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Gilbert, Michelle M., <u>Demographic responses of sagebrush-obligate songbirds to oil and natural gas development in western Wyoming</u>. M.S., Department of Zoology and Physiology, December 2010.

Oil and natural gas development in the Intermountain West of North America has expanded over the last two decades, primarily within sagebrush (*Artemesia spp.*) dominated landscapes. Although the effects of energy development on high profile game species such as the greater sage-grouse (*Centrocercus urophasianus*) have been documented, studies examining responses of non-game birds are lacking. Simultaneously, many songbirds that breed within sagebrush steppe habitats have shown range-wide population declines that are likely due to widespread habitat loss and alteration. I evaluated songbird abundance, species richness, nest survival and offspring quality across gradients of oil and natural gas development intensity at three energy fields in the Upper Green River Basin, WY, USA during 2008–2009. While simultaneously accounting for important habitat attributes, increased well density was associated with decreases in Brewer's sparrow (*Spizella breweri*), sage sparrow (*Amphispiza belli*), and vesper sparrow (*Pooecetes gramineus*) abundance. Horned larks (*Eremophila alpestris*) increased with well density in the Pinedale Anticline natural gas field. Sage thrashers (*Oreoscoptes montanus*) showed no response to energy development. Species richness was not significantly affected by well density. Additionally, I tested two alternative hypotheses for why oil and natural gas development influences songbird populations in western Wyoming: increased nest predation or food limitation. The probability of daily nest survival for Brewer's sparrow, sage sparrow, and sage thrasher decreased with greater well densities and increased proximity to well pads, and avian nest predator abundance increased slightly across energy development gradients, supporting a nest

1

predation hypothesis. Additionally, shrub vigor decreased with increasing energy

development, which could decrease insect prey availability and impact parental

investment in offspring through decreases in clutch size and (or) offspring provisioning.

Clutch size did not vary with energy development, but average nestling mass for the sage

thrasher (the largest of the study species) decreased significantly with increasing

development, lending partial support to the food limitation hypothesis. My results

indicate that regional declines of some songbird species, especially sagebrush-obligates,

may be exacerbated by increased energy development and suggest that avian declines

within energy fields may be influenced by increased susceptibility to nest predation and

changes in food resource availability.

DEMOGRAPHIC RESPONSES OF SAGEBRUSH-OBLIGATE SONGBIRDS TO OIL

AND NATURAL GAS DEVELOPMENT IN WESTERN WYOMING

by

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It was passed from one bird to another,
the whole gift of the day.
~Neruda

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TABLE OF CONTENTS

PREFACE

Oil and natural gas development in the Intermountain West of North America has expanded over the last two decades, primarily within sagebrush (*Artemesia spp.*) dominated landscapes (Knick et al. 2003). Development infrastructure such as drill pads, waste pits, access roads, and pipelines convert and fragment sagebrush habitats (Weller et al. 2002), and habitat condition can be impacted by altered air quality (Talluto and Suding 2008). Sagebrush ecosystems have historically been fragmented and degraded by anthropogenic activities (Connelly and Braun 1997, Knick et al. 2003), and are critical to the survival of many species which rely on these habitats during part or all of their life-cycle (Holloran 2005). For example, the Brewer's sparrow (*Spizella breweri*), sage sparrow (*Amphispiza belli*), and sage thrasher (*Oreoscoptes montanus*), are three songbird species generally considered sagebrush-obligates, and which are showing range-wide population declines (Sauer et al 2008). Hence, this is an excellent model system with which to examine the impacts of oil and natural gas development, a relatively novel anthropogenic change.

To date, research on sagebrush shrub nesting bird responses to oil and natural gas development activities has focused primarily on greater sage-grouse (*Centrocercus urophasianus*). Adverse effects to greater sage-grouse due to oil and natural gas development include decreased lek recruitment, nest survival, and chick survival, and increased adult mortality and infrastructure avoidance behavior (Naugle et al. in press). Although efforts to understand habitat relationships of non-game sagebrush birds have increased recently, a comprehensive analysis of energy development effects on non-game songbirds is still lacking.

Objectives

The primary objective of this study was to (1) assess the relationship between energy development intensity in sagebrush habitat and songbird populations and avian community composition. Specifically, I evaluated the relative abundance and species richness of songbirds across gradients of oil and natural gas well density and habitat variation. If a relationship was detected, my secondary objective was to (2) identify potential mechanisms which drive the impacts of energy development on avian population and community dynamics. Specifically, I focused on whether energy development affects two critical limiting factors of reproductive success and thus population size of nesting songbirds: nest predation and food availability.

Thesis Organization

The objectives outlined above are addressed in Chapters 1 and 2 of my thesis. These chapters are tied together; Chapter 2 explores potential mechanisms for the findings described in Chapter 1. Chapter 1 is to be published in *The Journal of Wildlife Management* (The Wildlife Society, Bethesda, MD, USA), and is presented here verbatim to the accepted manuscript, with Anna D. Chalfoun as a co-author. Minor copyediting changes to this manuscript may occur prior to final publication by *JWM*. Chapter 2 is written in *Ecological Applications* (Ecological Society of America, Ithaca, NY) format with Anna D. Chalfoun to be included as a co-author. References to Chapter 1 results within the Chapter 2 manuscript are stated as "(Gilbert and Chalfoun in press)".

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CHAPTER 1. ENERGY DEVELOPMENT AFFECTS POPULATIONS OF SAGEBRUSH SONGBIRDS IN WYOMING

ABSTRACT

Oil and natural gas development in the Intermountain West region of North America has expanded over the last two decades, primarily within sagebrush dominated landscapes. Although the effects of energy development on high profile game species such as the greater sage-grouse (*Centrocercus urophasianus*) have been documented, studies examining responses of non-game birds are lacking. Simultaneously, many songbirds that breed within sagebrush steppe habitats have shown range-wide population declines that are likely due to widespread habitat loss and alteration. We evaluated songbird abundance and species richness across gradients of oil and natural gas development intensity, as indexed by well density, at 3 energy fields (2 natural gas and 1 oil) in the Upper Green River Basin, WY, USA during 2008–2009. While simultaneously accounting for important habitat attributes, increased well density was associated with significant decreases in Brewer's sparrow (*Spizella breweri*) and sage sparrow (*Amphispiza belli*) abundance, particularly in the Jonah natural gas field. Vesper sparrows (*Pooecetes gramineus*) were also negatively influenced by increased well density. Horned larks (*Eremophila alpestris*) increased with well density in the Pinedale Anticline natural gas field, and sage thrashers (*Oreoscoptes montanus*) showed no response to energy development. Species richness was not significantly affected by well density. Results suggest that regional declines of some songbird species, especially sagebrush-obligates, may be exacerbated by increased energy development. Understanding the

specific mechanisms underlying responses to energy development is an important next step and will aid land managers in the development of effective mitigation and management strategies for the maintenance of stable bird communities in sagebrush habitat.

KEY WORDS avian abundance, Brewer's sparrow, natural gas, oil, species richness, sage sparrow, sage thrasher, shrubsteppe.

In press. The Journal of Wildlife Management

INTRODUCTION

Habitat loss, fragmentation, and alteration due to anthropogenic activities are major factors contributing to wildlife population declines and biodiversity loss across a variety of ecosystems (Saunders et al. 1991, Wilcove et al. 1998). Rapid loss, fragmentation and severe degradation of sagebrush communities (Knick and Rotenberry 2000) have been primarily due to human activities including: agricultural conversion (Braun et al. 1976, Vander Haegen et al. 2000), livestock overgrazing (Beck and Mitchell 2000), invasive species such as cheatgrass (*Bromus tectorum* L.; Monsen and Shaw 2000, Rich et al. 2005), and altered fire regimes (Connelly and Braun 1997). Simultaneously, many wildlife species dependent on sagebrush have declined or been locally extirpated due to loss of historical habitat, behavioral avoidance of disturbance, increased predation risk, and decreased annual survival, reproductive success, and recruitment (Braun et al. 2002, Knick et al. 2003, Holloran 2005, Vander Haegen 2007).

Concurrent with increased anthropogenic land use in North American sagebrush habitats, shrubland and grassland bird populations have declined faster than other avian

species groups (Paige and Ritter 1999, Knick et al. 2003). In particular, the Brewer's

sparrow (*Spizella breweri*), sage sparrow (*Amphispiza belli*), and sage thrasher

(*Oreoscoptes montanus*), three migratory passerine species generally considered

sagebrush-obligates during the breeding season (Braun et al. 1976), have shown average

annual declines in nationwide abundance between 1980–2007 of 1.5%, 0.2%, and 1.1%,

respectively (Sauer et al. 2008). Indeed, species dependent on a single habitat type are

usually more sensitive to anthropogenic habitat modifications than generalists (Saab and

Rich 1997). Although efforts to understand habitat relationships of non-game sagebrush

birds have increased recently, we still know little about the impacts of specific types of

habitat change on individual habitat use, reproductive success, and annual survival, or

how anthropogenic changes may interact with critical habitat components to influence

populations.

Oil and natural gas development has expanded across the Intermountain West

over the last 2 decades, primarily within sagebrush dominated landscapes (Knick et al.

2003). In Wyoming, for example, as of 2008 there were over 2 million ha of producing

oil and gas leases, and a total 5.5 million ha authorized for production (U.S. Department

of the Interior [USDI] 2009; Fig. 1). Energy development infrastructure such as drill

pads, waste pits, access roads, and pipelines convert and fragment sagebrush habitats

(Weller et al. 2002), often negatively impacting wildlife populations (Walker et al. 2007,

Doherty et al. 2008, Sawyer et al. 2009, Holloran et al. 2010).

Research focusing on effects of energy development on sagebrush birds has

centered on the greater sage-grouse (*Centrocercus urophasianus*; Walker et al. 2007,

Doherty et al. 2008, Holloran et al. 2010). Adverse effects of energy development on this

high-profile game species are well documented and include decreased recruitment to or abandonment of leks, avoidance of nesting near infrastructure, decreased nest and chick survival, and increased adult mortality due to increasing disease prevalence, vehicle collisions, and raptor predation (Naugle et al. in press). Yet studies examining responses of the rest of the sagebrush bird community to oil and natural gas development are lacking (Inglefinger and Anderson 2004). Understanding how songbird populations may be impacted by anthropogenic disturbance, and how disturbance impacts may interact with critical habitat features, is an important step in developing effective recommendations for management strategies geared towards the maintenance of stable sagebrush bird communities.

Our objective was to assess the relationship between energy development intensity in sagebrush habitat and songbird populations and avian community composition. Specifically, we evaluated the relative abundance and species richness of songbirds across gradients of oil and natural gas well density and habitat variation.

STUDY AREA

Our study was conducted within sagebrush habitat coinciding with energy development in the Upper Green River Basin (42˚60´N, 109˚75´W) of southwestern WY, USA (Fig. 1). Specifically, our 3 study areas were: the northern portion of the Pinedale Anticline Project Area (PAPA) natural gas field, the Jonah natural gas field, and the northern portion of the Big Piney-LaBarge (LaBarge) oil field (Fig. 2). Located south of Pinedale, WY, PAPA and Jonah rank among the most highly concentrated and productive natural gas fields in North America (USDI 2006, 2008). The LaBarge area is an aggregation of

oil fields south of Big Piney, WY. The Upper Green River Basin landscape is dominated by big sagebrush (*Artemisia tridentata* spp.) with a primarily native understory of grasses and forbs (Lyon and Anderson 2003). Yearly precipitation averaged 27.5 cm (Western Regional Climate Center 2010).

