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RESEARCH ARTICLE

Nontarget effects on songbirds from habitat manipulation for Greater Sage-Grouse: Implications for the umbrella species concept

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ABSTRACT

The “umbrella species” concept is a conservation strategy in which creating and managing reserve areas to meet the needs of one species is thought to benefit other species indirectly. Broad-scale habitat protections on behalf of an umbrella species are assumed to benefit co-occurring taxa, but targeted management actions to improve local habitat suitability for the umbrella species may produce unintended effects on other species. Our objective was to quantify the effects of a common habitat treatment (mowing of big sagebrush [*Artemisia tridentata*]) intended to benefit a high-profile umbrella species (Greater Sage-Grouse [*Centrocercus urophasianus*]) on 3 sympatric songbird species of concern. We used a before–after control-impact experimental design spanning 3 yr in Wyoming, USA, to quantify the effect of mowing on the abundance, nest-site selection, nestling condition, and nest survival of 2 sagebrush-obligate songbirds (Brewer’s Sparrow [*Spizella breweri*] and Sage Thrasher [*Oreoscoptes montanus*]) and one open-habitat generalist songbird (Vesper Sparrow [*Pooecetes gramineus*]). Mowing was associated with lower abundance of Brewer’s Sparrows and Sage Thrashers but higher abundance of Vesper Sparrows. We found no Brewer’s Sparrows or Sage Thrashers nesting in the mowed footprint posttreatment, which suggests complete loss of nesting habitat for these species. Mowing was associated with higher nestling condition and nest survival for Vesper Sparrows but not for the sagebrush-obligate species. Management prescriptions that remove woody biomass within a mosaic of intact habitat may be tolerated by sagebrush-obligate songbirds but are likely more beneficial for open-habitat generalist species. By definition, umbrella species conservation entails habitat protections at broad spatial scales. We caution that habitat manipulations to benefit Greater Sage-Grouse could negatively affect nontarget species of conservation concern if implemented across large spatial extents.

Keywords: Greater Sage-Grouse, habitat management, mowing, nontarget effects, sagebrush songbirds, surrogate species, umbrella species

Efectos derivados en las aves canoras a partir de la manipulación del hábitat para *Centrocercus urophasianus*: Implicancias para el concepto de especie paraguas

RESUMEN

El concepto de especie paraguas es una estrategia de conservación en la cual se piensa que la creación y el manejo de áreas de reserva que satisfacen las necesidades de una especie benefician indirectamente otras especies. Se asume que la protección del hábitat a gran escala en nombre de una especie paraguas beneficia a los taxa que comparten el hábitat, pero las acciones de manejo encaradas para mejorar la aptitud del hábitat local para la especie paraguas pueden producir efectos indeseados en otras especies. Nuestro objetivo fue identificar los efectos de un tratamiento genérico de hábitat (segado de *Artemisia tridentata*) dirigido a beneficiar una especie paraguas de alto perfil (*Centrocercus urophasianus*) sobre tres especies simpátricas de aves canoras de preocupación para la conservación. Usamos un diseño experimental de control del impacto antes y después a lo largo de 3 años en Wyoming, EEUU, para cuantificar el efecto del segado en la abundancia, la selección del sitio de anidación, la condición del polluelo y la supervivencia del nido de dos aves canoras obligadas de *Artemisia* (*Spizella breweri* y *Oreoscoptes montanus*) y de un ave canora generalista de ambientes abiertos (*Pooecetes gramineus*). El segado estuvo asociado con abundancias más bajas de *S. breweri* y *O. montanus*, pero con abundancias más altas de *P. gramineus*. No encontramos nidos de *S. breweri* y *O. montanus* en el sitio segado post-tratamiento, sugiriendo la pérdida completa del hábitat de anidación para estas especies. El segado estuvo asociado con mejores condiciones de los polluelos y con una mayor supervivencia del nido para *P. gramineus*, pero no para las especies obligadas de *Artemisia*. Las prescripciones de

manejo que remueven biomasa arbustiva dentro de un mosaico de hábitat intacto pueden ser toleradas por las aves canoras obligadas de *Artemisia*, pero son probablemente más benéficas para las especies generalistas de ambientes abiertos. Por definición, la conservación de las especies paraguas implica la protección del hábitat a grandes escalas espaciales. Advertimos que las manipulaciones del hábitat que benefician a *C. urophasianus* podrían afectar negativamente especies no-objetivo de preocupación para la conservación si se implementan sobre grandes extensiones espaciales.

