Energy development and avian nest survival in Wyoming, USA: A test of a common disturbance index

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A R T I C L E   I N F O

Article history:
Received 15 August 2014
Received in revised form 4 February 2015
Accepted 7 February 2015
Available online 27 February 2015

Keywords:
Brewer’s sparrow
Energy development
Fragmentation
Habitat loss
Indices
Natural gas
Nest predation
Sage thrasher
Sagebrush sparrow
Sagebrush steppe

A B S T R A C T

Global energy demands continue to result in new and emerging sources of anthropogenic disturbance to populations and systems. Here, we assessed the influence of natural gas development on a critical component of fitness (nest survival) for Brewer’s sparrow (Spizella breweri), sagebrush sparrow (Artemisiospiza nevadensis), and sage thrasher (Oreoscoptes montanus), three species of sagebrush-obligate songbirds that are of conservation concern, and assessed the efficacy of a commonly used index of oil and gas development intensity (well density) for estimating habitat transformation and predicting species’ responses. During 2008–2009 and 2011–2012 we monitored 926 nests within two natural gas fields in western Wyoming, USA. We calculated landscape metrics (habitat loss, amount of edge, patch shape complexity, and mean patch size) to identify the aspect of landscape transformation most captured by well density. Well density was most positively associated with the amount of sagebrush habitat loss within 1 square kilometer. Nest survival was relatively invariant with respect to well density for all three species. In contrast, nest survival rates of all three species generally decreased with surrounding habitat loss due to energy development. Thus, although well density and habitat loss were strongly correlated, well density resulted in overly conservative estimates of nest survival probability. Our results emphasize the importance of careful evaluation of the appropriateness of particular indices for quantifying the effects of human-induced habitat change. For managers concerned about the effects of natural gas development or similar forms of human land use to co-occurring breeding birds, we recommend minimizing the amount of associated habitat conversion.

1. Introduction

Human modification of ecosystems remains one of the greatest threats to global biodiversity (Tilman et al., 1994; Pimm and Raven, 2000). As such, addressing the impacts of new and emerging sources of anthropogenic disturbance embodies one of the primary challenges in conservation biology. A rapidly growing source of habitat loss, fragmentation, and alteration is from alternative (e.g., solar, wind) and unconventional (e.g., shale gas, oil sands) energy development activities (McDonald et al., 2009; Northrup and Wittemyer, 2013). Global energy demand is forecasted to increase 40% in the next 20 years, with alternative and unconventional energy resources making up an increasingly larger share of the global energy budget (U.S. Energy Information Administration, 2013). Understanding how these activities can affect populations and systems is therefore increasingly important.

North America has been the epicenter of unconventional gas (tight gas, shale gas, and coal-bed methane via hydraulic fracturing), in both the exploitation of current reserves and the development of improved technologies. Accordingly, the number of unconventional gas wells in the United States has nearly doubled since 1990 (U.S. Energy Information Administration, 2013). As a consequence, surrounding habitats have been reduced and fragmented by the associated road networks, pipelines, drill pads, and waste pits. To date, however, quantification of landscape transformation from energy development has been restricted to coarse, regional scale assessments (McDonald et al., 2009; Northrup and Wittemyer, 2013). In addition, many studies examining organismal responses have relied on well density (number of active wells per some defined area) as an index for development intensity (Dale et al., 2008; Doherty et al., 2008, 2010; Carpenter et al., 2010; Harju et al., 2010; Gilbert and Chalfoun, 2011; Hamilton et al., 2011; Taylor et al., 2013). Well locations are...
accurately mapped and readily available for many regions in North America (e.g., Colorado Oil and Gas Conservation Commission, Montana Board of Oil and Gas Conservation, Alberta Energy Regulator), resulting in a convenient gradient of disturbance for comparisons. A potential problem, however, is that the relevance of well density has been presumed and not explicitly investigated. Well pad size and the number of wells on a drill pad can vary substantially (from 1 to >30) depending on drilling approaches, such as the amount of directional drilling employed. The spatial configuration of wells can therefore produce strikingly different landscape-scale habitat patterns \( \text{(Fig. 1)} \). The resulting landscapes may have similar well densities, but such variation may be decoupled from ecologically relevant parameters such as the degree of habitat loss or the spatial arrangement of remaining patches. Consequently, unanswered questions remain regarding what aspect(s) of habitat change well density most indexes, whether well density is suitable for characterizing landscape transformation, and if well density is an appropriate metric by which to accurately assess species’ responses.

