

FINAL REPORT

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Effects of pathways within Grand Teton National Park on avian diversity, abundance, distribution, nesting productivity, and breeding behaviors

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Summary:

Landbirds are an integral component of park ecosystems and serve a wide range of ecological roles from pollinating plants to controlling insect populations. Construction plans for a new pedestrian pathway through sagebrush habitats of Grand Teton National Park prompted research to investigate the potential impacts on avian diversity, abundance, habitat use, nesting productivity, and breeding behavior. I used a before-after/control-impact (BACI) design to investigate responses before (2007), during (2008), and after (2009-2010) pathway construction at 3 sets of paired experimental (straddling the highway and path) and control (> 500 m from the road and path) plots. Responses were also analyzed with respect to distance to the pathway. The construction and use of the pathway did not affect avian diversity or the abundance of Brewer's (*Spizella breweri*) or vesper (*Pooecetes gramineus*) sparrows. The proportion of nests on the pathway side of the highway and nest densities within 50 m of the path decreased, and average nest distances from the pathway increased post-construction, suggesting avoidance of the pathway for nesting. The primary cause of reproductive failure was nest predation. Surprisingly, Brewer's and vesper sparrows consistently fledged more young in experimental than control plots, though differences decreased after the construction year. Brewer's sparrow nest success also increased with proximity to the pathway in 2008 and 2009. These unpredicted patterns suggest a human-induced trophic cascade in which nesting birds close to the transportation corridor are indirectly benefitting due to changes in the nest predator community, though this hypothesis requires further testing. Nest predator species documented via infrared cameras included deer mice, chipmunks, weasels, elk, and garter snakes. Brewer's and vesper sparrow clutch size and Brewer's sparrow nestling mass were higher in experimental plots which may reflect the lower nest predation risk in those areas. There were no significant effects of proximity to the pathway on Brewer's sparrow egg mass, incubation rhythms, nestling feeding rates or nestling mass, suggesting that pairs that nested near the path did not alter parental investment. Brewer's sparrow site fidelity across years was unrelated to the pathway treatment, but rather appeared to reflect habitat (shrub cover) differences. However, 83% of inter-annual switches in highway side for nesting were from the pathway to the non-pathway side. The primary impact of the new pathway on nesting sagebrush birds therefore appears to be habitat loss and effective habitat loss, as gauged by the tendency of birds to avoid nesting near the transportation corridor post-pathway construction, with no evidence of acclimation over time.

Introduction

Human-induced changes to natural landscapes have become ubiquitous, resulting in exposure of wildlife populations to many novel stressors (Munns 2006). While it is clear that changes such as habitat loss can directly impact wildlife species, less clear is the extent that human presence itself functions as a disturbance that indirectly influences wildlife populations by eliciting avoidance and/or altering behaviors with fitness consequences. Animals clearly respond to perceived risk of predation by natural predators via, for example, fleeing, or altering foraging and/or breeding habitat selection (Marzluff 1988, Hakkarainen et al. 2001, Frid and Dill 2002, Blumstein 2006, Borkowski et al. 2006, Fontaine and Martin 2006*a*). Such responses can alter access to important resources, energy budgets, and therefore attributes such as body condition (Bechet et al. 2004) with potential impacts to survival and reproductive output. Changes in habitat use and breeding behaviors can therefore ultimately influence population dynamics and community structure via differential fitness. Of critical importance to the management of wildlife populations is therefore to determine whether wildlife species perceive human presence as predation risk, and how individuals respond to such risk (Beale and Monaghan 2004).

Birds alter behaviors in response to perceived predation risk (e.g., Marzluff 1988, Hakkarainen et al. 2001; Fontaine and Martin 2006*a*, 2006*b*) and direct experience with offspring predation (Chalfoun and Martin 2010*b*) by reducing investment in offspring. Such responses may be driven by the need to conserve resources for future nest attempts (Slagsvold 1984) and/or reduce activities at nests that can attract predators (Martin and Briskie 2009). If birds perceive human presence as predation risk, they may respond similarly, with consequences for the quantity and quality of offspring produced in disturbed areas. Studies of avian parental care responses with respect to human disturbance, however, have been rare (but see Delaney et al. 1999, Steidl and Anthony 2000, Verhulst et al. 2001).

I evaluated the potential impacts of a novel disturbance, the construction and use of a new multi-use, non-motorized pathway in Grand Teton National Park, on sagebrush songbird species that breed along the pathway route. Many sagebrush songbird species are declining throughout their range due to extensive habitat loss and alteration (Knick et al. 2003) and therefore represent an important focal group. Landbirds are also an integral component of park ecosystems and serve a wide range of ecological roles from pollinating plants to controlling

insect populations. Wildlife responses to human disturbance appear to be highly context-dependent (Beale and Monaghan 2004) and studies of wildlife and pedestrian pathways are sparse. I therefore focused on a diverse suite of potential response variables (Table 1) representing one of the most comprehensive studies of multiple impacts of different types of human disturbance on a breeding bird community. While a large literature documents behaviors such as flight initiation distances (e.g., Smith-Castro and Rodewald 2010) for birds in response to human presence, no researchers to my knowledge have simultaneously and/or experimentally examined multiple response variables, many representing actual components of breeding bird fitness.

Objectives

The overall goal of the research was to evaluate the potential impacts of pathway development and use by pedestrians and cyclists on breeding bird species composition, relative abundance, habitat use, reproductive success, and breeding behaviors.

Specific objectives developed in consultation with Park biologists were to identify the impacts of pathway construction and subsequent human use on avian:

1. Diversity, abundance, and community composition
2. Spatial and temporal habitat use
3. Breeding productivity and reproductive strategies
4. Site fidelity

In 2009 I initiated additional work focused on the identification and relative abundance of nest predators within the study area, to better understand observed patterns of nest predation.

Approach

Study area and focal species

The study area was located along the Teton Park Road within Grand Teton National Park, Wyoming, from the Moose entrance station extending north approximately 11 km to South Jenny Lake Junction. The paved pedestrian pathway was approximately 4 m wide and meandered along the existing transportation corridor within a varying distance of approximately 2-50 m from the highway. Focal study species were migratory songbirds (Table 2) that nest within the big sagebrush (*Artemisia tridentata*) habitats through which the pathway largely traverses. The

Brewer’s sparrow (*Spizella breweri*), a declining sagebrush-obligate (Sauer et al. 2008), was the most abundant and widespread species within the study area and therefore the focus of many of the more detailed demographic and behavioral parameters (Table 1).

Table 1. Response metrics examined during the avian pathways study, with associated focal study species, sample sizes, and whether responses were examined as part of the Before-After/Control-Impact design (BACI) or distance-to-pathway analyses (right-hand columns). BRSP and VESP are abbreviations for the Brewer’s and vesper sparrow, respectively; the only two species observed at every site during every year of the study.

Metric	Focal species	Sample sizes	BACI	Dist. to path
Abundance	BRSP, VESP	84 transect surveys	✓	
Diversity	All	84 transect surveys	✓	
Proportion nests path-side [†]	All	730 nests		
Nest densities (50 m path)	All	127 nests		
Nest distances to path	All	730 nests		
Probability of nest success	All	1149 nests	✓	✓
No. of young fledged/nest	BRSP, VESP	684, 274 nests	✓	✓
Nest predator ID	BRSP	10 video IDs		
Nest predator abundance	Mammals	466 scent station-nights		
Clutch size	BRSP, VESP	600, 238 clutches	✓	✓
Egg mass	BRSP	232 clutches	✓	✓
Incubation rhythms	BRSP	109 nests		✓
Nestling feeding rates	BRSP	172 nests	✓	✓
Nestling mass	BRSP	257 broods	✓	✓
Site fidelity	BRSP	281 banded birds	✓	
Habitat analysis	All	147 points		

[†] Proportion of nest sample on the pathway side of the highway in experimental plots

Experimental design

Because the study commenced prior to pathway construction, I had a unique opportunity to examine responses of breeding birds to a novel disturbance using an experimental approach. Two main types of analyses were conducted. First, I used a rigorous Before-After/Control-

Impact (BACI) study design (Smith 2002) to quantify response metrics before pathway construction (2007), during construction (2008), and for two years (2009-2010) with pedestrian use. The 2010 data were important in terms of documenting potential acclimation effects (e.g., Steidl and Anthony 2000). Using GIS, I randomly established three paired sets of 25-ha study plots along the pathway route (Figure 1). One plot in each pair straddled the road and pathway, and the other was placed in similar habitat/topography but ≥ 500 m from the highway. Data collected within control plots served to separate possible annual and habitat effects from pathway effects. All plots were separated by ≥ 1 km, and placed no closer than 50 m from nearby forest or riparian edges to limit potential confounding effects of habitat. The two northernmost experimental plots (Timbered Island and South Jenny) could not be exactly centered across the transportation corridor due to the adjacency of forest edges on the west side. The Timbered Island plot extended 140 m and the S. Jenny site 100 m west of the highway.

