decreased predation rates. However, at the same time, nest-site selection seemed to adversely affect nest survival from nest-microclimate and nestling size perspectives. I observed apparent tradeoffs in fitness consequences between nest-site selection based on predation risk and that based on nest-microclimate conditions. Because I could not conduct experiments, it is very difficult to differentiate predation and food abundance effects from a microclimate effect; however, my results plausibly explained the relationship between vegetation features and nest survival, or nestling mass. To understand this phenomenon in more detail, experimental manipulations will be necessary.

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Table 1. All abbreviations and scales or layer of vegetation variables which were in models of nest survival and nestling mass model selections.

Variable name	Abbreviation	Scales or layer
Average shrub height	aveshtt	Nest patch
Potential nest shrub density	shdensity	Nest patch
Canopy cover	canopyc	Nest patch
Average grass height	avegraht	Understory layer
Average grass/forb ground cover	avegraforb	Understory layer
Average bare/rock ground cover	avebarock	Understory layer
Nest height	nestht	Nest shrub
Nest shrub height	nshht	Nest shrub
Nest shrub size	shsize	Nest shrub
Nest cover overhead	ovrcov	Nest shrub
Nest cover north	ncovern	Nest shrub
Nest cover east	ncovere	Nest shrub
Nest cover south	ncovers	Nest shrub
Nest cover east	ncovere	Nest shrub
Nest average cover	avecover	Nest shrub

Table 2. The candidate models and associated scales or layer for evaluation of vegetation effects on nest survival of Brewer's Sparrows.

Model id	Approximating model	Scales or layer
1	aveshht	Nest patch
2	canopyc	Nest patch
3	shdensity	Nest patch
4	canopyc+shdensity	Nest patch
5	canopyc+aveshht	Nest patch
6	aveshht+shdensity	Nest patch
7	aveshht+shdensity+canopyc	Nest patch
8	avegraht	Understory layer
9	avebarock	Understory layer
10	avegrafort	Understory layer
11	avegrafort+avegraht	Understory layer
12	avegrafort+nestht	Understory layer
13	shsize	Nest shrub
14	shsize+avecover	Nest shrub
15	nshht+nestht	Nest shrub
16	nshht+avecover+nestht	Nest shrub
17	avecover	Nest shrub
18	ovrcov	Nest shrub
19	ovrcov+ncovere+ncovers	Nest shrub
20	year	
21	constant	
22	global	

Table 3. Summary of the result of model selection for the vegetation effects on nest survival of Brewer's Sparrows.

Model id	K	AIC	Δ AIC	AIC Weight	Deviance
7	6	749.70	0	0.1466	737.70
4	5	749.82	0.12	0.1380	739.82
5	5	750.11	0.41	0.1194	740.11
1	4	750.13	0.43	0.1182	742.13
2	4	750.53	0.83	0.0968	742.53
6	5	751.81	2.11	0.0510	741.81
20	3	751.84	2.14	0.0503	745.84
15	5	752.36	2.66	0.0388	742.36
12	5	752.64	2.94	0.0337	742.64
17	4	753.17	3.47	0.0259	745.17
13	7	753.33	3.63	0.0239	739.33
3	4	753.68	3.98	0.0200	745.68
8	4	753.76	4.06	0.0193	745.76
9	4	753.76	4.06	0.0193	745.76
10	4	753.77	4.07	0.0192	745.77
16	6	753.77	4.07	0.0192	741.77
18	4	753.84	4.14	0.0185	745.84
21	1	754.39	4.69	0.0140	752.39
14	8	754.40	4.70	0.0140	738.40
11	5	755.61	5.91	0.0076	745.61
22	18	757.33	7.63	0.0032	721.33
19	6	757.35	7.65	0.0032	745.35

Table 4. Estimated parameters, and variables and standard errors in parenthesis of the best-approximating model to eighth ranked model for the effects of vegetation features on nest survival of Brewer's Sparrows.

Model id	Parameter estimates with 1 SE
7	$\text{Log}_e(s/[1-s])=5.851-0.015(\text{aveshht}, 0.010)+0.891(\text{shdensity}, 0.596)-0.024(\text{canopyc}, 0.012)$
4	$\text{Log}_e(s/[1-s])=4.908-0.028(\text{canopyc}, 0.011)+0.938(\text{shdensity}, 0.593)$
5	$\text{Log}_e(s/[1-s])=6.309-0.014(\text{canopyc}, 0.010)-0.016(\text{aveshht}, 0.010)$
1	$\text{Log}_e(s/[1-s])=5.901-0.019(\text{aveshht}, 0.010)$
2	$\text{Log}_e(s/[1-s])=5.310-0.018(\text{canopyc}, 0.010)$

Table 5. The candidate models and associated scales or layer for evaluation of vegetation effects on nestling mass of Brewer's Sparrows.