North American sagebrush steppe habitats and the associated wildlife species are ideal and timely foci with which to examine the relationships between energy development, landscape-scale habitat patterns, and ecological processes. Sagebrush steppe is regarded as one of the most altered ecosystems in North America as a result of extensive agricultural conversion, overgrazing, non-native grass encroachment, and other human activities such as energy development \( \text{(Braun et al., 1976; Vander Haegen et al., 2000; Knick et al., 2003)} \). Three songbird species closely associated with this system, Brewer’s sparrow (\textit{Spizella breweri}), sagebrush sparrow (\textit{Artemisiospiza nevadensis}), and sage thrasher (\textit{Oreoscoptes montanus}) are species of conservation concern for many state and federal agencies and have shown concomitant declines in the majority of their range \( \text{(Sauer et al., 2012)} \). As an important first step, recent work documented significant declines in abundance of Brewer’s sparrows and sagebrush sparrows in areas with higher densities of natural gas wells \( \text{(Gilbert and Chalfoun, 2011)} \). A critical next step, however, is the identification of potential mechanisms underlying observed declines.

The effects of habitat loss and fragmentation on nesting birds have received considerable attention, particularly patterns of increased nest predation in habitat fragments and near edges \( \text{(Robinson et al., 1995; Chalfoun et al., 2002)} \). Predation is the primary cause of nest failure in birds and an important factor limiting reproduction and population viability \( \text{(Martin, 1992)} \). Thus, as an important process that influences a key component of fitness, nest predation may affect patterns of abundance, such as those previously documented for sagebrush songbirds in natural gas areas \( \text{(Gilbert and Chalfoun, 2011)} \). Therefore, assessing nest predation patterns in relation to ecologically-based metrics offers insight into the development of mitigation strategies for effective conservation and management of songbirds affected by unconventional energy development activities.

The specific objectives of our study were to (1) identify which landscape metric was most closely associated with natural gas well density, (2) determine if well density was a reliable predictor of landscape transformation, and (3) evaluate sagebrush songbird nest survival in relation to natural gas extraction using both well density and the landscape metric most associated with well density.

**Fig. 1.** Aerial imagery of selected study regions inside the (A) Pinedale Anticline and (B) Jonah natural gas fields, Sublette County, Wyoming, USA. Raster images, (a) and (b), of the same locations depict digitized drill pads, road networks, pipelines, reclaimed grass areas (all in black), and sagebrush habitats (grey) as distinct patches. Image (a) contains: 115 active wells, 5 distinct patches, and approximately 12% habitat loss. Image (b) contains: 75 active wells, 21 distinct patches, and approximately 30% habitat loss. Thus, image (a) has 50% more wells than (b) but half the amount of habitat loss, demonstrating the disconnect that can occur with an oft-used index (well density) and associated metrics of habitat alteration.
density. With increasing demand for domestic and cleaner sources of energy, a critical next step in understanding the mechanisms underlying species' responses to ongoing energy development activities requires linking actual landscape patterns with ecological processes that have important fitness consequences.

2. Materials and methods

2.1. Study area

Our study took place within sagebrush (*Artemisia tridentata* ssp.) habitats undergoing unconventional natural gas extraction activities in Sublette County, Wyoming, USA. The Jonah-Pinedale Development Area (JPDA) consists of two large natural gas fields, the Pinedale Anticline Project Area (PAPA) and the Jonah Field (hereafter Jonah), which rank among the most concentrated and productive energy fields in the country (U.S. Energy Information Administration, 2011). In 2008, we randomly selected eight 25–ha study plots distributed evenly across the following four well density strata in the JPDA using a GIS: no development (0 wells/ km²), light (1–6 wells), moderate (7–15 wells), and heavy development (>15 wells) (Wyoming Oil and Gas Conservation Commission, 2008). Well density was defined as the number of wells within one square kilometer and was identified using a moving window over a raster of 30 × 30 meter cell resolution in ArcMap (ESRI, Redlands, California). In 2011 we added four additional study plots within each energy field; PAPA and Jonah, for a total of 12 plots) to more fully capture the range of well density within each site. To ensure the presence of nesting birds, study plots were ground-truthed to meet the following a priori criteria regarding vegetation structure: (1) minimum shrub cover of 20% and (2) average shrub height of 35 cm or greater (Wiens et al., 1987; Chalfoun and Martin, 2007).