A second analytical approach focused on avian responses with respect to distance from the pathway. For these analyses, a fourth experimental site in high quality sagebrush habitat just north of the Moose entrance station was included in order to increase replication of plots close to the pathway and examine avian responses with respect to proximity to the pathway using only the four experimental plots.

Data collection

Between May 15 - June 15 of each year I quantified avian diversity and abundance within the study plots using line transect surveys, with detections truncated to 100 m. Line transects were 1 km in length and centered within each study plot (Figure 1). In control plots, transects were oriented in a randomly chosen cardinal direction, whereas experimental transects were oriented perpendicular to the road and pathway. Surveys began within one-half hour of official sunrise and continued no later than 10 a.m., and each plot was surveyed 3 times per year by at least 2 different surveyors to account for potential surveyor bias. Surveyors slowly walked transects and recorded all visual and aural detections of all avian species. The distance and bearing to each detection were recorded to avoid double-counting of individuals. For species diversity comparisons, I used the Shannon-Weiner estimator (e.g., Hollenbeck and Ripple 2007) which accounts for both species richness and evenness: $H = -\sum P_i(\ln P_i)$, where P_i is the proportion of each species in the sample. For abundance I used mean detections per survey visit within a

plot and year. Brewer's and vesper sparrows were the only two species present in every plot during every year and with sufficient detections for individual abundance analyses.

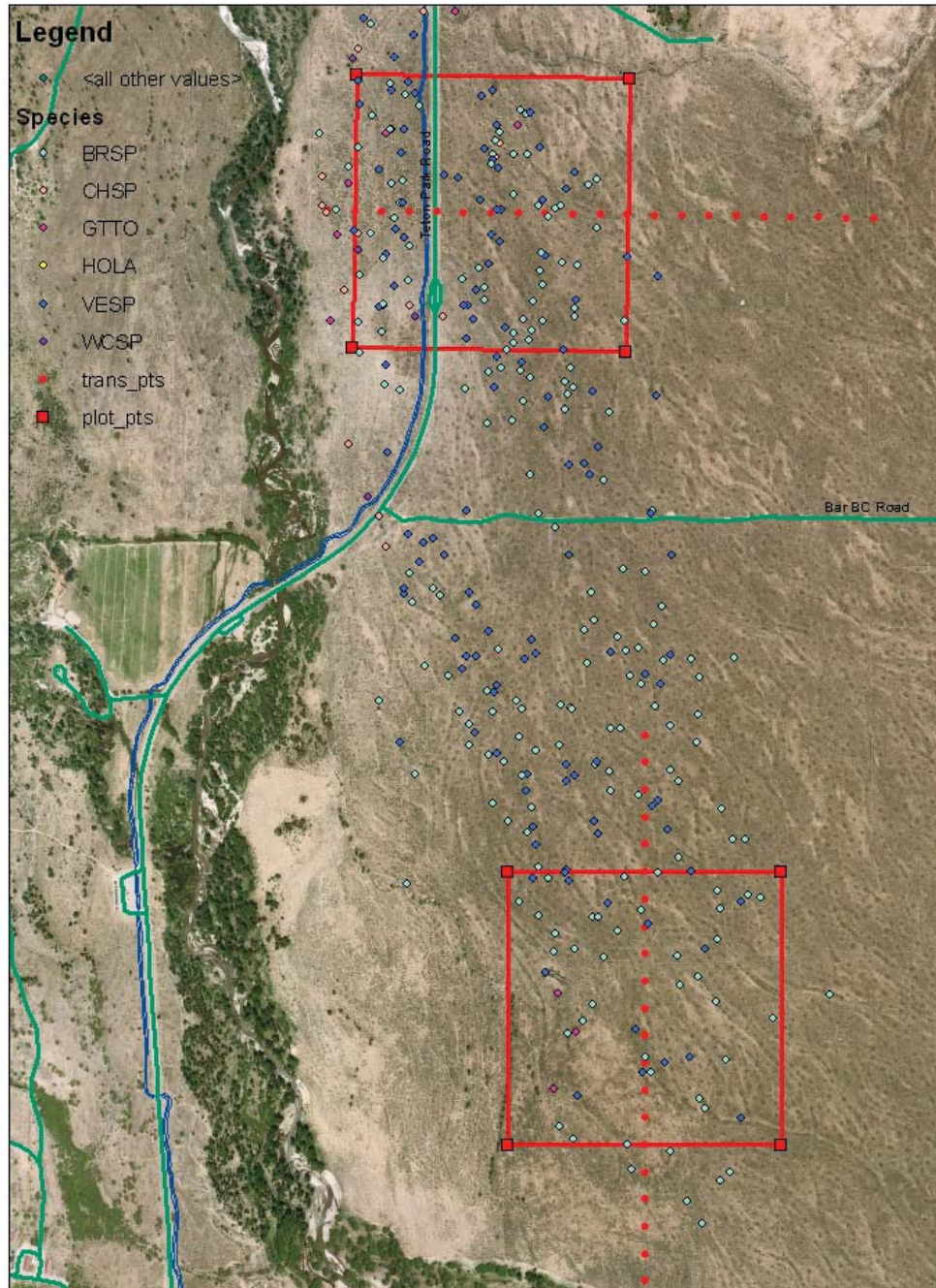


Figure 1. GIS image of one set of paired plots (Timbered Island area), with associated survey transects and all nest locations by species from 2007-2010.

To quantify reproductive success, within each plot each year I searched for nests and monitored the outcome (failure or fledge) every 2-3 days following standardized protocols (Martin and Geupel 1993). Field assistants were instructed to expend an approximately equal amount of time and nest-searching effort in control versus experimental plots, and in all areas within each plot. Some nests were inevitably located outside of plot boundaries (while hiking to adjacent plots etc.), and were included in analyses when ≤ 400 m from the transportation corridor for experimental plots and ≥ 500 m for control plots. Nest locations were recorded using GPS, and the distance to the pathway and highway calculated for each nest using GIS. Reproductive success was assayed via two metrics: a binary value of successful versus unsuccessful for each nest and the total number of offspring fledged per nest. Nest survival probability analyses were conducted on Brewer's sparrows individually and non sagebrush-obligate species pooled. Fledglings per nest attempt were only possible for the Brewer's and vesper sparrows.

Table 2. Songbird species present in the study area and raw nest sample sizes by year.

Species		Nest sample sizes				
Common name	Scientific name	2007	2008	2009	2010	Total
Brewer's sparrow	<i>Spizella breweri</i>	170	130	212	175	687
Vesper sparrow	<i>Pooecetes gramineus</i>	55	39	97	84	275
Green-tailed towhee	<i>Pipilo chlorurus</i>	12	24	20	54	110
Chipping sparrow	<i>Spizella passerina</i>	9	11	16	9	45
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	4	5	6	4	19
Horned lark	<i>Eremophila alpestris</i>	3	2	3	5	13
Total						1149

In 2009 I initiated 24-hour infrared video monitoring at a sub-set of Brewer's sparrow nests to identify nest predator species in the study area. Video set-ups were composed of a camouflaged weatherproof bullet surveillance camera equipped with infrared diodes, connected to a DVR recorder and sealed lead acid battery. Camera set-ups were visited every day and the batteries switched every other day. Data were stored on 8 gigabyte memory cards that were downloaded as soon as a predation event occurred at the nest.