Palabras clave: aves canoras de *Artemisia*, *Centrocercus urophasianus*, efectos derivados, especie paraguas, especie subrogante, manejo del hábitat, segado

INTRODUCTION

Surrogate species conservation, wherein conservation action directed at one species benefits other species indirectly, holds promise as a fruitful frontier in conservation biology (Caro 2010). Conservation approaches that employ surrogate species (e.g., umbrella, keystone, and flagship species) provide appealing conceptual shortcuts that may extend conservation benefits to previously neglected species (Caro 2010). One form of surrogacy, the “umbrella species” concept, entails creating and managing reserve areas to meet the conservation needs of one species (the umbrella species), with the assumption that doing so will indirectly meet the needs of other species that co-occur with the umbrella species (Wilcox 1984, Noss 1990). We follow the terminology of Caro (2003, 2010) to refer to the species that live in the same geographic area as an umbrella species (and therefore the species expected to benefit from the conservation of the umbrella species) as “background species.”

The key mechanism underlying the umbrella species concept is the protection of large areas (Caro 2003, 2010). It may be difficult to imagine how the wholesale protection of sizable landscapes in the name of an umbrella species could be harmful to background species; however, what happens when managers undertake efforts to modify the habitat within umbrella reserves solely to meet the needs of the umbrella species? In general, wildlife management actions can have unexpected and diverse effects throughout an ecosystem. For example, common management actions such as supplemental feeding (Morris et al. 2010), control of invasive or pest species (Hoare and Hare 2006), hunting (Grignolio et al. 2011, Dinges et al. 2016), and habitat management (Norvell et al. 2014, Gallo and Pejchar 2016) have all been shown to affect species other than those targeted by the management action. Despite these examples, careful empirical examinations of how background species fare under management scenarios geared toward an umbrella species are generally lacking (Roberge and Angelstam 2004, Seddon and Leech 2008, Branton and Richardson 2014, Norvell et al. 2014, Gallo and Pejchar 2016).

Habitat management or manipulation is a key tool in wildlife conservation and management (Bailey 1984,

Krausman 2002). The effects of habitat management on nontarget species, however, are not usually documented (Gallo and Pejchar 2016). Habitat management actions on behalf of umbrella species will benefit background species only if there is congruence between the species’ responses to the management action, and they could also conflict directly (Simberloff 1998, Roberge and Angelstam 2004, Seddon and Leech 2008, Branton and Richardson 2014). Investigating the response of nontarget species to such actions will therefore be critical for evaluating whether active management practices are at odds with the general concept of conservation via surrogate species.

The Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”) has been the focus of unprecedented research and conservation attention in western North America in recent decades (Knick and Connelly 2011), and the sage-grouse is often considered an umbrella species for the conservation of other components of sagebrush (*Artemisia* spp.)-steppe ecosystems—especially sagebrush-associated wildlife species (Rich and Altman 2001, Rowland et al. 2006, Hanser and Knick 2011, Gamo et al. 2013, Copeland et al. 2014). The Greater Sage-Grouse is listed as endangered in Canada under the federal Species at Risk Act and has been petitioned at least 7 times for listing under the U.S. Endangered Species Act (ESA; Stiver 2011). Although the U.S. Fish and Wildlife Service (USFWS) recently determined that ESA listing was not warranted (USFWS 2015), state- and federal-level management for the species continues to be a priority across large portions of the western United States (USFWS 2013, Crist et al. 2017).

The sage-grouse is considered a sagebrush-obligate species but uses a variety of microhabitats across broad landscapes over the course of its annual life cycle (Connelly et al. 2000, 2011, Fedy et al. 2012, 2014, Gibson et al. 2016). Habitat management actions intended to produce or enhance suitable conditions for certain seasonal habitats (hereafter “habitat treatments”) are common practices in sage-grouse management (Beck et al. 2012). For example, habitat treatments implemented to enhance brood-rearing habitat for sage-grouse often entail reducing the biomass of woody vegetation (e.g., sagebrush) and commonly take the form of herbicide application, mechanical treatments, or prescribed burning (Beck et al.

2012). Such treatments have a long history of use in sagebrush ecosystems, although their efficacy remains uncertain (Knick et al. 2003, Beck et al. 2012, Smith and Beck 2018).