2.2. Nest searching and monitoring

Nest searching efforts were focused on the three most abundant sagebrush-obligate songbird species; Brewer’s sparrow, sagebrush sparrow, and sage thrasher, during May–August, 2008, 2009, 2011, and 2012. Nests were located using behavioral observations of adults and systematic searches. We monitored active nests every 2–3 days until failure or success (Martin et al., 1997). Nest fledging was confirmed by visual observations of fledglings, scolding adults carrying food, or the sounds of fledgling begging calls. A nest was considered successful if at least one nestling fledged. Only successful nests and those that failed due to predation were included in analyses (95.7% of all nests). Additional sources of nest failure were attributed to abandonment due to researcher activities (3%) and weather (1%).

2.3. Indices of habitat modification

We used ArcGIS 10.0 to calculate the number of wells within 1 km² (564-m radius) for each nest using geographic locations of wells. In addition, we hand-digitized drill pad boundaries from aerial imagery (Wyoming Geographic Information Science Center, 2012) at a fixed scale of 1:5000 to create a drill pad feature class. A 10-m buffer was applied to existing road and pipeline layers to accurately reflect their footprint in 2 dimensions. These features were combined to generate a binary raster reflecting sagebrush habitat versus non-habitat (roads, drill pads, buried pipelines, and reclaimed areas). We categorized reclaimed areas (in which sagebrush had been removed during the construction process and that consisted mainly of native or non-native grasses or forbs) as non-habitat because our focal species forage, nest, and perform territorial displays almost exclusively within the shrub layer (Martin and Carlson, 1998; Reynolds et al., 1999; Rotenberry et al., 1999).

We used the SDMTools library in R (R Development Core Team, 2013) to generate four a priori landscape metrics within a 1 km² buffer around each nest: amount of habitat loss (the complement of total amount of sagebrush habitat), meters of edge, patch shape complexity (shape index), and mean patch size. We chose these metrics because they offered simple yet comprehensive interpretations of different landscape patterns (Gustafson, 1998; McGrigal et al., 2012).

2.4. Data analysis

To identify which of our a priori habitat modification metrics was most closely indexed by well density (i.e., which metric should be used in subsequent analyses), we first built four general linear models. We used each metric as the lone predictor of well density, with a Poisson distribution, and ranked models using Akaike’s Information Criterion (AIC). We only considered the single best landscape metric (lowest AIC score) in subsequent analyses because of the high degree of correlation among all metrics (Table 1) as well as a desire to maintain straightforward interpretations of models and effects. We tested the strength of the relationship between well density and the most supported habitat modification metric using a set of linear mixed models and the nlme package in program R (Pinheiro et al., 2014; R Core Team, 2013). We followed recommendations from Zuur et al. (2009) to first identify the structural form of the random component, and then identify the structural form of the fixed components. We built 3 models to assess the structural form of the random component; a model containing no random effects which implied nests within a study plot were uncorrelated, a random intercept model which acknowledged correlations among nests within a study plot but not assumed the relationship between well density and habitat modification was the same across all study plots, and a random intercept and slope model which acknowledged correlations, but enabled the relationship between habitat modification and well density to differ at each study plot. Fixed effects included well density, site (PAPA versus Jonah), and their interaction to test for differences in the relationship between habitat modification and well density across energy fields. We evaluated the relative strength of each model with AIC. Finally, we removed insignificant fixed effects using restricted maximum likelihood estimators to select a final model.

We used the logistic exposure method (Shaffer, 2004) to test for potential effects of energy development on the daily nest survival rates of our three focal species. The logistic exposure method is a generalized linear model that does not require assumptions about when nest losses occur during the nesting period. Further, this method allows unique covariates to be specified for each nest and the ability to build and rank candidate model sets that best describe variation in nest survival. However, we also report the total observation days and number of failed nests for each species because of the high degree of correlation among all metrics to enable the calculation of Mayfield (1975) estimates and facilitate comparisons between our results and those of previous studies that used the Mayfield method to calculate nest survival.