METHODS

Site Selection

To ensure sampling spanned a gradient of energy development intensity, we stratified each study area into 4 levels of development based on existing variation in well density: none (0 wells/km^2), light (1–6 wells), moderate (7–15 wells), and heavy (>15 wells) development. We used aerial imagery and geographic locations of wells (Wyoming Geographic Information Science Center, Laramie, WY; USGS Fort Collins Science Center, Fort Collins, CO) to spatially map well density in each energy field (Fig. 2) and randomly selected potential sampling sites within those strata.

Songbird habitats in sagebrush steppe have been characterized by measures of patch size, spatial homogeneity, and shrub attributes (Rotenberry and Wiens 1980; Wiens and Rotenberry 1981; Petersen and Best 1985*a*, *b*; Knopf et al. 1990). We ground-truthed potential sampling sites to ensure they consisted of ≥20% shrub cover (Wiens and Rotenberry 1981, Chalfoun and Martin 2007), average shrub height ≥35 cm (Rich 1980; Petersen and Best 1985*a*, *b*), and average shrub crown vigor ≥50% (Petersen and Best 1985*a*, *b*; Chalfoun and Martin 2009). Within each development strata at each study area, we chose the first 5 randomly selected sites which met these habitat criteria for placement of our point count clusters. Clusters consisted of 4 points in the shape of a

8

square with 200 m spacing between points; if habitat minimums at points were not met, points were adjusted outward with a maximum spacing of 400 m. By selecting sites that met habitat minimums we sought to survey only potentially suitable nesting and foraging habitat within areas of differing energy development intensity.

Avian Abundance and Species Richness

We evaluated avian abundance and species richness using point count sampling (Reynolds et al. 1980) from May through July, 2008–2009. We surveyed a total of 20 clusters per energy field (with 5 point count clusters in each of the 4 well density strata), for a total of 240 points. During each 10-min survey we recorded all birds seen or heard and distance to observer using digital rangefinders, taking care to avoid double-counting individuals. We recorded flyovers but excluded them from analyses. Surveys began at sunrise on mornings without rain or strong winds and were completed within 3 hours. We repeated surveys 3 times in 2008 and twice (due to persistent rain) in 2009, varying observer and time of visit among surveys. We surveyed the same sites in both years, except where creation or expansion of drilling infrastructure encroached on 7 point count clusters (2 in PAPA and 5 in Jonah) in 2009, which required the relocation of 10 survey points. In most cases we moved just one point per cluster and reassessed well density for the cluster for that year. Two additional clusters in PAPA could not be resurveyed in 2009 because the entire cluster area was developed, and were excluded from analyses.

We used program DISTANCE (Thomas et al. 2010) to fit detection-probability functions for species with sufficient detections at each study area. We pooled data across years, truncated the furthest 10% of distances, and fit detection functions for a uniform model with cosine expansions, a uniform model with simple polynomial expansions, and

9

a half-normal model with hermite polynomial expansions (Somershoe et al. 2006,

Thomas et al. 2010). We used Akaike's Information Criterion (Burnham and Anderson

2002) to select the model with the best relative fit, and adjusted our relative abundance

estimates using the model-generated detection probabilities (Table 1). However, the low

calculated detection probabilities for Brewer's sparrows (0.224–0.298) produced

unrealistically high abundance estimates, based on minimum territory sizes of

approximately 0.5 ha (Wiens et al. 1985, Chalfoun and Martin 2007). We therefore

truncated the Brewer's sparrow data at 100 m rather than the furthest 10% of detections.

We summarized adjusted detections for each species by cluster, averaged over the

number of visits each year. We summarized species richness as the average number of

breeding songbird species detected per cluster visit in each year.

Well Density

We used well density as a proxy for energy development intensity. Using aerial imagery

and geographic locations of wells, we calculated the number of well locations within a 1

km^2 area (564-m radius) around each point count center using ArcGIS 9 and averaged

these values to estimate well density for each cluster.

Habitat Characteristics

Because abundance of sagebrush songbirds is influenced by habitat characteristics at

breeding sites, we quantified habitat variation at our sampling sites to control for habitat

when examining energy development effects. We measured habitat attributes within 5-m

radius circular plots (Martin et al. 1997; Chalfoun and Martin 2007, 2009) placed at two

locations with randomly selected direction and distance up to 50 m from each point count

center. We completed habitat measurements during a 3-week period beginning mid-July

of each year, surveying half of each cluster in 2008 and the remainder in 2009. We quantified shrub cover using the line intercept method (Lucas and Seber 1977) along two 10-m transect lines oriented in the cardinal directions. For each intersected shrub we measured: (1) height of the main crown (cm), and (2) percent crown vigor (proportion of the crown that was live). In each quadrant designated by the transect lines, we recorded total shrub density and the density of potential nest shrubs (PNS density), which we defined as shrubs with the proper quantitative and qualitative attributes to potentially accommodate a nest of a Brewer's sparrow (Chalfoun and Martin 2007, 2009), the most common species at our sites. We averaged habitat data collected at each point count cluster, combined across years, to obtain one value per cluster for each habitat variable.

Correlation analysis revealed significant positive relationships between many of our habitat variables (Table 1). For sparrows in sagebrush habitat, shrub vigor has merit as a proxy for increased insect food abundance (Wenninger and Inouye 2008) and nest concealment (Rich 1980), two critical resources for shrub-nesting birds (Knopf et al. 1990). Shrub vigor is also important in identifying nest shrubs used by both Brewer's sparrows and sage sparrows (Petersen and Best 1985*a*, *b*). We therefore chose average shrub vigor as our habitat covariate for most species. For Brewer's sparrows, however, we used PNS density instead of shrub vigor, as PNS density influences nest site selection and reproductive success of Brewer's sparrows (Chalfoun and Martin 2007, 2009) and PNS density was correlated with most other habitat characteristics (Table 1). For horned larks (*Eremophila alpestris*), a ground-nesting species more associated with grasslands than shrublands (Beason 1995), we used shrub cover as our habitat covariate, as we anticipated that horned lark abundance would be inversely related to big sagebrush cover.

Statistical Analyses

After abundance and species richness data were checked for normality and homogeneity of variances, we analyzed abundance of each species and overall species richness across energy development gradients using repeated-measures general linear mixed models in SPSS 17 (SPSS Inc., Chicago, IL). Year was treated as a repeated measure on the experimental units (clusters)**,** using cluster identification as a random effect to acknowledge the potential correlation in songbird abundance at locations across years. Site was included as a fixed factor, and well density/km^2 was our covariate of interest. A covariate representing habitat characteristics (PNS density for Brewer's sparrow, average shrub cover for horned larks, average shrub vigor for all others) was included to account for habitat effects. Dependent variables were average species detections (adjusted) and average species richness per cluster per survey visit.

RESULTS

We conducted 1184 point count surveys during 2008–2009. The most common species were, in order of abundance: Brewer's sparrow, horned lark, sage sparrow, vesper sparrow (*Pooecetes gramineus*), and sage thrasher. These 5 species accounted for 95% of songbird detections. Detection probabilities ranged from 0.300–0.581 (Table 2). Other breeding songbird species included in species richness calculations were Brewer's blackbird (*Euphagus cyanocephalus*), green-tailed towhee (*Pipilo chlorurus*), loggerhead shrike (*Lanius ludovicianus*), western meadowlark (*Sturnella neglecta*), and white-crowned sparrow (*Zonotrichia leucophrys*).

Brewer's sparrow abundance decreased significantly with increased well density (Table 3), albeit to differing extents across sites and between years (Table 4, Fig. 3). Indeed, we observed significant site effects in all species' abundance models (Table 3), and because we were interested in which types of energy fields may influence bird populations most strongly, we further analyzed responses individually by site. Sage sparrows, sage thrashers, horned larks, and species richness lacked a significant year×site interaction (Table 3); for these, we pooled data across years and analyzed site responses using general linear models. Abundance of Brewer's sparrows decreased with increased well density most steeply at the Jonah natural gas field and the response was more pronounced in 2008 than in 2009 (Table 4, Fig. 3).

Sage sparrow abundance was also inversely related to well density (Table 3), with the strongest declines at Jonah (Table 4, Fig. 3). Similarly, abundance of vesper sparrows was negatively related to well density (Table 3), though to differing extents across sites and between years (Table 4, Fig. 3). Vesper sparrow abundance at PAPA decreased in response to increasing well densities, with mixed responses in LaBarge across years and consistently low detections at Jonah (Table 4, Fig. 3). Horned lark abundance increased with increasing well density at PAPA (Table 4, Fig. 3), but showed no significant responses at Jonah or LaBarge. Abundance of sage thrashers was unrelated to well density (Table 3), but responses differed among study sites (Table 4, Fig. 3). Habitat covariates did not influence responses of any of the 5 species we evaluated (Table 3). Species richness at clusters was unrelated to increasing well density (Table 3, Fig. 3); this response was consistent among study sites (Table 4).

13

DISCUSSION

Increased energy development intensity, as estimated by well density/km^2, was associated with decreased abundances of Brewer's sparrows, sage sparrows, and vesper sparrows. Declines were strongest for Brewer's sparrows and sage sparrows at the Jonah field, with an average decrease of 0.3 individuals per well/km^2 (Table 4). This translates to average losses of 2.5 individuals at clusters with densities of 8 wells/km^2 for both these sagebrush-obligates. Approved spacing of 16 well pads per 2.6-km^2 section (USDI 2006) readily yields these and higher well densities at Jonah.

Sage thrashers did not respond significantly to increased well density in our study, despite sage thrashers being the largest-bodied species with the largest average territory size of those we studied. Sage thrashers have also shown a lack of response to other disturbances such as fire treatments (Castrale 1982, Knick and Rotenberry 2000), suggesting they may be less sensitive to habitat change. An alternative explanation is high annual site fidelity (Wiens and Rotenberry 1985, Knick and Rotenberry 2002), regardless of habitat changes, though this hypothesis requires explicit testing. If site fidelity is strong, population responses could take longer to detect due to turnover times of individuals creating a lag effect, which has been shown in greater sage-grouse population responses to energy development (Walker et al. 2007, Harju et al. 2010). Site fidelity within altered habitats, moreover, could reduce population size in the future if these habitats are of lower quality and result in lower fitness of remaining individuals.

We provide evidence that not all energy fields are created equal; significant site effects for all species evaluated suggest that characteristics of an energy development field may influence avian species responses. Effects were typically stronger in the Jonah

and PAPA natural gas fields, developing energy fields that contained multiple disturbance sources in contrast to the LaBarge oil field that had been in production for several decades (McDonald 1976, Holloran 2005). Time since the initiation of development, spatial configuration of energy fields (Fig. 2), and higher human activity levels and drilling infrastructure presence may contribute to patterns of songbird abundance.

Human activity and vehicle traffic levels, for example, are highest on active drilling pads (Sawyer et al. 2009), and varied between our energy fields. On the growing PAPA and Jonah natural gas fields, manned drilling rigs were common on the landscape throughout the breeding season. In contrast, active drilling rigs were rare in LaBarge during our study. Likewise, traffic volume around an active well pad in the PAPA averaged 112 vehicles per day (Sawyer et al. 2009), and traffic on main haul roads in Jonah has exceeded 600 vehicles per day (Ingelfinger and Anderson 2004), whereas traffic at LaBarge rarely exceeded 5 vehicles per day during our study (M. Gilbert, personal observation).