Mammalian nest predator species were surveyed for relative abundance in 2009 and 2010 using track plates with a scent attractant. Scent stations were comprised of two 0.3 x 0.8 m aluminum track plates sooted by an acetylene torch flanking a fatty acid scent tablet (Roughton and Sweeny 1982, Chalfoun et al. 2002). Trials were run between June 20 and August 1 of both years. Five scent station locations were randomly chosen using GIS for each plot for each trial. Stations were placed in the field in the afternoon, and retrieved the following afternoon. Each plot was sampled four times each season except the two northern plot sets in 2010 which could only be sample three times due to recurring rain. Control and experimental plots within a pair were sampled concurrently, and the same sites were run \geq a week apart. Visitations were recorded as one individual per species at a station, regardless of the number of tracks of the same species, unless tracks were clearly distinguishable on the basis of size. Scent station data were summarized as the total number of visitations at the 5 stations within a plot during a trial.

Potential changes in the distribution of nests with the addition of the pathway were evaluated using three different approaches. First, I tested whether the proportion of nests on the pathway side of the highway within the four experimental plots decreased following pathway construction. Second, I determined the densities of nests within 50 m of the pathway for all four experimental plots each year. Fifty meters approximates the radius of the median area of a Brewer's sparrow territory (0.5-1 ha; Wiens et al. 1986, Chalfoun and Martin 2007), and edge effects on birds commonly permeate 50 m from a habitat edge (Paton 1994). All areas within 50 m of the highway and pathway at each site each year were intensively systematically searched by walking 2-m wide transects at least once during the peak nesting period (June 1- July 1). Nests on the pathway side of the highway and nest densities within 50 m of the pathway were calculated as a proportion of the total number of nests located within a plot and year to account for variation in annual nest densities and sample sizes. Finally, I also evaluated the average distance of nest locations to the pathway during all four years to test whether nest locations shifted farther from the pathway after the control year.

Clutch size (total number of eggs laid in a nest attempt) was recorded for every nest for which at least two sequential nest observations were obtained post clutch-completion. For the Brewer's sparrow, I also recorded egg mass, incubation rhythms, nestling feeding rates, and nestling mass. To control for changes due to evaporative water loss I only measured egg mass within 1-3 days of clutch completion. I used a portable electronic balance sensitive to 0.005 g

that was recalibrated following each re-location. In 2007 I measured incubation rhythms, including nest attentiveness (percent time on eggs) and mean on- and off-bout lengths, by placing Ibuttons (Maxim Corp.) in the lining of nests and recording temperature changes associated with a parent sitting on the nest. However, the minimum data recording frequency (1 minute) of the Ibuttons was too long to capture the subtle temperature changes when parents switched bouts. During 2008-2010 I therefore documented incubation behaviors by video-taping nests (Martin 2002, Chalfoun and Martin 2010*b*). Unfortunately, because incubation data were not collected during the control year, appropriate BACI analysis was impossible. Incubation rhythm data were therefore restricted to distance-to-pathway analyses. Video cameras were placed on tripods no closer than 3 m to nests and hidden from view with camouflaged material so that parents were not disturbed by the presence of the camera. Incubation videos began within one hour of official sunrise and ran continuously for four hours. I filmed nests during mid-incubation (day 4-7 of ≈ 10) to control for potential stage effects. Incubation metrics were calculated in the lab by transcribing behaviors observed in the videos. Attentiveness was derived by adding all partial and complete on-bouts and dividing by the total available tape time. Average on- and off-bout lengths were calculated using only complete bouts.

Nestling feeding rates (parent trips/hour) were recorded by video-taping nests using a similar methodology to the incubation films. Nestling films were restricted to day 5, 6 or 7 (of 8-10) of the nestling period and modal brood sizes of 3-4 to control for potential age and brood size effects (Chalfoun and Martin 2010*b*). Nestling mass was measured as a proxy for offspring growth and quality. Using the same portable balances as for egg mass measurements, I restricted nestling measurements to nests with known hatch dates and day 5 of the nestling period to control for growing time and lower the risk of force-fledging that can occur with older nestlings.

Birds are more likely to be site-faithful to habitats perceived as higher quality (Schmidt 2001; Lima 2009). In order to estimate annual site fidelity of the Brewer's sparrow in relation to the pathway treatment, I target-netted and color-banded a sub-set (5-10) of focal pairs within each site and year that were intensively monitored within and across seasons. Target-netting consisted of setting up 3 or 6-m mist nets within 1 m of nests and either flushing off incubating parents or attracting males to nets using playbacks of territorial songs. I took morphological measurements (mass, tarsus and wing length) of each captured bird and affixed a U.S. Fish and Wildlife Service aluminum band and three colored bands in unique combinations. Proportional

return rates as assayed by re-sights of color-banded birds on sites in subsequent years were summarized by site and year.

Microhabitat features known to influence the abundance, nest site selection and nest success of breeding sagebrush birds (Noson et al. 2006, Chalfoun and Martin 2007) were quantified at each plot during August 1-15, 2007 to examine habitat similarity between paired plots and/or with increasing proximity to the pathway. Habitat was sampled every 50 m along the 1 km avian transects (total $N = 21$ habitat points per plot; Figure 1). From each point I flipped a coin to select the side of the transect to sample, and generated a random distance between 1-200 m from the transect (at a perpendicular angle) to place the habitat point. At the center of each point I established a 5-m radius circular plot by arranging two ropes in the cardinal directions. I assessed percent understory cover (native and non-native graminoids, native and non-native forbs) using a small (0.25m) Daubenmire frame placed at plot center and the center of each rope end. Shrub cover was estimated using the line intercept method (Lucas and Seber 1977). For each shrub intersecting the four rope arms I measured the maximum height of the live crown. Within each plot quadrat I conducted live shrub counts by species and size class (0-20, 21-50, 51-100 and > 100 cm) to quantify shrub density.

Predictions

Inference that can be gained from the BACI design rests on observed differences between the control and experimental plots throughout the progression of pathway construction and use. I predicted that if pathway construction influenced avian responses, differences in response metrics between control and experimental sites should significantly increase in 2008 compared to 2007. Similarly, if human use of the pathway elicited responses, the differences between control and experimental plots in 2009 and 2010 should be significantly greater than in 2007. If acclimation occurred two years post construction, I predicted that differences in 2010 should relax back towards 2007 values. If the existing highway itself constitutes a disturbance, metrics should differ in a consistent direction between the experimental and control plots during all four years. If neither the road nor pathway has any effect, metrics should be similar across treatments during all four years.

If avian responses only occur at smaller spatial scales (i.e., with greater proximity to disturbance), I predicted that effects would only be evident in the within-experimental plot (distance-to-pathway) analyses.

Statistical analyses

All percentage/proportion data (nests on the pathway side of the highway and within 50 m of the pathway, incubation attentiveness, site fidelity) were arcsine square root transformed prior to analyses to ensure homogeneity of variances (Dytham 2003), though I present actual data for ease of interpretation.

BACI

BACI analyses for all response metrics (Table 1), with the exception of nest survival probability, were conducted using General Linear Mixed Models (GLMMs) with treatment (experimental versus control), year, and the treatment by year interaction as fixed factors. In addition, each set of paired plots ($N = 3$) was treated as a block (i.e., site). Block and block nested within a year were treated as random factors and included in models to account for within-site variation not attributable to the pathway treatment. Additional covariates in models included sagebrush cover for the Brewer's sparrow abundance model (Chalfoun and Martin 2007), Julian date of nest initiation for all nest-centered metrics (i.e., reproductive success and parental investment components), clutch size and female (parent) mass in the egg mass model, and brood size in the nestling feeding rate and mass models. The probability of Brewer's sparrow and non sagebrush-obligate (species pooled) nest survival was evaluated via logistic regression with treatment, year, and block as categorical (indicator) variables, treatment by year as an interaction term, and Julian date as a continuous variable.