We considered 3 background species of migratory songbirds that co-occur with sage-grouse in sagebrush ecosystems during the breeding season and have experienced population declines in recent decades (Rosenberg et al. 2016): Brewer's Sparrow (*Spizella breweri*), Sage Thrasher (*Oreoscoptes montanus*), and Vesper Sparrow (*Pooecetes gramineus*). Brewer's Sparrows and Sage Thrashers breed almost exclusively in sagebrush-steppe habitats of western North America and are considered sagebrush-obligate species (Reynolds et al. 1999, Rotenberry et al. 1999). By contrast, Vesper Sparrows breed in a variety of open, grass-associated habitats (e.g., sagebrush steppe, prairie grasslands, montane meadows) across North America (Jones and Cornely 2002) and served as a reference species. Brewer's Sparrows and Sage Thrashers are both species of conservation concern in the western United States (Knick et al. 2003) and are listed as species of greatest conservation need in Wyoming (Wyoming Game and Fish Department 2010), where our study took place. Since 1970, range-wide population sizes have declined by 35% for Brewer's Sparrows and by 44% for Sage Thrashers (Rosenberg et al. 2016). Vesper Sparrows do not share the same general level of conservation concern, but their range-wide population declined by 30% during the same period (Rosenberg et al. 2016).

Our objective was to assess how habitat manipulation in the form of shrub mowing to benefit sage-grouse affected the abundance, nest-site selection, nestling condition, and nest survival of Brewer's Sparrows, Sage Thrashers, and Vesper Sparrows. Because Brewer's Sparrows and Sage Thrashers rely on the sagebrush shrub layer for nesting, foraging, and breeding displays, we predicted that these 2 sagebrush-obligate species would decrease in abundance, have reduced nesting habitat, and have poorer reproductive outcomes in response to shrub removal by mowing, because the availability of potential nest sites would be more limited (Chalfoun and Martin 2009). We expected the inverse responses for Vesper Sparrows, given that they nest on the ground and often utilize more open habitats.

METHODS

Study Area

We worked in central Wyoming, USA (42.65°N, 108.18°W), near Sweetwater Station. The study area was within the state-designated Greater South Pass Core Population Area of sage-grouse (State of Wyoming 2011, 2015) and federally designated Priority Areas for Conservation of sage-grouse (USFWS 2013). The mean annual temperature and precipitation during 1981–2010 were

5.73°C and 30.40 cm (PRISM Climate Group 2012), and the soil was characterized as cool-dry, with moderate resilience to disturbance and resistance to invasive annual grasses (Chambers et al. 2016, Maestas et al. 2016). Elevation ranged from 2,046 to 2,172 m (Gesch et al. 2002). The area was predominantly sagebrush steppe, with overstory communities dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*). Black sagebrush (*A. nova*) and rabbitbrush (*Ericameria nauseosa* and *Chrysothamnus viscidiflorus*) were also present in some areas. Understory communities were dominated by bunchgrasses and forbs.

Habitat Treatments and Experimental Design

A goal of wildlife management is to provide habitat that fulfills the food requirements of all age classes of animals throughout the year (Bailey 1984). Young sage-grouse chicks are dependent on insects and forbs during the first few months of life (Johnson and Boyce 1990), and the habitats used by brood-rearing sage-grouse during summer tend to have relatively fewer shrubs and more herbaceous plants than the habitats used in other life stages or seasons (Connelly et al. 2011). With the goal of improving brood-rearing habitat of sage-grouse in the area, a multi-stakeholder group interested in sage-grouse conservation applied mechanical mowing designed to reduce shrub cover and promote herbaceous plant growth. Such habitat treatments intended to produce or enhance suitable sage-grouse habitat have been commonplace in areas of sagebrush steppe (Beck et al. 2012, Smith and Beck 2018). The mowing treatments were applied during January–February 2014, while snow covered the ground, using a tractor-pulled mowing implement ([Supplemental Material Figure S1](#)). Winter application is thought to reduce the risk of introducing invasive plants and limit the direct exposure of wildlife that are present in non-winter months. The mowing implement was set to a height of ~25 cm; however, due to snow cover and uneven topography ([Supplemental Material Figure S1](#)), the height to which shrubs were mowed was not strictly uniform across the study area (LeVan et al. 2015). The general effects of the mowing were to convert taller shrubs to woody stumps and to remove the top but leave the lower leafy branches of shorter shrubs ([Supplemental Material Figures S2 and S3](#)). The mowing also introduced a large amount of coarse woody debris in areas with a high density of mature shrubs ([Supplemental Material Figures S2 and S3](#)). Treatments were applied in a patchy, mosaic pattern (Figures 1 and 2), such that all treated areas were within 60 m of unmowed sagebrush (Dahlgren et al. 2006). Treatment application followed state guidelines for treating habitat in sage-grouse core areas, including guidance about the seasonal timing of treatment and buffers around occupied leks (Wyoming Game and Fish Department