Field age or spatial configuration may factor into response differences between the PAPA and Jonah natural gas fields. Development began on PAPA approximately 10 years ago and the northern portion of the field was configured in a linear band of development (Fig. 2), primarily employing directional drilling technology with multiple wells drilled on a well pad (Sawyer et al. 2009). Approximately 30 km^2 of our 170-km^2 PAPA study area contained moderate to high well densities of ≥ 8 wells/km^2. The Jonah field, where species declines were steepest, lies directly south of PAPA but is older, with development authorized in the late 1990s, and had a wide central area that was densely

developed (Fig. 2), particularly where infill drilling occurred among existing wells (USDI 2006). As a result, nearly 70 km^2 of our 210-km^2 Jonah study area contained moderate to high well densities (≥ 8 wells/km^2). Interestingly, overall abundance estimates for several species at the LaBarge field, the oldest of our study areas, were lower than at the other two sites (Fig. 3), suggesting that effects may compound over time at energy fields rather than showing patterns of acclimation or recovery after initial disturbances. The specific effects of such anthropogenic disturbance on wildlife are still unclear. Other studies have shown that mule deer avoidance of well pads on PAPA increased with higher levels of traffic (Sawyer et al. 2009), and greater noise at energy development facilities reduced passerine density and altered songbird community composition (Bayne et al. 2008, Francis et al. 2009). Even so, some species may show partial acclimation to human activity over time, thus long-term effects at the community level are unknown.

Our results corroborate those of other studies showing decreased occurrence and abundance of several grassland birds near oil and gas development edges (Linnen 2008) and decreased sagebrush songbird density adjacent to natural gas development roads (Ingelfinger and Anderson 2004). Higher well densities result in a greater number and proportion of well pads, roads, and other anthropogenic infrastructure, which can intensify edge effects (Fletcher 2005) and may negatively impact songbirds via decreased nest success or altered species interactions. Horned larks can be associated with disturbed vegetation communities (Knick and Rotenberry 2002), and the increased horned lark abundance we observed at PAPA, coupled with decreased sparrow populations, could signal a fundamental change in the bird assemblage of shrubsteppe habitats surrounding energy development.

Songbird population declines may be driven by increased nest predation risk as generalist predators become more abundant in human-altered areas (Chalfoun et al. 2002). Common ravens (*Corvus corax*) are widespread and effective nest predators (Andren 1994), and energy field encroachment upon undeveloped sagebrush areas appears to facilitate increases in breeding raven abundance (Bui et al. 2010). Increased raven numbers in sagebrush systems negatively affected greater sage-grouse nest survival, particularly in areas with relatively sparse shrub cover (Coates and Delehanty 2010). Data on the identification, abundance, and distribution of dominant nest predators in relation to energy development would shed light on nest predation as a potential mechanism for decreased sagebrush songbird abundance in energy fields.

Landscape-scale habitat alteration associated with energy development may also lead to songbird population declines via decreased food availability (Howe et al. 1996). Reduction of the amount of intact sagebrush habitat surrounding territories via conversion can limit foraging opportunities. Alternatively, if the condition of remaining sagebrush patches is altered, associated insect prey assemblages could decrease in abundance. Breeding songbirds rely heavily on such insect prey for their own maintenance and ability to provision young. We found no significant relationship between the habitat characteristics we measured and sagebrush obligate abundance, but this is likely an artifact of selecting our sampling locations above set minimums of shrub cover and vigor. That we found significant effects of energy development while simultaneously accounting for important microhabitat components suggests, moreover, that energy development independently affects non-game birds.

17

In conclusion, we documented a pattern of declining sagebrush songbird abundance with increasing well densities in energy development fields. An important next step is to examine the consequences of energy development for songbird demographic and population processes in order to clarify mechanisms for declines. Understanding patterns of population responses coupled with specific causes for declines will facilitate the development of effective management strategies for the maintenance of sagebrush bird communities.

MANAGEMENT IMPLICATIONS

Sagebrush-obligate songbirds are an important component of the biodiversity of the western United States, and can serve as barometers of sagebrush ecosystem integrity due to their dependence on sagebrush and sensitivity to habitat alteration (Dobkin and Sauder 2004). The long-term impact of oil and natural gas development on songbirds in sagebrush habitat is unclear (Ingelfinger and Anderson 2004), but our data suggest that increasing energy development intensity will further exacerbate regional declines of sagebrush songbirds.

Current restrictions and mitigation requirements on energy fields in Wyoming focus on game birds and large mammals, but we document that energy fields may also negatively impact a suite of non-game birds. Others have recommended management actions minimizing well density where possible and maintaining large tracts of undeveloped sagebrush habitats with moderate to high canopy cover and a large presence of tall, mature sagebrush shrubs (Connelly et al. 2000, Doherty et al. 2008, Holloran et al. 2010). We suggest that these recommendations would also benefit songbirds. For fields

in early development stages, or expansions to existing fields such as the anticipated addition of 4,399 wells on up to 600 well pads in the PAPA (USDI 2008), it will be imperative for future studies to evaluate well placement configurations so as to assess their impacts on wildlife. Furthermore, explicit hypothesis tests focused on impacts to important limiting resources such as refugia from nest predation and food availability will be critical for determining underlying mechanisms through which energy development impacts songbirds, and ultimately for developing appropriate mitigation strategies.

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Table 1. Correlation matrix of habitat measurements collected at 3 energy fields in southwestern Wyoming, USA, 2008–2009, averaged per point count cluster (1 cluster = 4 points). Data are 2-tailed Pearson correlation *(r)* and *P*-values, *n* = 118.

		PNS Density	Shrub Height	Shrub Cover	Shrub Density
Shrub Vigor	*r*	0.212	0.017	− 0.166	0.147
	P	0.021	0.857	0.072	0.112
PNS Density	*r*		0.305	0.619	0.553
	P		0.001	≤ 0.001	≤ 0.001
Shrub Height	*r*			0.149	0.258
	P			0.106	0.005
Shrub Cover	*r*				0.461
	P				≤ 0.001

Table 2. Detection probabilities calculated using program Distance for the 5 most common

songbird species at 3 energy fields in southwestern Wyoming, USA, 2008–2009.

	Jonah	PAPA	LaBarge
Brewer's sparrow	0.378	0.384	0.448
Sage sparrow	0.423	0.300	0.359
Sage thrasher	0.361	0.323	0.493
Vesper sparrow	0.432[a]	0.432	0.565
Horned lark	0.508	0.555	0.581

[a]Detections at Jonah were insufficient (≤ 50 individuals) for

estimation of vesper sparrow detection probabilities, so we

assumed this value was similar to that on the adjacent PAPA

site.

Table 3. Between-subjects effects (top 3 lines) and within-subject contrasts (lower 3 lines) from repeated measures general linear mixed models examining effects of energy development density (wells/km^2) on abundance of the 5 most common passerine species and species richness at 3 energy fields in southwestern Wyoming, USA, 2008–2009. $n = 57$ point count clusters for Brewer's sparrow and 58 for all other species and richness.

	df	Brewer's sparrow		Sage sparrow		Sage thrasher		Vesper sparrow		Horned lark		Richness	
		F	P	F	P	F	P	F	P	F	P	F	P
Well Density	1	5.247	0.026	7.995	0.007	0.144	0.706	3.055	0.086	0.795	0.377	0.43	0.515
Habitat[a]	1	2.437	0.125	1.786	0.187	1.059	0.308	0.682	0.413	0.03	0.864		
Site	2	38.871	≤0.001	6.953	0.002	7.722	≤0.001	36.175	≤0.001	19.78	≤0.001	12.663	≤0.001
Year	1	14.218	≤0.001	0.01	0.92	0.088	0.768	0.601	0.442	0.037	0.847	13.556	0.001
Year × Well Density	1	0.745	0.392	0.071	0.792	0.848	0.361	0.064	0.802	0.162	0.689	3.662	0.061
Year × Site	2	13.970	≤0.001	0.673	0.515	0.613	0.546	4.265	0.019	0.346	0.709	0.169	0.845

[a]Potential nest shrubs for Brewer's sparrow, shrub cover for horned lark, and average shrub vigor for other species.

Table 4. Parameter estimates, 95% confidence intervals, and *P*-values for effects of well density (wells/km^2) in 2 natural gas fields (Jonah and PAPA) and 1 oil field (LaBarge) in western WY, USA on the abundance of the 5 most abundant passerine species and species richness by year and site from repeated measures general linear mixed models, or by site with years combined from general linear models.

		Jonah			**PAPA**			**LaBarge**		
		B	*CI*	*P*	*B*	*CI*	*P*	*B*	*CI*	*P*
Brewer's sparrow	2008	–0.311	(–0.528, –0.095)	0.008	–0.011	(–0.327, 0.306)	0.943	–0.017	(–0.222, 0.188)	0.865
	2009	–0.348	(–0.717, 0.022)	0.063	–0.147	(–0.431, 0.136)	0.286	–0.070	(–0.371, 0.231)	0.629
Sage sparrow		–0.294	(–0.436, –0.152)	≤0.001	–0.060	(–0.255, 0.135)	0.536	–0.144	(–0.335, 0.047)	0.134
Sage thrasher		0.057	(–0.052, 0.165)	0.296	–0.062	(–0.197, 0.073)	0.358	0.077	(–0.034, 0.189)	0.168
Vesper sparrow	2008	0.001[a]	(–0.012, 0.013)	0.929	–0.043	(–0.152, 0.065)	0.407	–0.139	(–0.333, 0.050)	0.149
	2009	–0.012[a]	(–0.031, 0.007)	0.183	–0.141	(–0.331, 0.050)	0.136	0.024	(–0.155, 0.202)	0.781
Horned lark		–0.024	(–0.569, 0.041)	0.739	0.125	(0.012, 0.238)	0.031	0.005	(–0.131, 0.142)	0.937
Richness		–0.013	(–0.029, 0.002)	0.096	–0.002	(–0.018, 0.014)	0.816	–0.018	(–0.049, 0.013)	0.248

[a]Estimates based on very low numbers of vesper sparrow detections at Jonah (<20 individuals over 2 years).

Figure 1. *Top Panel*: Sagebrush habitats (light gray shading) are predominant throughout

Wyoming (U.S. Geological Survey 2001). *Bottom Panel*: Producing (medium

gray) and authorized (dark gray) oil and natural gas leases (as of 2008; Wyoming

Geographic Information Science Center 2009), showing extensive overlap with

sagebrush habitats across the state. Our study of sagebrush songbird population

responses to energy development took place in Sublette County (outlined in bold),

Wyoming, USA, 2008–2009.

Figure 2. Three energy fields in Sublette County, southwestern Wyoming, USA (inset),

used to examine the relationship between oil and natural gas development and

sagebrush songbird abundance and richness, 2008–2009. Four *a priori* categories

of well density (wells/km^2) used to stratify point count sampling sites are

represented by light to dark shading.