Spatial nesting habitat use

The proportion of nests located on the pathway side of the highway, proportion of nests within 50 m of the pathway, and average nest distances from the path were calculated for each of the 4 experimental plots each year for the Brewer's sparrow individually and all other (non sagebrush-obligate) species combined. Responses were analyzed using GLMs with year and site as fixed factors and the year by site interaction. Least Significant Difference post hoc tests were used to compare differences among each set of years when year was significant.

Distance-to-Pathway

Distance-to-pathway analyses were conducted using data exclusively from the four experimental plots. Distance to the pathway for each nest during each year was the continuous explanatory variable. Binary nest success (successful versus unsuccessful) was examined separately for each year using logistic regression with site included as a categorical variable.

Other response variables were analyzed using GLMMs with year and site as fixed factors, distance to the path as a covariate, and year by distance as an interaction term. Additional covariates in models were the same as in the BACI analyses.

Nest Predator Abundance

Scent station visitations by mammalian nest predator species were analyzed using a GLMM with treatment and year as fixed factors, treatment by year as an interaction term, and block (site) and block within a year as random factors.

Site Fidelity

The transformed proportions of returned banded Brewer's sparrows within a site and year during 2008-2010 were analyzed using a GLM with year and site as fixed factors.

Habitat Analysis

Habitat metrics (% grass cover, % forb cover, shrub cover, shrub height and shrub density greater than 20 cm) were compared across the 6 paired plots using Multiple Analysis of Variance (MANOVA) with site as a fixed factor and Least Significant Difference post hoc tests. To examine whether habitat metrics co-varied with distance to the pathway route I conducted a MANCOVA with site as a fixed factor and distance to the pathway as a covariate, and site by distance to the pathway as an interaction term. For shrub height, the interaction between site and pathway distance was significant. Therefore, I also ran individual regression models of shrub height with respect to distance-to-pathway for each site.

Results

Diversity and abundance

Species richness ranged from 2-6 species within a plot. Species diversity (Shannon-Weiner H) varied across sites ($F_{2,16} = 5.30, P = 0.047$) but not years ($F_{3,16} = 1.51, P = 0.31$) or treatment ($F_{1,16} = 2.25, P = 0.17$), regardless of pathway stage (year x treatment: $F_{3,16} = 1.38, P = 0.32$).

Brewer's sparrow abundance varied annually ($F_{3,17} = 91.96, P < 0.001$) and by site ($F_{2,17} = 15.30, P = 0.001$), and increased with sagebrush cover ($F_{1,17} = 31.73, P = 0.001$), but was invariant with respect to the pathway treatment ($F_{1,17} = 2.20, P = 0.18$) regardless of pathway stage (year x treatment: $F_{3,17} = 0.36, P = 0.78$). Vesper sparrow abundance similarly varied

across years ($F_{3,16} = 20.90, P = 0.001$) and sites ($F_{2,16} = 8.68, P = 0.02$), but not by treatment ($F_{1,16} = 0.01, P = 0.92$) regardless of pathway stage (year x treatment: $F_{3,16} = 1.20, P = 0.37$).

Spatial patterns of nests

The proportion of Brewer's sparrow nests located on the pathway side of the highway decreased monotonically after the control year ($F_{3,15} = 3.90, P = 0.049$; Figure 2) regardless of site ($F_{3,15} = 2.29, P = 0.15$). The control year had significantly higher pathway-side nests than the two pathway use years (2009: $P = 0.04$; 95% CI: 0.02-0.48; 2010: $P = 0.01$; 95% CI: 0.10-0.56) but not the construction year (2008: $P = 0.20$; 95% CI: -0.09-0.37). The proportion of non sagebrush-obligate species' nests located on the pathway side varied similarly with pathway stage albeit not significantly (Year: $F_{3,15} = 2.60, P = 0.12$; Figure 2). The control year had significantly higher pathway-side nest proportions than the second pathway use year (2010: $P = 0.04$; 95% CI: 0.02-0.44), but not the construction year (2008: $P = 0.91$; 95% CI: -0.20-0.22) or first year of use (2009: $P = 0.40$; 95% CI: -0.13-0.29).

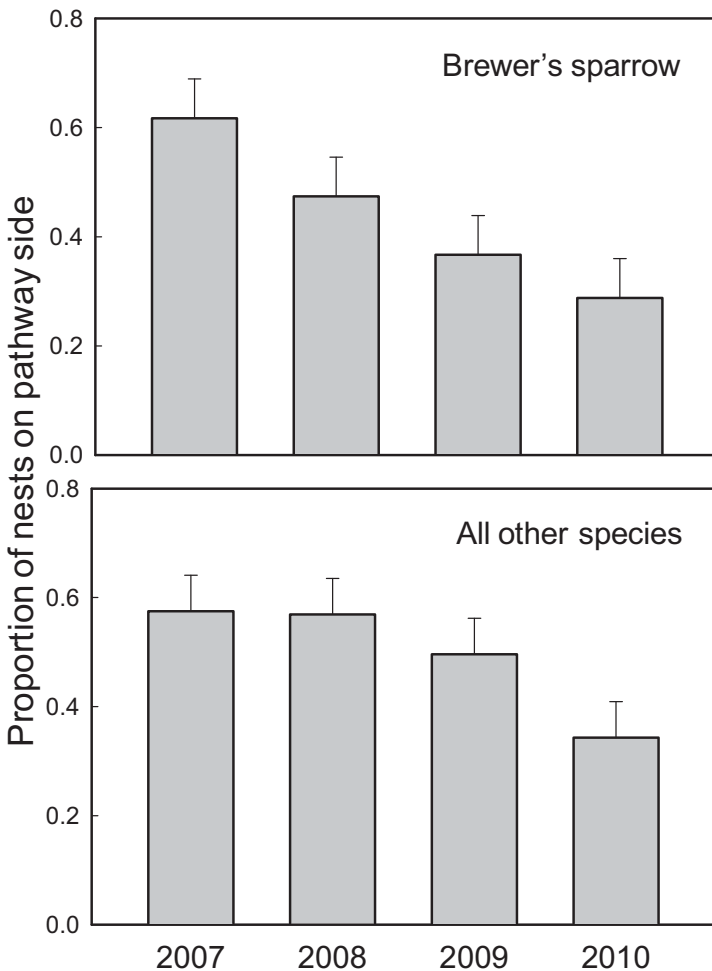


Figure 2. The proportion of Brewer's sparrow (top panel) and all other non sagebrush-obligate species' (bottom) nests located on the pathway side of the highway in relation to total nest sample sizes during each year of the study. Data are marginal means and associated standard errors from the general linear mixed models (see text) holding site (which was not significant) constant.

The density of Brewer's sparrow nests within 50 m of the pathway decreased with pathway progression (Year: $F_{3,15} = 3.92$, $P = 0.048$), with variation across sites ($F_{3,15} = 6.62$, $P = 0.01$) (Figure 3). The proportion of nests near the pathway differed significantly between the control year and the two pathway use years (2009: $P = 0.03$; 95% CI: 0.03-0.21; 2010: $P = 0.01$; 95% CI: 0.04-0.22) but not the construction year (2008: $P = 0.22$; 95% CI: -0.03-0.15). The density of all other species' nests within 50 m of the path also decreased with pathway progression (year: $F_{3,15} = 3.97$, $P = 0.047$; Figure 3). However, only the second pathway use year differed significantly from the control year (2010: $P = 0.01$; 95% CI: 0.04-0.30).