Initially, we assessed whether well density and the best habitat modification metric provided comparable estimates of daily nest survival. We generated nest survival estimates by fitting separate logistic exposure models for each species using PROC GENMOD (SAS Institute 2010). To test the consistency of patterns across space and time, we built candidate model sets that included combinations of year, site (PAPA versus Jonah), and one of our energy development indices (Table 2). We ran separate model sets, replacing well density with the best habitat modification metric, in order
to examine potential mismatches in model support. We ranked candidate models using Akaike’s Information Criterion scores, adjusted for small sample sizes (AICc) and computed model weights (Burnham and Anderson, 2002). We used model averaging to obtain parameter estimates from the entire candidate set. The Hosmer–Lemeshow goodness of fit test was used to ensure the model fit the data. Wald’s Chi-square test statistic was used to evaluate the significance of individual predictors in candidate models. We did not consider models that were within 2 AICc units and differed from the top model by 1 parameter as informative (Arnold, 2010). We converted model coefficients to odds ratios as subset data.

In 2012, Brewer’s sparrows breeding within 2 study plots in Jonah experienced a complete reproductive failure (n = 26 nests). Nest predation rates were far higher than anything observed from any study plot in all prior years. Logistic exposure models estimated that nests had a 0.1% and 0.05% chance of completing the nesting cycle, respectively. Both plots represented low well density sampling areas for the Jonah site, and their inclusion or exclusion significantly altered model rankings and interpretation of energy development effects. We suspected that these failures were anomalous and unrelated to energy development, however, we did not want to exclude them completely. Consequently, for Brewer’s sparrows, we present results with and without nests from those 2 study plots in 2012. Models and interpretations from data excluding nests from those sampling areas are hereafter referred to as subset data.

### Results

#### 3.1. Indices of habitat modification

The amount of habitat loss was the landscape metric most closely associated with well density (R² = 0.46, Table 1). Amount of edge, shape complexity, and mean patch size were each more than 150 AIC units greater than the habitat loss model. The random intercept and slope form of the random effects component had higher support than the random intercept model and the model lacking random effects; AIC values were 4399, 4585, and 6325, respectively. Thus, the relationship between well density and habitat loss differed among study plots. Neither the well density by site (PAPA versus Jonah) interaction term (F₁,873 = 1.347, P = 0.246), nor the additive effect of site (F₁,10 = 0.748, P = 0.407), however, were significant. Well density was significantly related to the amount of habitat loss within 1 km² (F₁,874 = 4.320, P = 0.038). On average, every well added per km² resulted in 1.2 (±0.6 SE) hectares of habitat loss.

#### 3.2. Nest survival

During 2008–2009 and 2011–2012, we monitored 926 nests of our three focal species. Thirty-nine failures (4.3% of nests) were not due to predation and were excluded from analyses. In total, 536 Brewer’s sparrow, 178 sagebrush sparrow, and 173 sage thrasher nests were used in survival analyses, of which, 191 (36%), 80 (45%), and 62 (36%) failed, respectively. Nest cycle lengths used in overall nest survival calculations were 23 (mean = 23.1, n = 346), 25 (mean = 24.9, n = 100), and 29 (mean = 28.6, n = 111) days, and total observation days were 7479, 2566, and 2799, for Brewer’s sparrows, sagebrush sparrow, and sage thrashers, respectively. Among candidate model sets, the global model fit the data for each species: Brewer’s sparrow complete (χ² = 8.55, P = 0.382), Brewer’s sparrow subset (χ² = 8.04, P = 0.429), sagebrush sparrow (χ² = 10.31, P = 0.244), and sage thrasher (χ² = 8.22, P = 0.412).

### Table 1

<table>
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<th>Habitat metric</th>
<th>Δ AIC</th>
<th>Meters edge (per km²)</th>
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<th>0.782</th>
<th>0.989</th>
<th>0.531</th>
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<td>169</td>
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<td></td>
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<td>&lt;0.001</td>
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- a Pearson’s correlation (r) and P-values; n = 887.
- b AIC score from GLM with habitat loss predicting well density was 12424.