Figure 3. Relative abundance of Brewer's sparrow (BRSP), sage sparrow (SAGS), sage

thrasher (SATH), horned lark (HOLA), and vesper sparrow (VESP), and

passerine species richness in relation to well density at the Jonah (circles and solid

lines), PAPA (squares and dashed lines), and LaBarge (triangles and dotted lines)

energy fields, southwestern Wyoming, USA, 2008–2009. Open symbols

designate oil fields, shaded symbols are natural gas fields. Data are average

number of individuals or species detected per survey visit per cluster (sum of 4

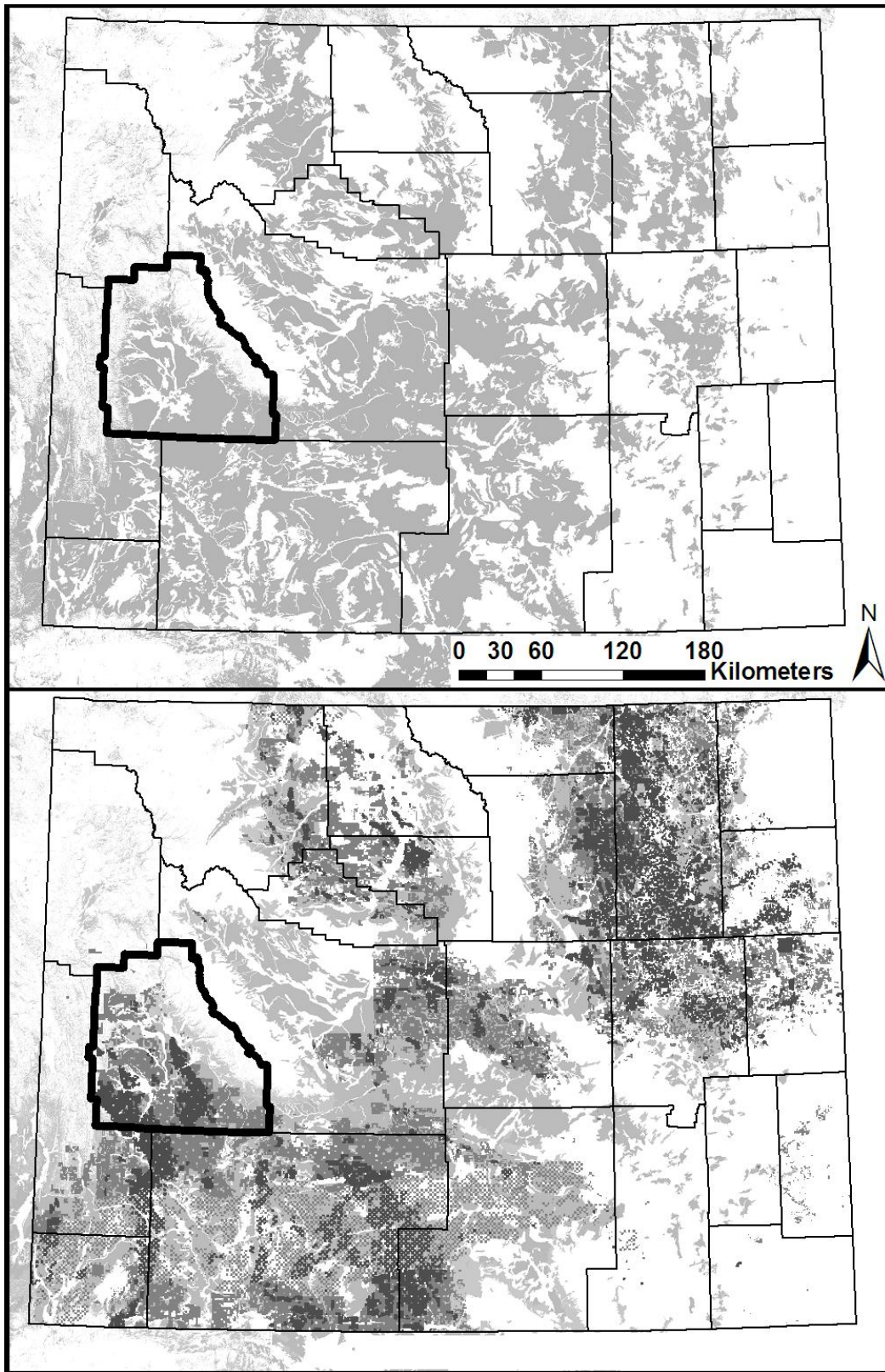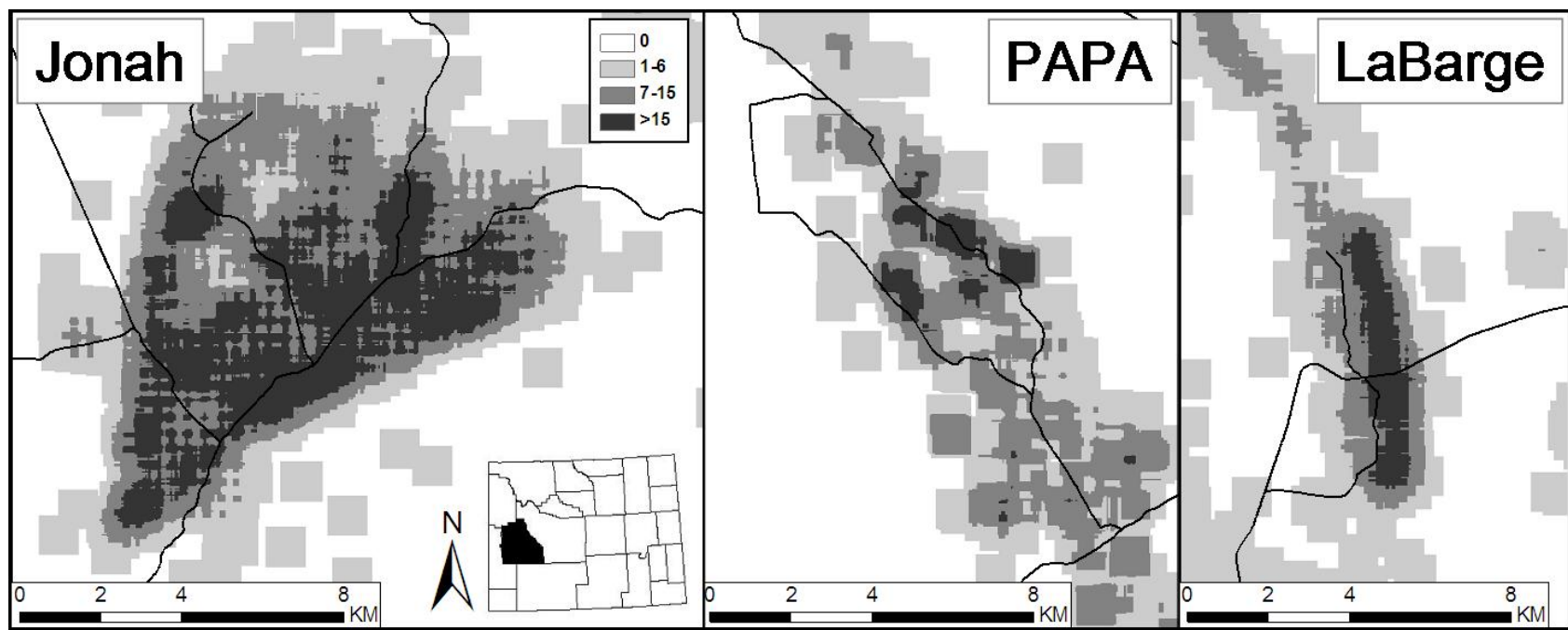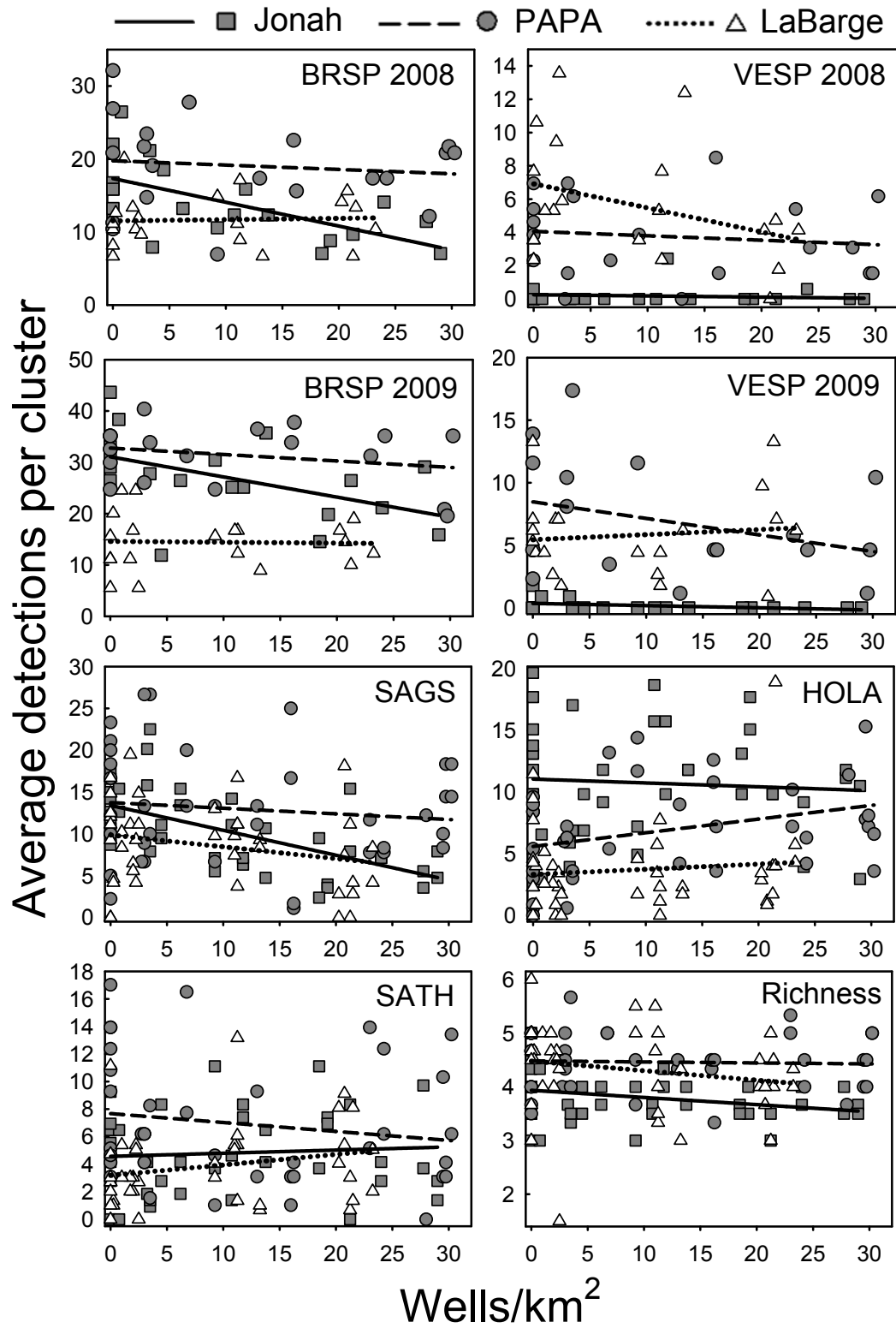100-m radius point counts), adjusted for detection probabilities.

Figure 1.

Figure 2.

Figure 3.

CHAPTER 2. INCREASED NEST PREDATION AND FOOD LIMITATION AS POTENTIAL MECHANISMS UNDERLYING SAGEBRUSH-OBLIGATE SONGBIRD DECLINES WITHIN ENERGY DEVELOPMENT FIELDS.