Model id	Approximating model	Scales or layer
1	aveshht	Nest patch
2	canopyc	Nest patch
3	shdensity	Nest patch
4	canopyc+shdensity	Nest patch
5	canopyc+aveshht	Nest patch
6	aveshht+shdensity	Nest patch
7	aveshht+shdensity+canopyc	Nest patch
8	avegraht	Understory layer
9	avebarock	Understory layer
10	avegrafort	Understory layer
11	avegrafort+avegraht	Understory layer
12	avegrafort+nestht	Understory layer
13	shsize	Nest shrub
14	shsize+avecover	Nest shrub
15	nshht+nestht	Nest shrub
16	nshht+avecover+nestht	Nest shrub
17	avecover	Nest shrub
18	ovrcov	Nest shrub
19	ovrcov+ncover+ncoverw	Nest shrub
20	ovrcov+ncover+ncoverw+ncoverw	Nest shrub
21	grazing+year+parasite	
22	constant	
23	global	

Table 6. Summary of the results of model selection for the vegetation effects on nestling mass of Brewer's Sparrows.

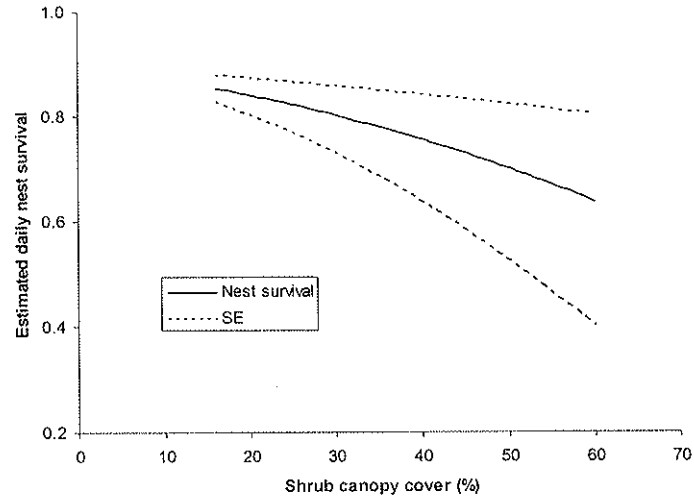
Model id	K	AIC	AICc	Δ AICc	AICc Weights	Deviance
14	11	311.45	313.83	0.00	0.7532	289.45
13	10	314.27	316.23	2.40	0.2262	294.27
16	9	321.21	322.80	8.97	0.0085	303.21
17	7	324.16	325.13	11.30	0.0026	310.16
15	8	324.31	325.57	11.74	0.0021	308.31
10	7	325.22	326.19	12.36	0.0016	311.22
9	7	325.99	326.96	13.13	0.0011	311.99
21	6	326.24	326.96	13.13	0.0011	314.24
12	8	326.91	328.17	14.34	0.0006	310.91
8	7	327.30	328.27	14.44	0.0005	313.30
11	8	327.15	328.41	14.58	0.0005	311.15
18	7	327.93	328.90	15.07	0.0004	313.93
3	7	328.00	328.97	15.14	0.0004	314.00
1	7	328.09	329.06	15.23	0.0004	314.09
2	7	328.21	329.18	15.35	0.0003	314.21
19	9	329.23	330.82	16.99	0.0002	311.23
6	8	329.87	331.13	17.30	0.0001	313.87
4	10	329.89	331.85	18.02	0.0001	309.89
5	10	330.02	331.98	18.15	0.0001	310.02
23	24	320.44	332.68	18.85	0.0001	272.44
20	11	330.81	333.19	19.36	0.0000	308.81
7	9	331.70	333.29	19.46	0.0000	313.70
22	2	353.04	353.14	39.31	0.0000	349.04