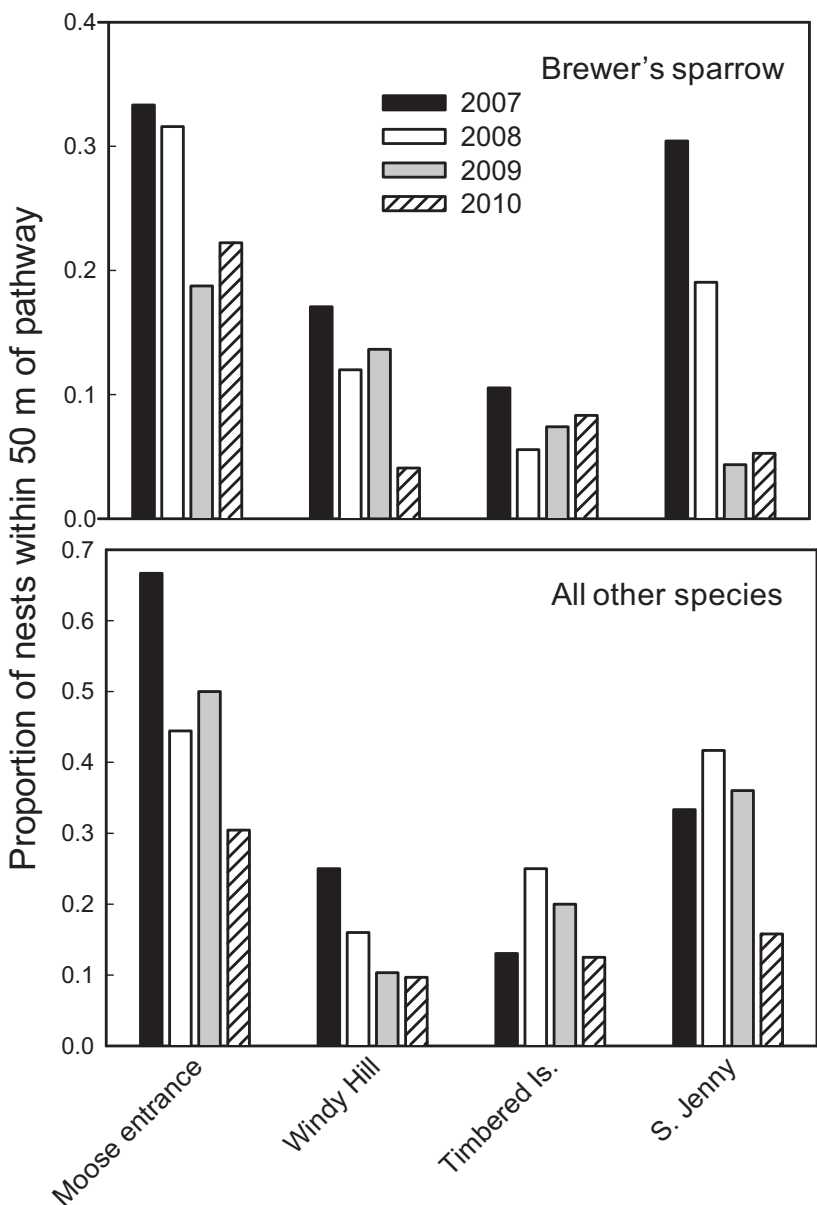


Figure 3. The proportion of Brewer's sparrow (top) and other non sagebrush-obligate (bottom) nests located within 50 m of the pathway in relation to total nest sample sizes within a site and year, at the four experimental study plots (straddling highway and pathway) in 2007-2010.

Distances of Brewer's sparrow nests from the pathway increased significantly after the control year (Year: $F_{3,388} = 11.69$, $P < 0.001$) albeit to different extents across sites (year x site: $F_{9,388} = 5.11$, $P < 0.001$) (Figure 4). Nests in the construction year were not consistently farther from the pathway than the control year (2008: $P = 0.64$; 95% CI: -43.87-26.78). Nests in both pedestrian use years, however, were significantly farther from the pathway than in 2007 (2009: $P = 0.04$; 95% CI: -64.79- -1.20; 2010: $P < 0.001$; 95% CI: -92.47- -26.32).

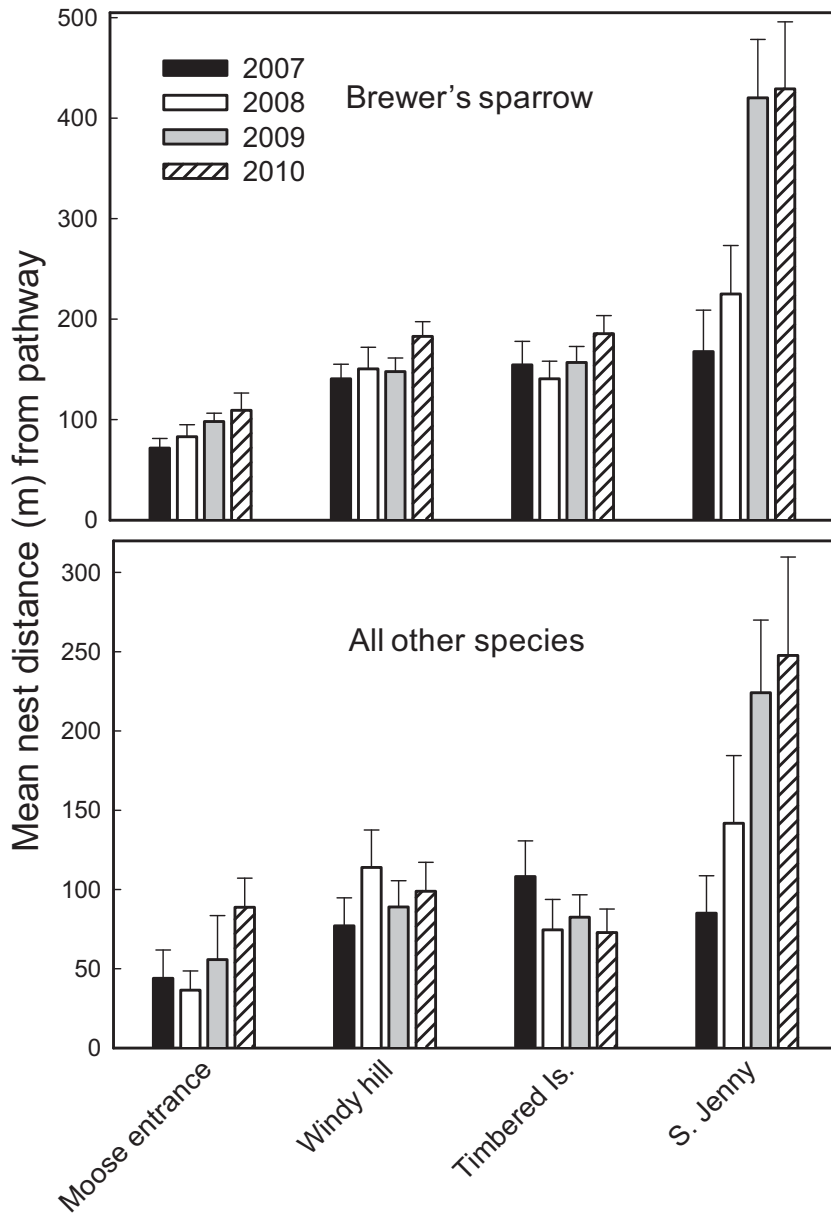


Figure 4. Mean ($\pm 1SE$) nest distances in meters from the pathway during 2007-2010 for the Brewer's sparrow (top) and all other species combined (bottom) at the four study sites.

The mean difference across sites in nest distances from the path for the Brewer's sparrow between 2007 and 2010 was 59.4 m. Non sagebrush-obligate species' nest distances from the path also increased after the control year ($F_{3,301} = 4.03$, $P = 0.008$) to different extents across sites (year x site: $F_{9,301} = 3.10$, $P = 0.001$) (Figure 4). Both 2009 ($P = 0.04$; 95% CI: -79.63- -1.29) and 2010 ($P = 0.05$; 95% CI: -77.94- -0.23) but not 2008 ($P = 0.83$; 95% CI: -48.24- 38.58) nests were farther from the pathway than the control year. The mean difference in nest distances from the path for non sagebrush-obligates between 2007 and 2010 was 40.5 m.