ABSTRACT

Understanding the mechanisms underlying species responses to anthropogenic disturbances is essential for the development of effective wildlife management and conservation regimes. Energy development, which has rapidly expanded within sagebrush habitats in the western United States, has been associated with decreased abundance of sagebrush-obligate songbirds. However, mechanisms for such declines remain unclear. We tested two alternative hypotheses for why oil and natural gas development influences songbird populations in western Wyoming: increased nest predation and food limitation. The probability of daily nest survival for Brewer's sparrow (*Spizella breweri*), sage sparrow (*Amphispiza belli*) and sage thrasher (*Oreoscoptes montanus*) decreased with greater well densities and increased proximity to well pads, and avian nest predator (common raven, *Corvus corax*) abundance increased slightly across energy development gradients, supporting a nest predation hypothesis. Additionally, shrub vigor decreased with increasing energy development, which could decrease insect prey availability and impact parental investment in offspring through decreases in clutch size and/or offspring provisioning. Clutch size did not vary with energy development, but average nestling mass for the sage thrasher (the largest of our study species) decreased significantly with increasing development, lending partial support to the food limitation hypothesis. Our results indicate that energy development

can impact songbird demography, and we suggest that avian declines within energy fields may be influenced by increased susceptibility to nest predation and changes in food resource availability.

INTRODUCTION

Human modification of natural environments is a global threat to the maintenance of wildlife populations and biodiversity (Turner 1996, Gill 2007). Anthropogenic disturbance can result in habitat loss, increased fragmentation, and/or degradation of remaining habitat (Saunders et al. 1991, Lin et al. 2006). Such disturbances are often comprised of both physical changes to habitats and increased human activity, and can potentially impact wildlife via a number of non-mutually exclusive mechanisms. Yet, while studies often quantify levels of disturbance, specific mechanisms underlying disturbance impacts to wildlife are rarely explicitly examined (Klein 1993, Hill et al. 1997).

Encroachment by human development can result in modified community structure and altered species interactions (Schmiegelow and Monkkonen 2002). For example, human developments are commonly accompanied by an influx of generalist species capable of exploiting novel anthropogenic resources (Chalfoun et al. 2002, Leu et al. 2008). Increased presence and/or activity of predators may alter the abundance, distribution, and demography of prey species via increased predation risk in altered habitats (Kristan and Boarman 2007, Coker et al. 2009, Bui et al. 2010).

Habitat structure, condition and complexity can also influence resources such as food availability (Hixon and Menge 1991, Halaj et al. 2000). Therefore, human activities

that alter attributes of remaining habitats may lead to food limitation for individuals in disturbed areas. Food limitation can affect the physiological condition of parents, which in turn can influence reproduction and survival through, for example, a reduced investment in offspring. Parents in disturbed environments may therefore reduce the number of reproductive attempts, number of offspring produced per attempt, and/or provisioning rates to young (Martin 1987, Koskela et al. 1998, Zanette et al. 2006, White 2008).

Sagebrush habitats, and the passerines that are obligates to this system, are an excellent model system with which to examine the effects of anthropogenic change on wildlife. Across western North America, sagebrush habitats have been fragmented and degraded through livestock overgrazing, exotic species invasion, altered fire frequency and agricultural conversion (Braun et al. 1976, Connelly and Braun 1997, Dobkin and Sauder 2004, Rich et al. 2005), which has resulted in concomitant population declines of many breeding birds (Sauer et al. 2008). More recently, sagebrush landscapes have been converted or altered due to a rapid increase in infrastructure for oil and natural gas extraction (Knick et al. 2003, Holloran et al. 2010). Habitat loss and fragmentation are among the ecological impacts from drill pads, waste pits, networks of access roads and pipelines (Weller et al. 2002), and vegetative condition could be impacted if air quality is altered (Westman 1979, Talluto and Suding 2008).

Species dependent on a single habitat type, such as sagebrush obligates, may be more sensitive to habitat modification than generalist species (Saab and Rich 1997, Bui et al. 2010). Indeed, previous work suggests that energy development can negatively impact sagebrush-specialists (Sawyer et al. 2009, Holloran et al. 2010, Naugle et al. in

38

press). We documented decreases in sagebrush songbird abundance across gradients of
energy development intensity (Gilbert and Chalfoun in press), yet specific mechanisms
for these declines remain unknown. In this study, we tested alternative hypotheses for
potential mechanisms underlying the impacts of energy development on populations of
three sagebrush obligates: the Brewer's sparrow (*Spizella breweri*), sage sparrow
(*Amphispiza belli*) and sage thrasher (*Oreoscoptes montanus*). Specifically, we focused
on whether energy development affects two factors that can limit the reproductive
success and thus population size of nesting songbirds: nest predation and food
availability.

Nest predation hypothesis

Increased nest predation in disturbed habitats is often attributed to changes in
assemblages of generalist predators able to take advantage of human-altered
environments (Andren 1994, Chalfoun et al. 2002). For example, the common raven
(*Corvus corax*) is an effective nest predator capable of benefitting from anthropogenic
disturbance, and may increase in abundance in landscapes with frequent human activity,
such as energy development fields (Kristan and Boarman 2007, Leu et al. 2008, Bui et al.
2010). The increased nest predation hypothesis suggests that energy development
infrastructure may be subsidizing nest predator assemblages, resulting in increasing nest
predation risk. Under this hypothesis, we predicted higher rates of nest predation and
greater abundance of synanthropic nest predator species with increased energy
development.

Resource depletion hypothesis

Landscape-scale habitat alteration associated with energy development may also impact songbird populations via decreased food availability (Howe et al. 1996). Wyoming big sagebrush (*Artemisia tridentata*) land cover is reduced where conversion to energy development occurs (Walston et al. 2009) which may alter overall prey availability in the landscape. Moreover, declines in metrics indicative of habitat condition such as shrub vigor (Talluto and Suding 2008) may affect associated insect communities (Wenninger and Inouye 2008, Burger et al 2003), which are the main diet of songbirds provisioning nestlings (Rotenberry and Wiens 1998, Chalfoun and Martin 2007). Decreased body condition, size, and/or growth rates of offspring as a result of food limitation can substantially lower survival probability (Sinervo 1993). The resource depletion hypothesis therefore suggests that energy development is affecting habitat availability and condition, thereby influencing prey (insect) abundance and nesting productivity. Under this hypothesis, we specifically predicted decreased shrub condition, and decreased clutch sizes and nestling mass, metrics known to be sensitive to food availability in nesting birds (Martin 1987), with increased energy development.

METHODS

Study Sites

We conducted our study during May to August 2008-2009 in sagebrush habitats within three energy development areas in the Upper Green River Basin of Wyoming. Study areas were contained within: (i) the northern portion of the Pinedale Anticline Project Area (PAPA) natural gas field, (ii) the Jonah natural gas field, and (iii) the northern portion of the Big Piney-LaBarge (LaBarge) oil field. These 3 fields were

representative of energy extraction activity in this region, and were also chosen in order to determine whether mechanisms may differ across energy field contexts. The Upper Green River Basin landscape is dominated by big sagebrush (*Artemisia tridentata* spp.) and a largely native forb and grass understory (Lyon and Anderson 2003, Holloran et al. 2010).

To examine responses across a gradient of energy development intensity, we stratified study areas into 4 levels of development based on existing variation in well density: no development (0 wells/km^2), light (1-6 wells), moderate (7-15 wells), and heavy development (>15 wells), using aerial imagery and geographic locations of wells (Gilbert and Chalfoun in press). We established 25-ha nest searching plots, one within each energy development strata at each study area, for a total of 12 nest searching plots. All plots were placed at randomly selected locations that also met minimums of habitat attributes important for nesting songbirds, including shrub cover, height, and vigor (Gilbert and Chalfoun in press), thus increasing our probability of surveying only suitable nesting and foraging areas.

Data collection

Nest searching and monitoring

We located nests within each site during each year via observations of adult behavior and systematic searches (Chalfoun and Martin 2007). Nests were monitored every 2-4 days until failure or fledging (Martin et al. 1997). Nests were considered fledged when found empty within a day or two of the expected fledge date, and/or when fledged chicks, adults with food, or agitated adults were seen near the nest. Nests were considered failed if found empty prior to the predicted fledge date, or if they contained

broken eggshells or dead chicks. To minimize disturbance while monitoring nests, observers spent minimal time at nests, and avoided visiting a nest if corvids were observed in the area. Nests with eggs that remained unhatched more than three days past the predicted hatch date were considered abandoned. Abandoned nests or failures due to weather were omitted from analyses. During 2008–2009, we monitored a total of 256 Brewer's sparrow, 93 sage sparrow, and 74 sage thrasher nests for use in nest survival analysis. Predation was the leading cause of nest failure, accounting for > 90% of failures. We used ArcGIS 9.3 (ESRI, Redlands, CA) to plot well locations and digitize well pad boundaries. For each nest, we measured the distance from the nearest well pad edge and calculated well density within a 1 km^2 (100 ha) buffer.

Avian nest predator abundance

While nest predator assemblages in sagebrush are often diverse (Vander Haegen et al. 2002, Chalfoun and Martin 2007), we chose to focus on corvid species as an indicator of nest predator response to energy development. Common ravens are an important nest predator known to be able to take advantage of human infrastructure (Leu et al. 2008, Bui et al. 2010, A. Holmes, unpublished data), and were observed taking eggs from greater sage-grouse (*Centroercus urophasianus*) nests during our study (M. Gilbert, personal observation). We used point count sampling (Reynolds et al. 1980) to evaluate raven abundance from early May through early July each year. We conducted 10-minute unlimited radius point counts at 5 point count clusters placed in each energy development strata in each study area (Gilbert and Chalfoun in press), with clusters consisting of 4 point count locations. Clusters were surveyed 3 times in 2008 and twice in 2009. Flyovers were included because ravens have large home ranges and commonly forage

long distances from their territories during the day (Linz et al. 1992). Moreover, our goal was to examine relative rather than absolute differences in raven abundance across energy development gradients. Energy field expansion encroached on 7 point count clusters (2 in the PAPA and 5 in Jonah) in 2009 and required us to relocate 10 survey points. Two additional clusters in the PAPA could not be resurveyed in 2009 due to development and were excluded from analyses. We conducted a total of 1184 point count surveys at 58 clusters during 2008–2009 to assess raven abundance. Average raven abundance per cluster was calculated by summing the counts of the 4 points in each cluster, averaged over the total visits each year.

Habitat Features

Relevant nest patch attributes were assessed for inclusion as covariates in nest predation analyses, and to examine habitat condition across energy development gradients. We measured habitat attributes within 5-m radius circular plots (Martin et al. 1997, Chalfoun and Martin 2007) placed at two locations of randomly selected direction and distance up to 50 m from each point count center (Gilbert and Chalfoun in press), and centered at each nest shrub. We quantified shrub cover using the line intercept method (Lucas and Seber 1977) along two 10-m transect lines oriented in the cardinal directions. Total shrub density was recorded in each quadrant. For each intersecting shrub we also measured: (1) height of the main crown (cm), and (2) vigor (visual estimate of the proportion of the crown that was live and green). We also recorded density of potential nest shrubs (PNS density), which we defined as shrubs with the proper quantitative and qualitative attributes to potentially accommodate a nest of a Brewer's sparrow, the most common species at our sites (Gilbert and Chalfoun in press). PNS density can influence

43

Brewer's sparrow nest site selection and reproductive success (Chalfoun and Martin 2007, 2009) and was correlated with total shrub density at our sites ($r = 0.411$, $P < 0.001$). We conducted vegetation surveys at a total of 471 point count sites and 432 nest locations. Habitat data were averaged to obtain one value per nest site or point count cluster for each habitat variable measured.