### Table 2

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<tr>
<td>Energy development + site</td>
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<tr>
<td>Energy development + year</td>
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<tr>
<td>Site + year</td>
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<tr>
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<td>Site + year</td>
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<td>Energy development + year</td>
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<tr>
<td>Site + year + energy development</td>
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<table>
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<th>Δ AIC</th>
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<td>-0.705</td>
<td>-0.501</td>
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<tr>
<td>Habitat loss (ha/km²)</td>
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- a Pearson’s correlation (r) and P-values; n = 887.
- b AIC score from GLM with habitat loss predicting well density was 12424.
Among candidate model sets, the influence of both energy development metrics (well density and habitat loss) on nest survival varied by year and site (Tables 3 and 4). The probability of daily nest survival declined with increased energy intensity (well density and habitat loss) in 2 of 4 years (Fig. 3).

3.2.2. Brewer's sparrow subset

When nesting data from the two sites in 2012 with anomalously low nest survival were omitted, Brewer's sparrow nest survival was also uniform with respect to well density, with approximately 20% of nests successfully fledging overall (odds ratio 0.998, 95% CI: 0.975, 1.020, Fig. 2a). In contrast, nest survival significantly decreased with increased habitat loss ($\beta = -0.013 \pm 0.006$, $\chi^2 = 4.28$, $P = 0.039$, Fig. 2b). The probability of daily nest survival decreased by 1.3% (odds ratio 0.987, 95% CI: 0.975, 0.998) with every additional hecetare of habitat lost within 1 km$^2$. Thus, Brewer's sparrow overall nest survival was more than halved across the habitat loss gradient, from approximately 29% to 12% of nests successfully fledging.

Model rankings differed when using well density versus habitat loss as a predictor of Brewer's sparrow daily nest survival (Tables 3 and 4). Well density models again showed strong support for annual variation in the influence of energy development (Table 3 and Fig. 3). Habitat loss models, by contrast, predicted an additive year effect (Table 4). The probability of daily nest survival decreased 1.6% (odds ratio 0.984, 95% CI: 0.972, 0.996) with every additional hectare of habitat lost within 1 km$^2$ ($\beta = -0.016 \pm 0.006$, $\chi^2 = 6.31$, $P = 0.012$). Thus, nest survival was approximately halved across the habitat loss gradient within a given year.

3.2.3. Sagebrush sparrow

Sagebrush sparrow nest survival did not vary significantly with well density, with approximately 18% of nests successfully fledging overall (odds ratio 1.002, 95% CI: 0.989, 1.015, Fig. 2a). With increased habitat loss, overall nest survival decreased slightly from approximately 22% to 11% of nests successfully fledging (odds ratio 0.996, 95% CI: 0.980, 1.012, Fig. 2b). The null model of constant survival was most supported for sagebrush sparrow nests in both well density and habitat loss model sets (Tables 3 and 4), and there was no overwhelming support for a single model in either candidate suite.

3.2.4. Sage thrasher

Sage thrasher nest survival was relatively uniform in relation to well density, with approximately 16% of nests successfully fledging overall (odds ratio 0.997, 95% CI: 0.983, 1.011, Fig. 2a). The null model of constant survival was most supported in the well density model suite, and none of the models that included a well density predictor were considered informative (Table 3). In contrast, habitat loss was most supported when used as the energy development predictor (Table 4), and nest survival significantly decreased with increased surrounding habitat loss ($\beta = -0.032 \pm 0.015$, $\chi^2 = 8.28$, $P = 0.004$, Fig. 2b). The probability of daily nest survival decreased 3.2% (odds ratio 0.968, 95% CI: 0.941, 0.997) with every additional hectare of habitat lost within 1 km$^2$. Thus, sage thrasher nest survival decreased from approximately 35% in low habitat loss areas to approximately 3% of nests successfully fledging in the highest loss areas.

4. Discussion

Extraction of energy resources continues to be a form of HIREC (“human-induced rapid environmental change”; Sih et al., 2010) that can influence important fitness outcomes such as avian nest survival. Better understanding of the effects of HIREC necessitates careful quantification of species’ responses using meaningful indices of habitat change. We tested the relevance of well density (wells/km$^2$), a commonly used index of oil and gas development intensity, for estimating landscape transformation and predicting nest survival probability for three species of declining sagebrush-obligate passerines. Three general patterns emerged from our results. First, well density was a significant predictor of landscape transformation (amount of habitat loss) for our study area. Second, there was considerable variation in the ecological relevance of well density—reflected in mismatched model support for some species. In such cases well density and habitat loss suggested different responses of nest survival to energy development activities. Lastly, spatial and temporal patterns of species’ responses to energy development varied, but nest survival generally decreased with increasing surrounding habitat loss for all three species.