Reproductive success

Brewer's sparrow nest survival probability did not vary significantly with treatment (Wald = 2.02, df = 1, $P = 0.16$), though nest success was significantly higher in experimental than control plots during the control year (Wald = 5.08, df = 1, $P = 0.02$). The probability of Brewer's sparrow nest success decreased with proximity to the pathway location in 2007, though not significantly (Wald = 1.063, df = 1, $P = 0.30$; Figure 5). In 2008 (Wald = 2.88, df = 1, $P = 0.09$) and 2009 (Wald = 8.18, df = 1, $P = 0.004$) nest success increased with proximity to the pathway (Figure 5). By 2010, however, this relationship neutralized (Wald = 0.16, df = 1, $P = 0.69$; Figure 5). The probability of nest success of non sagebrush-obligate species was not significantly influenced by treatment (Wald = 0.51, df = 1, $P = 0.48$) during any year (treatment x year: Wald = 3.15, df = 3, $P = 0.37$). Non sagebrush-obligate nest success probability was also unrelated to distance to the pathway during all years (2007: Wald = 0.23; $P = 0.63$; 2008: Wald = 0.09; $P = 0.77$; 2009: Wald = 2.75; $P = 0.10$; 2010: Wald = 0.97; $P = 0.32$; all df = 1).

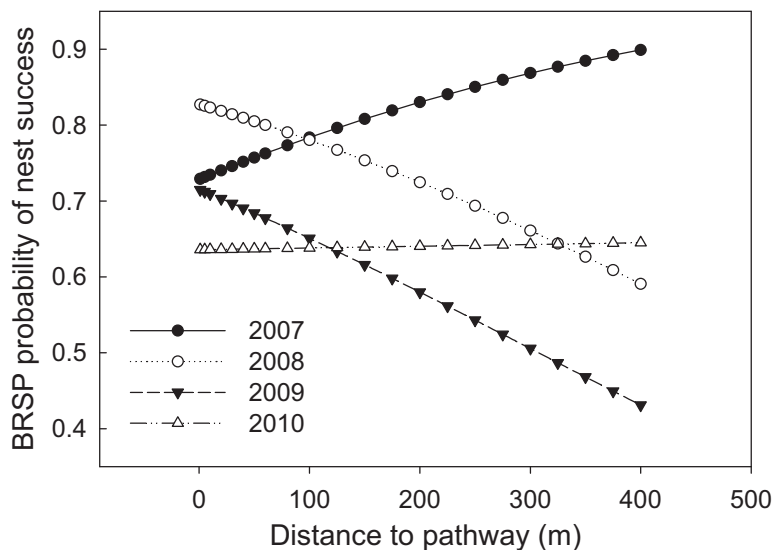


Figure 5. The probability of Brewer's sparrow nests surviving (fledging at least one young) as a function of the distance in meters from the pathway during 2007-2010 as calculated from back-transformed logistic regression parameter estimates. Prior to pathway construction in 2007, the probability of success increased with distance to the transportation corridor, but the pattern switched in 2007-2008 and neutralized in 2010.

The number of Brewer’s sparrow young fledged per nest was consistently higher in experimental than control plots ($F_{1,15} = 11.79, P = 0.001$; Figure 6), though differences decreased after 2007 (year x treatment: $F_{3,15} = 3.14, P = 0.03$; Figure 6). The number of Brewer’s sparrow fledglings per nest also increased with proximity to the pathway ($F_{1,411} = 4.70, P = 0.03$; $\beta = -0.001 \pm 0.001$) during all pathway stages (year x distance: $F_{3,411} = 1.87, P = 0.13$). The number of vesper sparrow young fledged per nest was also consistently higher in experimental plots ($F_{1,15} = 6.17, P = 0.01$) especially in the construction year, though differences dissipated by 2010 (Figure 6). The number of vesper sparrow fledglings did not vary with distance to the pathway ($F_{1,165} = 1.05, P = 0.31$) during any pathway stage (year x distance: $F_{3,165} = 1.65, P = 0.17$).

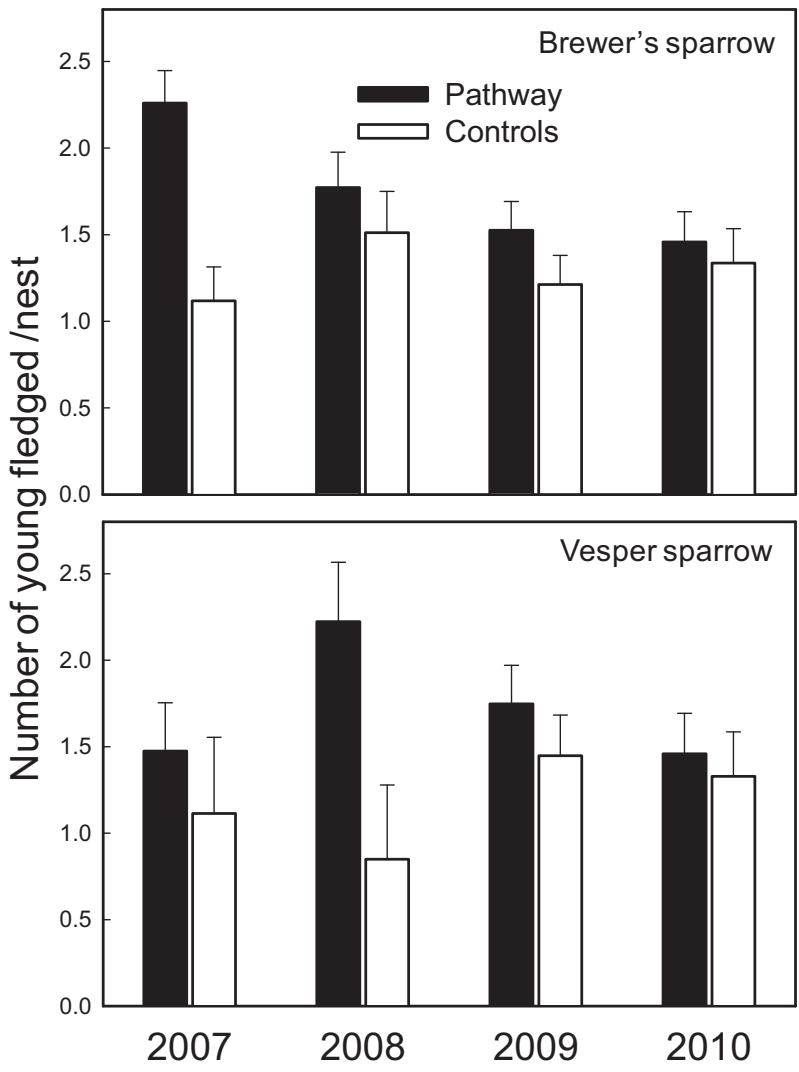


Figure 6. Number of young fledged per nest for the Brewer’s sparrow (top) and vesper sparrow (bottom) at pathway versus control plots during the control year (2007), construction year (2008) and two pedestrian use years (2009, 2010). Data are marginal means from general linear mixed models (see text) holding other factors constant.

Nest predator identification and abundance

Ten video confirmations of nest predator species were obtained at 10 different nests during 2009-2010 (Table 3). In addition to video evidence, garter snakes were observed digesting nest contents near depredated nests on two other occasions, and elk were identified as the likely predator in two other cases (trampling and fresh scat near nest; nest cup removed from shrub and placed in nearby shrub).

Table 3. Nest predator species identified via infrared cameras depredating Brewer's sparrow nests in 2009-2010. *N* is the number of observed cases.