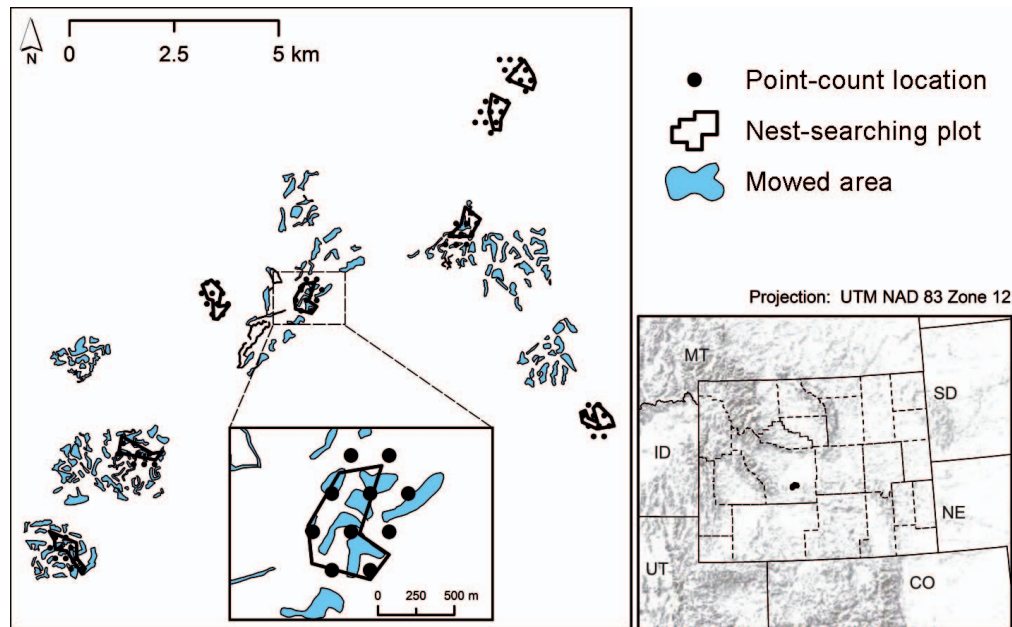


FIGURE 1. Map of the study area, mowed patches, and survey locations in central Wyoming, USA, 2013–2015. The inset, zoomed-in map shows finer-scale detail of the spatial context of the mowing treatments implemented for Greater Sage-Grouse. The regional map indicates the general study area in relation to county (dashed lines) and state boundaries. The point-count locations shown exclude the additional 40 point-count locations added for the secondary abundance analysis that were surveyed only posttreatment.

2011). The design, implementation, and vegetation-related effects of the mowing treatment are further detailed by LeVan et al. (2015) and Smith (2016).

We employed a before–after control-impact (BACI) experimental design (Stewart-Oaten et al. 1986, Stewart-Oaten and Bence 2001) to identify the effect of the mowing

treatment on songbird species that co-occur with sage-grouse in our study area during the breeding season. We surveyed treatment and reference sites (with units of replication defined separately by analysis) for 1 yr pretreatment (2013) and 2 yr posttreatment (2014 and 2015). We did not survey nestling condition pretreatment, so we employed a control-impact design for the nestling-condition portion of our experiment. The units of replication in our design were a point-count survey location (circle with 125 m radius) for the abundance analyses, a nest for the nest-site selection and nestling condition analyses, and a nest-check interval for the nest survival analyses. Prior to treatment, we established 8 nest-searching plots (each 24 ha; Figure 1), divided between portions of the study area selected for the mowing treatment ($n = 4$) and in nearby reference areas ($n = 4$; reference plots were 600–3,000 m from mowed patches posttreatment). Based on aerial imagery and ground truthing, we located and oriented plots in a manner that maximized within-plot habitat variability (i.e. each plot contained a relatively broad gradient of shrub height and cover; Chalfoun and Martin 2007). We established a cluster of 10 point-count locations at each nest-searching plot using a systematic grid with a random start location, arranged in offset rows with 250 m spacing between points within each row ($n = 80$ point-count locations; Figure 1). To increase our sample size for a secondary abundance analysis, we established 4 additional groups of 10 point-count locations each ($n = 40$) after the mowing treatment