Clutch and Nestling Size

We recorded clutch size for every nest for which we obtained 2 or more observations of the nest between the end of laying and hatch day. We measured nestling size at a subset of nests in each nest plot with known hatch dates and modal brood sizes (3-4 nestlings for the Brewer's sparrow and the sage sparrow, 4-5 nestlings for the sage thrasher). Nestlings were always measured between the hours of 1100 and 1400 on the same day of the nestling period (day prior to pin feather emergence; days 5, 6, and 7 for Brewer's sparrow, sage sparrow and sage thrasher, respectively) to control for growing time. Measuring nestlings just prior to pinbreak allows several days for growth under ambient food conditions while minimizing the risk that nestlings will force-fledge when handled. We measured a total of 372 nestlings from 68 Brewer's sparrow nests, 19 sage sparrow nests, and 19 sage thrasher nests during the study. Nestling size data were summarized as average nestling mass for each nest.

Statistical analyses

Nest survival

To model potential impacts of energy development on daily nest survival rates (DSR) for each of our three focal species, we used a logistic exposure approach (Shaffer 2004) which is based on a generalized linear model that does not require assumptions

about when nest losses occur during the nesting period or that nests be checked daily. Our sets of candidate models included combinations of year, site, Julian date of nest initiation (Jdate; day first egg laid), and an energy development variable, either well density (wells/km^2) or distance in meters to the nearest well pad (Table 1). Because our two energy development metrics were highly correlated ($r = -0.573$, $P < 0.001$), we analyzed them in separate model sets. Evaluating both of these metrics allowed us to assess the impacts of proximity to and relative density of human disturbance on birds, the results of which could inform different management objectives.

To determine if the any of the microhabitat variables we measured impacted songbird nest survival, we first used logistic regression to examine the nest success of each species in relation to: (1) shrub cover, (2) shrub height (3) shrub vigor, and (4) shrub density (or PNS density for Brewer's sparrows). The only significant habitat variable was shrub cover for sage thrashers (Wald $= 4.416$, df $= 1$, $P = 0.036$). Thus, we included shrub cover as a covariate in the logistic exposure model candidate sets for sage thrashers (Table 1).

We evaluated support for candidate models using PROC GENMOD (SAS version 9.2; SAS Institute, Cary, NC). We ranked candidate models based on Akaike's Information Criterion scores, adjusted for small sample sizes (AIC$_c$) and computed model weights (Burnham and Anderson 2002). We plotted DSR as a function of energy development variables from best fit models for each species to demonstrate effects on nest survival.

Avian nest predator abundance

To evaluate whether the avian nest predator population was augmented by energy development, we analyzed raven abundance in relation to each energy development variable (well density/km^2 or distance to nearest well pad edge) using repeated-measures general linear mixed models. Year was treated as a repeated measure on the experimental units (point count clusters) to acknowledge potential correlations in raven abundance at clusters across years, and site was included as a fixed factor.

Habitat condition

We used analysis of covariance to examine whether shrub vigor changed in relation to each energy development variable (well density/km^2 or distance to nearest well pad edge), with site included as a fixed factor. We used vigor data from point count clusters rather than from nest sites because songbirds routinely forage beyond their immediate nest patch and we felt that the randomly selected point count locations served as better samples of habitat condition across the landscape.

Clutch and nestling size

To explore which potential explanatory variables impacted reproductive investment and offspring quality for each species, clutch size and nestling mass were compared via analysis of covariance with year and site as fixed factors, and Jdate and well density or distance to well pad edge as covariates. Brood size was included as an additional covariate in the nestling mass models.

RESULTS

Nest survival

The probability of daily nest survival (DSR) declined with increasing well density (Fig. 1a) and decreasing distance to the nearest well pad (Fig. 1b) for all three species, albeit to differing extents. For the Brewer's sparrow, models including an energy development variable and Jdate received the most support per candidate set ($w_i \geq 0.46$; Tables 2, 3). Those best-fit models indicated that Brewer's sparrow DSR declined with increased density of wells ($\beta = -0.015 \pm 0.007$ SE; Wald $= 4.11$, $P = 0.04$; Fig. 1a) and increased with increased distance from the nearest well pad ($\beta = 0.4712 \pm 0.1697$ SE; Wald $= 7.71$, $P = 0.006$; Fig 1b).

For the sage sparrow, no nest survival model had overwhelming support. The null model performed the best, and 5 models in each set were within $\Delta \text{AIC}_c \leq 2$ (Tables 2, 3). The null model predicted an average DSR of 0.959 ± 0.005 SE, which translates to a 28% – 48% apparent nest success probability (23-day nest cycle). In the best fit energy development models (Tables 2, 3), sage sparrow DSR declined slightly with increased density of wells ($\beta = -0.009 \pm 0.011$ SE; Wald $= 0.56$, $P = 0.45$) and increased with increased distance from the nearest well pad ($\beta = 0.2594 \pm 0.2325$ SE; Wald $= 1.25$, $P = 0.26$).

For the sage thrasher, the model including shrub cover, Jdate, year and site received the most support ($w_i = 0.57$) in both energy development model sets (Tables 2, 3). Sage thrasher DSR increased with increased shrub cover ($\beta = 0.0509 \pm 0.0171$ SE; Wald $= 8.83$, $P = 0.003$). The best energy development models (Tables 2, 3) indicated that sage thrasher DSR declined slightly with increased density of wells ($\beta = -0.0191 \pm 0.0224$ SE; Wald $= 0.73$, $P = 0.39$) and increased slightly with increased distance from the nearest well pad ($\beta = 0.280 \pm 0.376$ SE; Wald $= 0.55$, $P = 0.46$).

Avian nest predator abundance

Common raven abundance increased marginally with well density ($F_{1,54} = 3.632$, $P = 0.062$; Fig. 3a) across all sites ($F_{2,54} = 0.76$, $P = 0.47$) and during both years of the study ($F_{1,54} = 0.36$, $P = 0.55$). Raven detections were not significantly related to distance to well pad edge ($F_{1,54} = 2.356$, $P = 0.131$; Fig. 3b) across sites ($F_{2,54} = 0.48$, $P = 0.62$), with variation across years ($F_{1,54} = 5.074$, $P = 0.028$).

Habitat condition

Shrub vigor was not related to increased well density ($F_{1,54} = 0.55$, $P = 0.46$), across all sites ($F_{2,} = 0.89$, $P = 0.42$; Fig 4a). Shrub vigor decreased marginally with decreasing distance to the nearest well pad edge ($F_{1,54} = 3.41$, $P = 0.07$) across all sites ($F_{2,54} = 0.81$, $P = 0.45$; Fig 4b). Average shrub vigor increased by 3.08 percent (SE = 1.67) for every 1 km increase in distance from a well pad edge.

Clutch and Nestling Size

Brewer's sparrow clutch size did not respond to well density ($F_{1,60} = 0.39$, $P = 0.54$) across sites ($F_{2,60} = 0.126$, $P = 0.88$), years ($F_{1,60} = 1.428$, $P = 0.34$) or nest initiation dates ($F_{1,60} = 0.862$, $P = 0.36$). Brewer's sparrow clutch size was also unrelated to the distance to the nearest well pad edge ($F_{1,60} = 0.226$, $P = 0.64$) across sites ($F_{2,60} = 0.105$, $P = 0.90$), years ($F_{1,60} = 1.324$, $P = 0.25$) and nest initiation dates ($F_{1,60} = 0.715$, $P = 0.40$).

Sage sparrow clutch size was unrelated to well density ($F_{1,11} = 0.002$, $P = 0.97$) across sites ($F_{2,11} = 0.209$, $P = 0.82$), years ($F_{1,11} = 1.316$, $P = 0.28$) and nest initiation dates ($F_{1,11} = 0.367$, $P = 0.56$). Sage sparrow clutch size was also unrelated to distance to

the nearest well pad edge ($F_{1,11} = 0.10$, $P = 0.76$) across sites ($F_{2,11} = 0.269$, $P = 0.77$), years ($F_{1,11} = 0.898$, $P = 0.36$) and nest initiation dates ($F_{1,11} = 0.176$, $P = 0.68$).

Sage thrasher clutch size was unrelated to well density ($F_{1,11} = 0.023$, $P = 0.88$) across sites ($F_{2,11} = 0.815$, $P = 0.47$), years ($F_{1,11} = 0.55$, $P = 0.47$) and nest initiation dates ($F_{1,11} = 1.44$, $P = 0.26$). Sage thrasher clutch size also did not respond to distance to the nearest well pad edge ($F_{1,11} = 0.546$, $P = 0.48$) across sites ($F_{2,11} = 0.605$, $P = 0.56$), years ($F_{1,11} = 1.01$, $P = 0.34$) and nest initiation dates ($F_{1,11} = 1.17$, $P = 0.30$).

Average Brewer's sparrow nestling mass was unrelated to well density ($F_{1,59} = 1.96$, $P = 0.17$) across sites ($F_{2,59} = 0.835$, $P = 0.439$) with a marginal effect of year ($F_{1,59} = 3.777$, $P = 0.06$). Nests with larger brood sizes tended to have smaller nestlings ($F_{1,59} = 6.125$, $P = 0.016$), and average nestling mass increased as the season progressed ($F_{1,59} = 18.683$, $P < 0.001$). Brewer's sparrow nestling mass was also unrelated to distance to the nearest well pad edge ($F_{1,59} = 1.01$, $P = 0.32$) across sites ($F_{2,59} = 0.562$, $P = 0.574$) and years ($F_{1,59} = 3.374$, $P = 0.07$). Again, nestling mass of Brewer's sparrow decreased with brood size ($F_{1,59} = 6.294$, $P = 0.015$), and increased through the breeding season ($F_{1,59} = 18.637$, $P < 0.001$).

Similarly, average nestling mass of sage sparrows was not related to well density ($F_{1,10} = 0.275$, $P = 0.611$), brood size ($F_{1,10} = 1.164$, $P = 0.306$) or nest initiation date ($F_{1,10} = 0.355$, $P = 0.565$) across all sites ($F_{2,10} = 0.578$, $P = 0.579$) and years ($F_{1,10} = 0.001$, $P = 0.98$). Sage sparrow nestling mass was also unrelated to distance to the nearest well pad edge ($F_{1,10} = 2.143$, $P = 0.174$) across all sites ($F_{2,10} = 1.416$, $P = 0.287$) and years ($F_{1,10} = 0.226$, $P = 0.644$). Neither brood size or nest initiation date were

related to sage sparrow nestling mass ($F_{1,10} = 1.043$, $P = 0.331$ and $F_{1,10} = 0.036$, $P = 0.853$, respectively).

Average nestling mass of sage thrashers, the largest of our study species, decreased with increasing well density ($F_{1,10} = 7.962$, $P = 0.018$) regardless of nest initiation date ($F_{1,10} = 0.852$, $P = 0.378$). Holding other factors constant, nestling mass decreased by 0.1 gram (SE = 0.03) with every additional well pad/km^2. Responses differed among sites and years (year*site $P = 0.028$); average sage thrasher nestling mass decreased marginally with well density at the Jonah ($F_{1,2} = 11.526$, $P = 0.077$) and Pinedale ($F_{1,2} = 9.487$, $P = 0.091$) natural gas fields, but not at the LaBarge oil field ($F_{1,2} = 1.128$, $P = 0.399$). Nests with larger brood sizes tended to have smaller nestlings ($F_{1,10} = 28.834$, $P < 0.001$). Average sage thrasher nestling mass also increased significantly with increasing distance from well pads ($F_{1,10} = 5.702$, $P = 0.038$) regardless of nest initiation date ($F_{1,10} = 0.046$, $P = 0.834$) or year ($F_{1,10} = 0.632$, $P = 0.445$), though there was a site effect ($F_{2,10} = 4.335$, $P = 0.044$). Average nestling mass of sage thrasher increased by 0.3 grams (SE = 0.1) for every 100-m increase in distance from the nearest well. Nestling mass of sage thrashers decreased with increasing brood size ($F_{1,10} = 20.298$, $P < 0.001$).