FIGURE LEGENDS

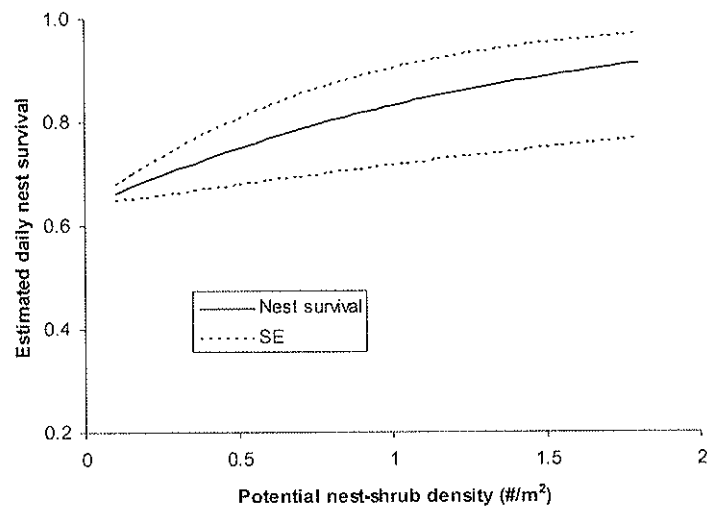
Figure 1. The relationships with estimated nest survivals of Brewer's Sparrows as a function of: a. shrub canopy cover; b. potential nest-shrub density; c. average nest-shrub height. Solid line represents mean and dashed line represents standard error of mean.

Figure 2. The relationships with estimated nestling mass of Brewer's Sparrows as a function of average nest cover. Solid line represents mean and dashed line represents standard error of mean.

a.



b.



c.

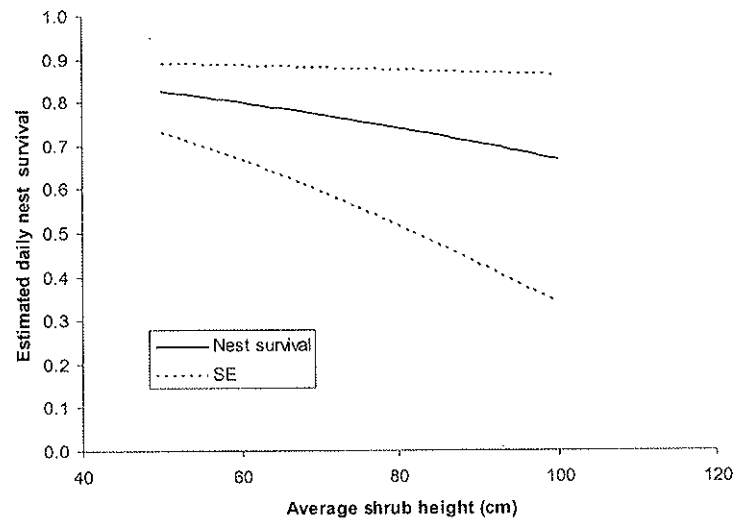


Figure 1

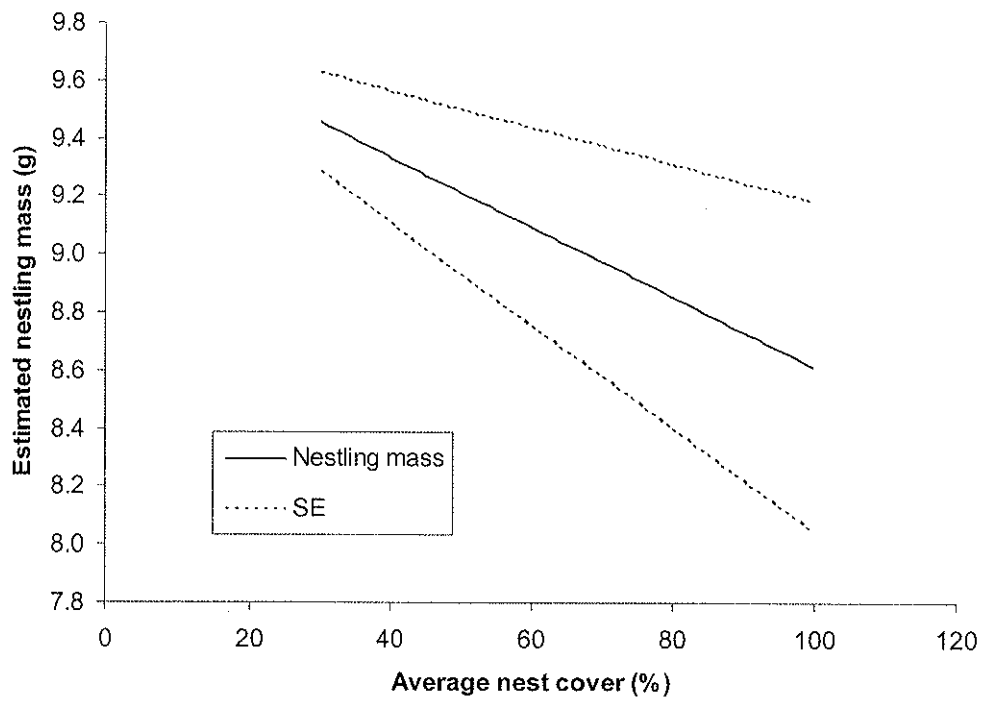


Figure 2