Common name	Scientific name	<i>N</i>
Chipmunk	<i>Tamias spp.</i>	3
Deer mouse	<i>Peromyscus maniculatus</i>	2
Weasel	<i>Mustela spp.</i>	2
Elk	<i>Cervus canadensis</i>	2
Garter snake	<i>Thamnophis sirtalis</i>	1

I obtained a total of 202 visits of nest predator species to scent stations out of 466 possible station-nights (Table 4). Predator visitations did not vary significantly by treatment ($F_{1,7} = 0.31$, $P = 0.58$), site ($F_{2,7} = 7.71$, $P = 0.12$) or year ($F_{3,7} = 1.00$, $P = 0.42$).

Table 4. Nest predator visitations to scent stations in 2009-2010 by species. *N* is number of observed cases.

Common name	Scientific name	<i>N</i>
Deer mouse	<i>Peromyscus maniculatus</i>	116
Chipmunk	<i>Tamias spp.</i>	50
Elk	<i>Cervus canadensis</i>	26
Weasel	<i>Mustela spp.</i>	3
Garter snake	<i>Thamnophis sirtalis</i>	3
Ground squirrel	<i>Spermophilus spp.</i>	2
Black bear	<i>Ursus americanus</i>	1
Coyote	<i>Canis latrans</i>	1

Parental investment and behavior

None of the assessed Brewer’s sparrow parental investment metrics showed different patterns with respect to the pathway treatment across years (Table 5). Both clutch size and nestling mass were consistently higher in experimental plots than controls (Table 5, Figure 7) and varied annually (Table 5). Clutch size also decreased seasonally (Julian date: $F_{1,16} = 101.87$, $P < 0.001$; $\beta = -.022 \pm 0.002$). Vesper sparrow clutch size decreased seasonally ($F_{1,16} = 40.98$, $P < 0.001$; $\beta = -.019 \pm 0.003$) but did not vary across treatments ($F_{1,16} = 0.008$, $P = 0.93$) regardless of year ($F_{3,16} = 1.26$, $P = 0.29$).

Table 5. Before-After/Control-Impact results of Brewer’s sparrow parental investment and care metrics in the pathway versus control treatment with pathway progression (2007-2010) at three sites (Windy Point, Timbered Is., South Jenny Lake) from general linear mixed models. *N* is the number of nests in each analysis.

Metric	Treatment x								
	Treatment		Year		year		Site		<i>N</i>
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Clutch size	7.06	0.008	4.39	0.05	0.09	0.97	6.86	0.03	528
Egg mass	1.87	0.18	0.29	0.83	1.82	0.15	2.16	0.19	76
Nestling feeding rates	0.60	0.44	0.48	0.71	0.76	0.52	0.70	0.53	141
Nestling mass	4.30	0.04	3.50	0.04	0.90	0.44	1.06	0.39	212

Brewer’s sparrow clutch size increased with proximity to the pathway during all four years (Table 6). Vesper sparrow clutch size similarly increased marginally with proximity to the path ($F_{1,142} = 3.03$, $P = 0.08$) regardless of pathway stage (distance x year: $F_{3,142} = 0.53$, $P = 0.67$). After accounting for female body mass ($F_{1,77} = 15.97$, $P < 0.001$; $\beta = 0.10 \pm 0.03$), Brewer’s sparrow egg mass did not vary with distance to the path, nor did incubation rhythms (Table 6). Neither nestling feeding rates nor mass varied with distance to the path (Table 6). Parents fed larger broods at a greater rate ($F_{1,115} = 15.42$, $P < 0.001$; $\beta = 2.52 \pm 0.64$).

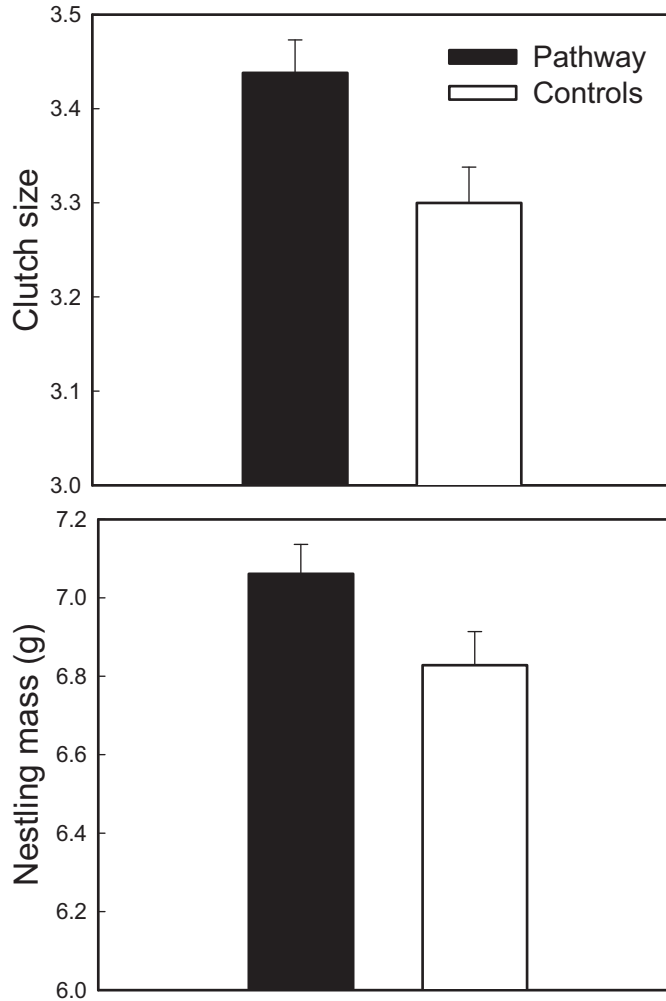


Figure 7. Brewer's sparrow clutch size (top) and nestling mass (bottom) were higher in experimental than control plots during all years of the study (2007-2010). Data are marginal means from the general linear mixed models (see text) holding other factors constant.

Table 6. Results from general linear mixed models of Brewer's sparrow parental care and investment metrics in relation to distance to the pathway. First set of *F* and *P* statistics is for the distance to the pathway factor and the second is for the year by distance interaction.

Metric	<i>F</i>	<i>P</i>	df _(dist)	<i>F</i>	<i>P</i>	df _(yr * dist)	df _(total)
Clutch size	5.57	0.02	1	0.93	0.43	3	361
Egg mass	0.76	0.39	1	0.77	0.51	3	77
Nest attentiveness	0.07	0.79	1	2.17	0.12	2	71
Incubation on-bout length	0.01	0.99	1	0.04	0.97	2	71
Incubation off-bout length	0.44	0.51	1	1.25	0.30	2	71
Nestling feeding rates	0.19	0.67	1	0.17	0.92	3	115
Nestling mass	1.22	0.27	1	1.34	0.26	3	169

Site fidelity

A total of 281 Brewer's sparrows (133 males, 148 females) were captured and individually color-banded during the study, 218 of which were banded during years 1-3 and therefore available for annual return-rate analysis. Thirty-eight birds (17%), 24 males and 14 females, were re-sighted at the same plot for at least one subsequent season. Sixteen birds were observed at the same plot in at least 2 subsequent seasons. Percent returns varied across plots ($F_{6,20} = 3.34$, $P = 0.04$) but not years ($F_{2,20} = 0.33$, $P = 0.73$). Twenty-seven (71%) of the returnees were based at one of the 3 southern-most plots (Moose entrance and Windy Hill areas) which have higher shrub cover (15-20%) than the other plots (13-17%). Return rates did not differ between control and experimental plots ($F_{1,20} = 1.19$, $P = 0.29$) in any year (treatment x year: $F_{2,20} = 0.88$, $P = 0.44$). When birds crossed the highway in subsequent years to nest, five out of six (83%) movements (3 females and 2 males) were from the pathway side to the non-pathway side.