DISCUSSION

Habitat loss, fragmentation, and/or degradation as a result of anthropogenic activities can lower the availability of limiting resources such as food or refugia from predation (Gill 2007, Chalfoun et al. 2002, Leu et al. 2008). Here, we examined two potential mechanistic hypotheses for why a large-scale contemporary land use, oil and

natural gas development, affects populations of sagebrush songbirds (Gilbert and Chalfoun in press).

The increased nest predation hypothesis suggests that nest predation risk increases with energy development, possibly as a result of subsidized nest predator assemblages. Under the increased nest predation hypothesis, we predicted higher rates of nest predation and increased abundance of nest predators with increased energy development intensity. We found that daily nest survival rates for all species decreased in areas with greater well density and with increased proximity to the nearest well pad, signaling a general increase in nest predation with increased energy development. For the Brewer's sparrow, our most abundant study species, an increase in well density from 1 to 16 reduced average nest survival rates (DSR) from 0.973 to 0.965, or a 5% decrease in apparent nest success given a 22-day nest cycle. Moreover, an increase in the distance from the nearest well pad edge from 50 meters to 1 kilometer increased DSR from 0.96 to 0.975, which translates to a 17% increase in apparent nest success. Sage thrasher nest survival probability was better explained by changes in shrub cover than energy development metrics in our logistic exposure model sets, consistent with a lack of sage thrasher abundance response to energy development at these study sites (Gilbert and Chalfoun in press). However, if energy development activities substantially decrease sagebrush shrub cover on the landscape over time, we would expect decreases in sage thrasher populations in those areas.

Concordant with decreases in nest survival, the abundance of common ravens, a focal nest predator species, was slightly higher with increased well pad density. The trend was strongest at the Jonah field, which has by far the greatest human activity level

51

of our three study areas (Gilbert and Chalfoun in press). And although raven abundance did not increase significantly with proximity to well pad edges in our study, all of our higher detections occurred at sites ≤ 800 m from a well pad edge (Fig. 3), suggesting increased avian nest predator presence and/or abundance in close proximity to energy development. In energy fields, ravens nest on artificial structures as much or more than natural substrates (Bui et al. 2010, Knight et al. 1993), and as a result, nearby songbird nests may be exposed to increased predation risk. Previous studies have documented increased raven abundance in the PAPA natural gas field relative to surrounding undeveloped sagebrush areas (Bui et al. 2010), and shown inverse relationships between corvid density and nest survival (Manser and Hannon 2005), particularly in areas with relatively sparse shrub cover (Coates and Delehanty 2010).

While we focused on avian nest predators as a potential index for nest predator responses to energy development, we recognize that the nest predator community is likely more diverse. For example, the study area includes populations of several small mammal species (I. Abernethy, unpublished data) capable of depredating sagebrush songbird nests (e.g., deer mice, *Peromyscus maniculatus* and least chipmunks, *Tamias minimus*, A. Chalfoun, unpublished video data). Future studies should identify specific nest predator species responsible for nest losses and their responses to energy development to further explore why nest predation risk is elevated within energy development fields.

We also tested the hypothesis that energy development affects shrubland habitat condition, thereby influencing food (insect) abundance (Wenninger and Inouye 2008) and the ability of parents to invest in young (Chalfoun and Martin 2007), which can affect the

number of surviving offspring and ultimately population growth. Under this food limitation hypothesis, we predicted decreased sagebrush shrub condition, clutch size, and nestling mass with increased energy development. Vigorous shrubs likely support more herbivorous insecs , the primary component of breeding sagebrush adult and nestling songbird diets (Rotenberry and Wiens 1998), and parental investment metrics such as clutch size and nestling mass are sensitive to variation in food availability (Martin 1987). We documented decreased shrub vigor with increasing proximity to well pads, which could negatively impact food availability and thus parental investment of nesting songbirds.

Contrary to our prediction, however, clutch size for all three species did not decrease with increasing energy development. While clutch size has been similarly invariant with respect to ambient nest predation risk (e.g., Rotenberry and Wiens 1989, Chalfoun and Martin 2007), clutch sizes of species in arid systems typically respond to increased intra-annual moisture levels which improve vegetative productivity (Patten and Rotenberry 1999, Chalfoun and Martin 2007). During the breeding season, however, food may often be "superabundant" in shrubsteppe ecosystems, and so birds may not typically be food limited (Rotenberry 1980). Moreover, even when food is limiting, productivity may not be affected if birds are able to compensate for lost resources through behavioral changes such as diet switching, foraging in larger areas, or increased time spent foraging (Adams et al. 1994, Howe et al. 2000), though these changes could elicit additional energetic costs.

Nestling mass of our two smaller focal species, Brewer's and sage sparrows, similarly did not vary with energy development. However, sage thrasher nestling mass

decreased significantly with increasing well density and decreasing distance from well pads. Sage thrashers have the largest body size and therefore the highest nestling food requirements of our study species. Hence, food limitation should manifest earliest in this larger songbird, and indeed, food reductions negatively impacted sage thrasher nestling size in another study (Howe et al. 1996). The decrease in sage thrasher nestling mass with energy development we observed suggests that landscape-scale habitat alteration associated with energy development may be influencing at least some songbird populations via depleted food resources, thereby lowering nestling quality (Howe et al. 1996) and potentially post-fledging survival prospects (Sinervo 1993). An alternative explanation for observed decreases in thrasher nestling mass, however, is that parental feeding visits were reduced in areas with energy development activites because parents perceived them as more risky (Lima 2009, Chalfoun and Martin 2010). Moreover, food and predators likely have combined, and potentially interactive, effects on nesting songbird demography (Nagy and Holmes 2004, Zanette et al. 2006).

In conclusion, our results suggest that already declining songbird populations (Knick et al. 2003) within areas influenced by oil and natural gas extraction may be susceptible to increased nest predation and decreases in the availability of food resources. Energy development has become and will likely continue to be a dominant activity within sagebrush habitats of the Intermountain West (Sawyer et al. 2009), and increases in scale and intensity of energy-related disturbances has implications not only for songbirds, but all sagebrush-associated wildlife . In Wyoming alone, more than 2 million ha are currently impacted, and that number could double if all leases authorized for oil and gas production come online (U.S. Department of the Interior [USDI] 2009; Fig. 1 *in* Gilbert

and Chalfoun in press). The cumulative effects of direct and indirect impacts of energy development on the sagebrush ecosystem will therefore likely render the management and conservation of sagebrush species increasingly challenging (Walston et al. 2009). Attempts, such as ours, however, to quantify potential mechanisms underlying impacts will facilitate the development of the most effective management strategies to limit further impacts of on-going and proposed energy development activities on vulnerable wildlife species.

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TABLE 1. Candidate set of logistic exposure models used to examine differences in nest survival of Brewer's sparrow, sage sparrow, and sage thrasher nests at energy development fields in western Wyoming, 2008–2009.

TABLE 2. Logistic exposure models describing the effect of site, year, Julian date of nest initiation (Jdate), and well density on daily nest survival rates of the Brewer's sparrow, sage sparrow, and sage thrasher within three energy development fields in Wyoming. K = number of parameters in the model including the intercept; ΔAIC_c = difference in Akaike's information criterion (AIC_c) values between the best-fitting model and model i; and w_i = Akaike weights indicating the relative support for each model.

TABLE 3. Logistic exposure models describing the effect of site, year, Julian date of nest initiation (Jdate), and distance to wellpad edge on daily nest survival rates of Brewer's sparrow, sage sparrow, and sage thrasher within three energy development fields in Wyoming. K = number of parameters in the model, including the intercept; ΔAIC_c = difference in Akaike's information criterion (AIC_c) values between the best-fitting model and model i; and w_i = Akaike weights indicating the relative support for each model.

TABLE 1.

Model
Constant
Site
Year
Julian date
Energy Development[a]
Site + Year
Site + Energy Development
Year + Energy Development
Julian date + Energy Development
Site + Year + Energy Development
Site + Year + Energy Development + Julian date
ShrubCover[b]
Julian date + ShrubCover
Site + Year + ShrubCover
Site + Year + ShrubCover + Julian date

[a]Energy development = Well density or Distance to nearest well pad (separate model sets).

[b]Models including Shrub cover were run in model sets for Sage Thrasher only.

TABLE 2.

Model	K	Brewer's Sparrow			Sage Sparrow			Sage Thrasher		
		AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i
Constant	1	868.95	20.742	0	339.47	0	0.25	206.41	12.096	0.001
Jdate	2	850.11	1.908	0.179	340.76	1.29	0.131	200.27	5.956	0.029
Site	3	868.27	20.067	0	343.28	3.808	0.037	209.85	15.537	0
Year	2	867.82	19.618	0	339.98	0.514	0.193	208.39	14.078	0
WellCount	2	867.18	18.976	0	340.93	1.465	0.12	207.50	13.193	0.001
Jdate WellCount	3	848.20	0	0.464	342.25	2.778	0.062	201.58	7.274	0.015
Site WellCount	4	867.77	19.561	0	344.88	5.409	0.016	210.96	16.647	0
Year WellCount	3	866.07	17.863	0	340.80	1.332	0.128	209.50	15.192	0
Site Year	4	866.86	18.656	0	343.46	3.994	0.034	211.85	17.544	0
Site Year WellCount	5	866.60	18.391	0	344.56	5.091	0.02	212.98	18.665	0
Site Year WellCount Jdate	6	848.74	0.533	0.356	346.32	6.853	0.008	203.80	9.486	0.005
ShrubCover	2							200.27	5.96	0.029
ShrubCover Jdate	3							195.44	1.126	0.325
Site Year ShrubCover	5							200.84	6.531	0.022
Site Year ShrubCover Jdate	6							194.31	0	0.571

65

TABLE 3.

Model	K	Brewer's Sparrow			Sage Sparrow			Sage Thrasher		
		AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i
Constant	1	868.95	25.552	0	339.47	0	0.227	206.41	12.096	0.001
Jdate	2	850.11	6.718	0.026	340.76	1.29	0.119	200.27	5.956	0.029
Site	3	868.27	24.878	0	343.28	3.808	0.034	209.85	15.537	0
Year	2	867.82	24.428	0	339.98	0.514	0.176	208.39	14.078	0
WellpadDistance	2	861.51	18.12	0	340.18	0.713	0.159	207.22	12.906	0
Jdate WellpadDistance	3	843.39	0	0.76	341.70	2.23	0.075	201.67	7.358	0.014
Site WellpadDistance	4	863.88	20.482	0	344.11	4.642	0.022	210.65	16.344	0
Year WellpadDistance	3	859.26	15.861	0	340.58	1.116	0.13	209.23	14.917	0
Site Year	4	866.86	23.467	0	344.47	5.003	0.019	211.85	17.544	0
Site Year WellpadDistance	5	861.67	18.273	0	346.30	6.835	0.007	212.67	18.358	0
Site Year WellpadDistance Jdate	6	845.94	2.545	0.213	343.46	3.994	0.031	204.22	9.908	0.004
ShrubCover	2							200.27	5.960	0.029
ShrubCover Jdate	3							195.44	1.126	0.326
Site Year ShrubCover	5							200.84	6.531	0.022
Site Year ShrubCover Jdate	6							194.31	0	0.572

FIGURE 1. Daily nest survival of the Brewer's sparrow (BRSP), sage sparrow (SAGS), and sage thrasher (SATH) decreased with oil and natural gas well density (a) and increased with distance from the nearest well pad (b) in southwestern Wyoming. Solid lines represent DSR estimated using beta values from best-fit energy development models; dashed lines represent 95% confidence intervals.