4.1. Habitat modification

We observed a 1.2% (1.2 ha) reduction in sagebrush habitat on average with every additional natural gas well within one square kilometer of nests. Of the published wildlife-energy development studies using well density, only Doherty et al. (2008) made reference to testing the relationship with landscape features, though nothing quantitative is mentioned and unpublished data are cited. Spatial analyses of oil and gas development have largely been restricted to regional-scale assessments of total area impacted (Weller et al., 2002; Copeland et al., 2009; McDonald et al., 2009; Walston et al., 2009; Finn and Knick, 2011), and all tell a similar story of reduced native vegetation concurrent with increased development. Interestingly, McDonald et al. (2009) used PAPA and Jonah as reference points for the most and least compact energy fields, respectively, when estimating land use requirements for oil and gas development across the United States. Thus, despite the recognition of clear differences in well density and landscape-scale habitat loss patterns that can occur, well densities have been assumed to be a sufficient proxy up to this point.

Despite well density and habitat loss being correlated, in some cases they generated different results when used to examine nest survival responses. Most alarming was the mismatch in model support for sage thrasher nest survival. Well density predicted no effect of energy intensity on probability of nest predation, whereas habitat loss due to energy infrastructure predicted significant declines in nest survival. This suggests that validating indices should not simply entail confirming a correlational relationship with some other (difficult to measure) metric. Had we only used well density, because it is easy to calculate and significantly related to the amount of habitat loss, we may have falsely concluded no effect of energy development on sage thrashers. Across taxa, the overwhelming majority of studies have documented negative responses from unconventional oil and gas development (reviewed in Northrup and Wittemyer, 2013). Interestingly however, of the three songbird studies that utilized well density (Dale et al., 2008, Hamilton et al., 2011, Gilbert and Chalfoun, 2011), two had at least one species that appeared to show no response to energy development intensity.

The weaknesses of well density as a meaningful corollary for landscape-scale habitat alteration in our study system may have been the result of the spatial variation in drill pad sizes and wells drilled per pad. Evident in the slope and standard error estimates ($\beta = 1.2 \pm 0.6 SE$), the relationship between well density and habitat loss exhibited a fair amount of variation across the range of sites sampled. Each well added within 1 square kilometer increased the amount of habitat lost by as much as nearly 2 ha or as little as 600 square meters. Akin to the single large or several small (SLOSS) debate regarding reserve design (Diamond, 1975), our energy field landscapes comprised either few, large drill pads with
many wells or several small drill pads with fewer wells per pad (Fig. 1). Thus, despite comparable well densities, the resulting landscapes varied in the degree of habitat loss and the spatial arrangement of remaining habitats. More importantly, from a conservation perspective, assuming one detects an ecological response using well density, what recommendations can be generated other than to reduce development? Such observations offer little in the way of specific mitigation strategies that could minimize impacts while accommodating human land uses. Conversely, asking questions such as whether fewer, large drill pads are better for species’ responses (such as avian nest survival) than many smaller drill pads have merit as practical management considerations.

4.2. Nest survival

We documented a general decrease in nest survival with increased energy development (as assayed by surrounding habitat loss) for all three songbird species. Sage thrashers showed the strongest and most consistent response to the amount of habitat loss, whereas effects on both Brewer’s and sagebrush sparrows showed some annual variation. Thus, in most years, habitat patches within energy fields appear to be acting as population sinks for breeding sagebrush songbirds. While we did not set out to test for an ecological trap (Schlaepfer et al., 2002) scenario, an examination of habitat preferences using nest initiation dates in our study sys-

Fig. 2. Daily nest survival rates of Brewer’s sparrow (BRSP), sagebrush sparrow (SAGS) and sage thrasher (SATH) nests in relation to (a) well density (wells/km²) and (b) amount of surrounding (1 km²) habitat loss within two natural gas fields in western Wyoming, USA, 2008–2009 and 2011–2012; n = 887 nests. Brewer’s sparrow subset data excludes 26 nests from 2012 within two sampling areas of exceptionally high nest failure (99.9% and 99.5%) in the Jonah Field.
Relative support for each model. Only models that were within 2 AIC units of the best model and with similar log-likelihoods, and thus considered uninformative (Arnold, 2010). Model weights from uninformative models should be added to the best model.