Habitat

The MANOVA for habitat variables across plots showed significant differences in percent grass cover ($F_{5,125} = 5.63$, $P < 0.001$), shrub density ($F_{5,125} = 17.86$, $P < 0.001$), and shrub height ($F_{5,125} = 8.25$, $P < 0.001$). Grass cover differed significantly between the experimental and control plot for one site pair (S. Jenny: $P < 0.001$, mean difference = -7.21 ± 1.81 SE). Shrub density differed between the experimental and control plot for the two northern site pairs, Timbered Island ($P = 0.01$, mean difference = 14.05 ± 5.59 SE) and S. Jenny ($P = 0.002$, mean difference = -17.90 ± 5.59). Shrub height only varied marginally between the paired plots at S. Jenny ($P = 0.06$, mean difference -8.48 ± 4.51 SE).

The site by distance-to-pathway interaction was significant for shrub height ($F_{3,76} = 3.74$, $P = 0.01$) because shrub height varied inversely ($\beta = -.03 \pm 0.01$) with distance from the pathway at one experimental site (S. Jenny; $F_{1,20} = 5.65$, $P = 0.03$).

Discussion

Many wildlife species respond to human disturbance by exhibiting vigilance and fleeing behaviors (Taylor and Knight 2003, Blumstein et al. 2005, Borkowski et al. 2006). Evidence that novel human disturbances influence actual fitness components, moreover, has been scarcer. At least some bird species respond to perceived predation risk by altering habitat use and/or

decreasing investment in offspring (Fontaine and Martin 2006a, 2006b; Chalfoun and Martin 2010a, 2010b). The ubiquity of such responses, and the extent to which different types of human activities are perceived as predation risk by wildlife, however, remains unclear (Beale and Monaghan 2004).

In this study, I used a comprehensive and experimental approach to examine the responses of breeding songbirds to a novel disturbance (new multi-use, non-motorized pathway) in Grand Teton National Park in order to further understand the impacts of different types of human activities (construction and recreational) on wildlife. Neither species diversity nor overall abundance of focal species was significantly associated with pathway construction or use activities. However, results clearly suggest avoidance of the pathway area for nesting activities, especially during pathway use, potentially reflecting perceived predation risk. The proportion of nests located on the pathway side of the highway and the density of nests within 50 m of the pathway route decreased, and the average distance of nests from the pathway increased, post control year with no signs of acclimation by year four. As further evidence of avoidance, 83% of the color-banded Brewer's sparrows who switched sides of the highway to nest in subsequent years shifted from the pathway to the non-pathway side.

The extent of shifts in nest distances from the pathway varied by habitat, with smaller shifts in the higher shrub cover southern plots, and averaged 59.4 m across sites. Adopting a conservative management scenario for the determination of effective nesting habitat loss would therefore entail multiplying the total length of the pathway (approximately 11 km) by the width of the pathway itself (≈ 4 m) plus 2×59.4 m (= 118.8) which yields a total area of influence (see Taylor and Knight 2003) of 135 ha. This represents enough area to accommodate between 135 and 270 Brewer's sparrow territories (Wiens et al. 1986, Chalfoun and Martin 2007). For non-sagebrush obligate species (vesper sparrow, chipping sparrow, white-crowned sparrow, green-tailed towhee, horned lark), shifts in nest distances from the pathway were lower but still averaged 40.5 m which yields an effective area loss of 93.5 ha.

Birds that placed nests close to the pathway did not appear to alter parental care behaviors or decrease investment in offspring. There were no differences in egg mass, incubation rhythms, or nestling feeding rates with proximity to the pathway during any year, and Brewer's sparrow clutch size and nestling mass were actually higher closer to the pathway. These somewhat unexpected results raise the possibility that pairs nesting near the existing

transportation corridor were those already acclimated or less sensitive to human disturbance. Alternatively, the higher clutch and nestling sizes may be a result of the nest predation patterns observed at the sites. Nest predation rates were consistently higher in plots away from rather than along the transportation corridor, and birds tend to reduce investment in young with increased predation risk, whether perceived (Fontaine and Martin 2010a) or directly experienced in previous nesting bouts (Chalfoun and Martin 2010b).

The results of previous work examining avian nest predation and distance to linear features such as roads and trails have been mixed, with positive (Barton and Holmes 2007), negative (Dietz 2006) and neutral (Ortega and Capen 2002) relationships observed. I speculate that the pattern of decreased nest predation along the pathway in Grand Teton National Park may be driven by a human-induced trophic cascade in which at least some nest predator species are less abundant along the transportation corridor thereby reducing predation risk to nesting birds. Nest predator species documented via video cameras during 2009-2010 and other evidence at nests included deer mice, chipmunks, weasels, elk, and garter snakes. A component of this diverse nest predator assemblage may avoid the disturbed area (e.g., Barton and Holmes 2007). Alternatively, some species such as canids may preferentially forage along the transportation corridor (but see Larivière 2003) which could decrease the abundance of other nest predators (e.g., rodents). I attempted to test these hypotheses using scent stations to assess nest predator relative abundance, but there were no significant differences in predator visitations across treatments. Scent station sample sizes may have been too low to perceive differences, and the method was not ideal for sampling the entire suite of mammalian predator species. Hypotheses for the observed patterns of nest predation in relation to the transportation corridor therefore require further testing. The differences in nest success between experimental and control plots decreased greatly post pathway construction, however, suggesting that the indirect benefit of birds nesting close to the transportation corridor is not large or temporally consistent.

The inclusion of two years of pathway use following implementation allowed investigation of potential acclimation of breeding birds to the new disturbance. Avoidance responses, however, as particularly indicated by the distribution of nests in relation to the pathway over time, did not dissipate during the study period. Rather, differences in response metrics across treatments were greatest in 2010 compared to the 2007 control year. Both types of disturbance stimuli (construction and pathway use) in the study were intermittent and therefore

somewhat unpredictable, which tend to be the types that elicit stronger wildlife avoidance responses (Borkowski et al. 2006, Thiel et al. 2007). The specific stimuli emitted by the human activities that elicited avoidance are unclear (i.e., noise, visual, movement), though recent work found no evidence for vehicle traffic noise causing negative effects of roads on breeding birds (Summers et al. 2011).

In addition to human disturbance, habitat structure and composition can be very influential in the distribution and reproductive success of nesting birds, and must be considered in the context of the pathway results. While some habitat attributes (grass cover, shrub density, shrub height) varied across paired plots, only the northernmost site (South Jenny Lake area) showed differences in all 3 habitat metrics. Moreover, shrub cover, one of the most influential sagebrush steppe attributes in determining avian distribution and success (Noson et al. 2006, Chalfoun and Martin 2007), was invariant across paired plots. Yet, patterns of avian response metrics that differed by treatment (nest distributions, reproductive success, clutch size, nestling mass) were largely consistent across sites. Moreover, only one habitat metric (shrub height) varied with distance to the pathway for one site (S. Jenny) suggesting no systematic pattern of habitat variation with distance to the path. Habitat features, especially sagebrush cover, influenced avian abundance and site fidelity similar to the results of other studies in shrubsteppe systems (Chalfoun and Martin 2007, Knick et al. 2008). However, given (1) that habitat did not vary systematically across experimental treatments and (2) the robust and experimental BACI design, I am confident that observed differences in avian response metrics to the transportation corridor were independent from habitat variation.

In conclusion, the primary impacts of the new pedestrian pathway through sagebrush habitats of Grand Teton National Park on breeding birds appear to be direct (actual habitat converted) and effective (via avian avoidance) habitat loss. It is unclear whether avoidance was elicited from construction activities that then carried over into subsequent years, or whether birds were responding to both types of human activities (construction and pedestrian use). Regardless of the specific mechanism, the addition of the pathway has increased the width of the zone of influence of the previously existing highway, with no sign of avian habituation since pathway implementation. Data herein provide insight into the width of the area of influence for future management scenarios involving construction projects with respect to avian species that breed in the park and beyond. The patterns observed in the study are worthy of conservation concern

especially in light of the extent of sagebrush conversion and alteration range-wide and concomitant migratory bird declines (Paige and Ritter 1999, Knick et al. 2003).

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