FIGURE 2. Daily nest survival of sage thrashers increased with increased shrub cover. The solid line represents DSR estimated using beta values from the best-fit logistic exposure model; dashed lines represent 95% confidence intervals.

FIGURE 3. Abundance of Common ravens increased marginally with increased well density (a) and proximity to the nearest well pad (b). Data are the number of individuals detected per point count per survey visit, averaged across clusters of 4 points.

FIGURE 4. Average shrub vigor decreased relative to increasing well density (a) and proximity to the nearest well pad edge (b) within three energy development fields in southwestern Wyoming.
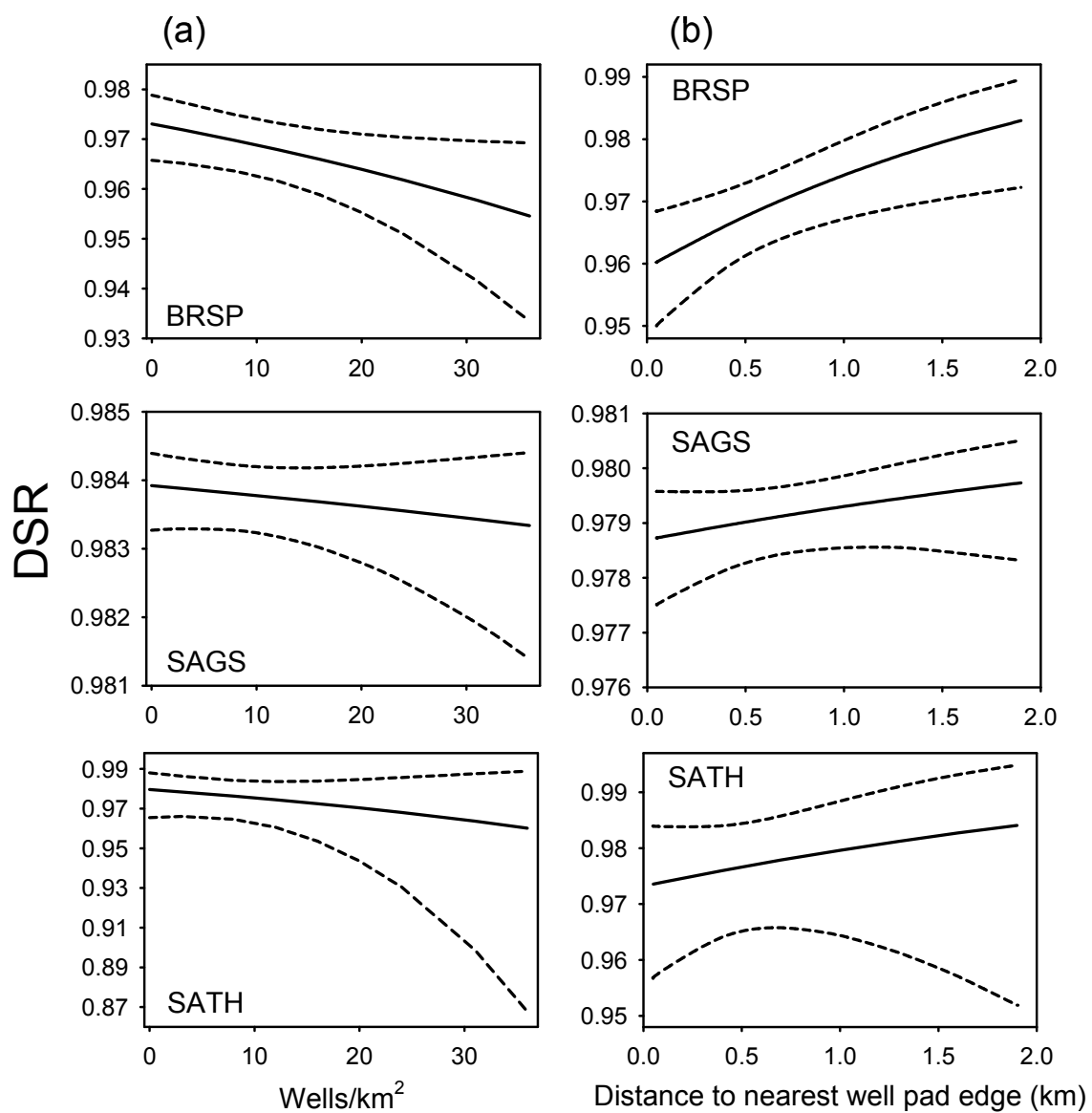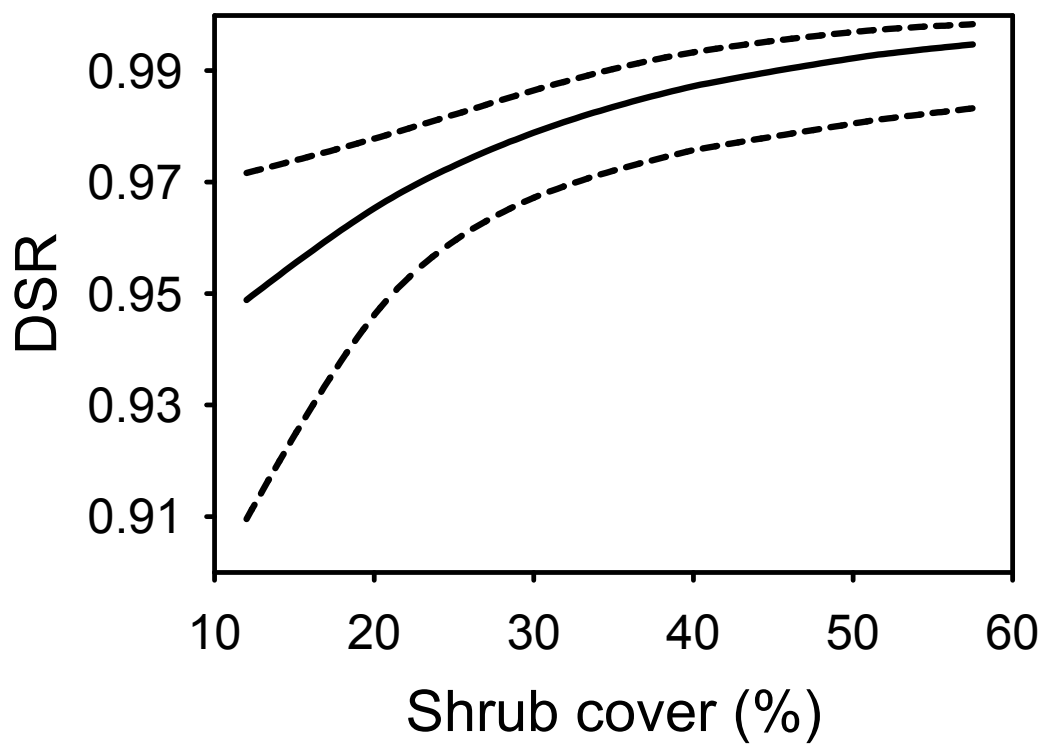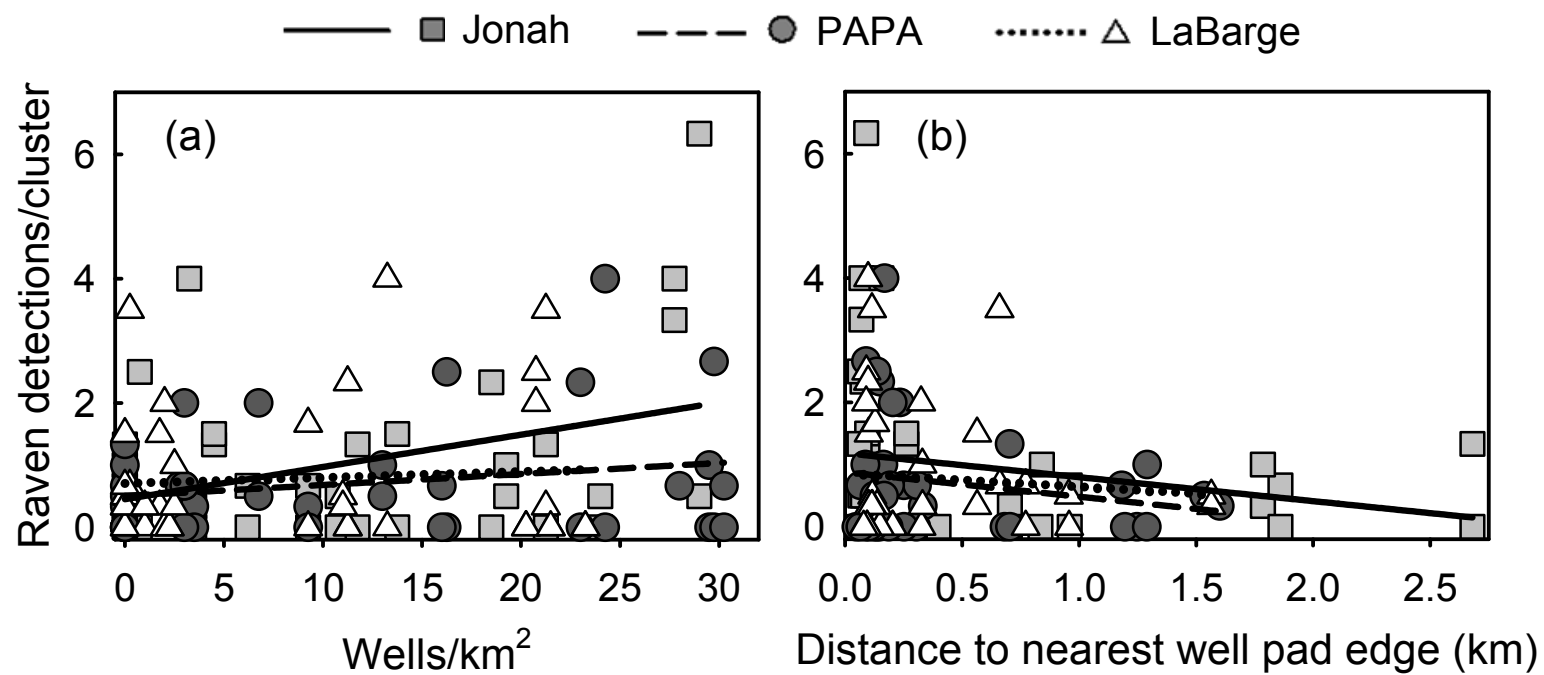
(a)

(b)

DSR

BRSP

SAGS

SATH

Wells/km^2

Distance to nearest well pad edge (km)

Figure 1.

Figure 2.

Figure 3.

Figure 4.