Model weights from uninformative models should be added to the best model.

<table>
<thead>
<tr>
<th>Competing model</th>
<th>log(L)</th>
<th>k</th>
<th>ΔAICc</th>
<th>wi</th>
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<tr>
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<td>1.02</td>
<td>0.21</td>
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<tr>
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<td>0.21</td>
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Logistic exposure models describing the effect of site (Jonah vs. Pinedale Anticline), year, and well density on daily nest survival rates of sagebrush songbird nests within two natural gas fields in western Wyoming, USA, 2008–2009 and 2011–2012. The log-likelihood values are denoted by log(L); k is the number of parameters in each model; ΔAICc is the difference in Akaike’s information criterion (AICc) values between the best-fitting model and model i; and w represents Akaike weights indicating the relative support for each model. Only models that were within 2 AICc units are shown. Models not in bold are within 2 AICc of the best model but with similar log-likelihoods and thus considered uninformative (Arnold, 2010). Model weights from uninformative models should be added to the best model.

The annual variation in nest survival exhibited by Brewer’s and sagebrush sparrows may reflect fluctuations in important nest predator species, such as small mammals, that are known to exhibit cyclic population fluctuations (Krebs, 1966). As part of a separate study at the same sites, we documented that rodent species (mice, chipmunks, and ground squirrels) were the main nest predators, and most of these species were more abundant in areas with more habitat loss due to natural gas infrastructure (Hethcoat and Chalfoun, unpublished data). Increased abundance of some nest predators in habitat fragments and/or near edges, moreover, has generally been invoked as a mechanism underlying increased avian nest predation rates, though such assertions require careful study within focal systems (reviewed in Chalfoun et al., 2002). A critical next step is to test why nest survival is lower in remaining habitat fragments within energy development areas.

Shrubland songbirds are among the most rapidly declining groups of species in North America, resulting from substantial habitat loss and alteration (Knick et al., 2003; Sauer et al., 2012). Prior work within the same natural gas fields as the current study documented reduced densities of sagebrush-obligate songbirds with well density (Gilbert and Chalfoun, 2011). The increased nest predation with increased habitat loss due to natural gas extraction we documented suggests one potential mechanism for previously observed declines in abundance.

Unconventional gas resources exist on every continent, and are poised to become a major global energy sector (International

![Fig. 3. Annual variation in daily nest survival rates of Brewer's sparrow nests in relation to well density (wells/km²) and amount of surrounding (1 km²) habitat loss within two natural gas fields in western Wyoming, USA, 2008–2009 and 2011–2012. Subset data excludes 26 nests from two sampling areas in 2012 with exceptionally high nest failure (99.9% and 99.5%) in the Jonah Field.](image-url)
Energy Agency, 2012). Moreover, the ecological patterns we have observed the potential to manifest in other systems affected by expanding energy infrastructure. Based on the nest survival relationships in this study and abundance patterns in Gilbert and Chalfoun (2011), we suggest that energy development effects on breeding birds may be minimized by reducing the conversion of habitat surrounding well pads during initial construction activities as much as possible. This suggestion is further bolstered by the recent finding that reclamation of well pads back to mature sagebrush habitat can take greater than 50 years (Minnick and Alward, 2015). In many cases, habitat conversion may be minimized by employing more directional drilling, and/or restricting the addition of new wells to existing well pads, as depicted, for example in Fig. 1A. The U.S. alone is anticipated to develop 200,000 km² of new land for energy development by 2035 (McDonald et al., 2009). The clarification of specific mechanisms responsible for species’ responses will be essential to effectively address the conservation and management challenges posed by intensifying energy development activities worldwide.

Acknowledgements

This project was supported by grants from The Wyoming Landscape Conservation Initiative (U.S. Geological Survey) and The Wyoming Game and Fish Department. We thank T. Alleger, J. Berndt-Plaisted, J. Butch, T. Docherty, R. Haynam III, A. Stevens, and K. Urban for assisting with field data collection. S. Albeke was instrumental in compiling the fragmentation indices. S. Knick and four anonymous reviewers provided valuable feedback on earlier versions of the manuscript. Any use of trade or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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