FIGURE 2. Photograph of a mowed patch (left foreground with no visible shrubs) and an unmowed patch (right foreground with visible shrubs) in July 2015, nearing the end of the second growing season, following a shrub-mowing habitat manipulation for Greater Sage-Grouse in central Wyoming, USA. The mowing took place during January–February, 2014. Photo credit: Jason D. Carlisle

(2014), in mowed areas that were not covered by nest-searching plots. The location of these additional point-count locations adhered to the same systematic grid used for the initial point-count locations. Nest-searching plots and point-count locations were ≥ 100 m from trafficked roads, ≥ 1 km from oil or gas wells, and on public land. Nest-searching plots and point-count locations in the control group were ≥ 600 m from mowed areas, such that they were likely beyond the treatment's influence, yet close enough to be influenced by the same range of natural phenomena (e.g., weather) that could result in temporal changes in songbird populations (Stewart-Oaten et al. 1986).

Collection of Field Data

Abundance. We used point-count surveys following a distance-sampling protocol to survey the abundance of each species (Buckland et al. 2001). During each point-count visit, we conducted a 6 min unlimited-distance point-count survey between sunrise and 2.5 hr post-sunrise, recording all birds seen or heard. We surveyed each point-count location once in 2013 (between June 13 and 15) and twice per year in 2014 and 2015 (first between May 30 and June 5, second between June 6 and 22). Surveyors were randomly assigned to point clusters (10 nearby point-count survey locations; Figure 1) and surveyed one cluster per day, excluding days with precipitation or high winds. Distances to detected groups were recorded using laser rangefinders, either Nikon Prostaff 550 (Nikon, Melville, New York, USA) or Bushnell Yardage Pro Sport 450 (Bushnell Outdoor Products, Overland Park, Kansas, USA). To minimize bias in distance estimates for individuals detected aurally but not seen, observers attempted to identify the shrub from which the bird vocalized, then measured the distance to that shrub using the laser rangefinder (Hanni et al. 2012). Although it was rare for the same individual to be observable from multiple point-count locations, due to the spacing of our systematic grid and the truncation of observations >125 m, observers noted the location of birds detected near the outer edge of the point-count survey area (approximately 100–125 m) to ensure that individuals that had moved after being initially detected were not double counted at an adjacent point-count location (Buckland et al. 2001, Hanni et al. 2012).

Nest-site selection and nest survival. We located songbird nests at nest-searching plots between mid-May and mid-July, 2013–2015, searching for nests every 2 days. Nests were located by either accidental flushing of an adult bird from the nest while systematically walking through the plot or through intensive searching of an area where nest-building, courtship, or food-carrying behavior was observed (Reynolds and Rich 1978, Martin and Geupel 1993, Ralph et al. 1993). We took standard precautions to

minimize impacts on nesting activity due to observers, including limiting the amount of time spent at a nest, not approaching nests known to be under construction, not using flagging to mark nest locations, and varying walking paths within the plot (Martin and Geupel 1993, Ralph et al. 1993). We endeavored to standardize nest-searching effort among and within plots by ensuring that all observers visited all plots over the course of the season, and by searching all portions of each plot, including mowed areas. We recorded the location of each nest with a handheld GPS unit (Garmin GPSmap 62s or 62sc; Garmin, Olathe, Kansas, USA; accuracy ± 2 –10 m). We included only nests where active breeding activity (e.g., eggs or nestlings) was observed, and we excluded any nest found >10 m outside a plot boundary. A nest was considered successful if ≥ 1 nestling fledged from it, and we checked nests daily if nestlings appeared likely to fledge before the next scheduled visit (Martin and Geupel 1993, Ralph et al. 1993). Nest success was determined by examining the nest and immediate vicinity for signs of predation or fledging of young (Martin and Geupel 1993, Ralph et al. 1993). We concluded that young had fledged if we observed any of the following when finding no young in the nest after confirming their presence previously: (1) fledglings of the appropriate age nearby; (2) food-carrying adults within ~ 10 m of the nest; (3) fecal droppings on the nest rim or below the nest; (4) excessive flattening of the nest rim; or (5) nestlings having reached the typical fledging age, with no evidence of nest predation (e.g., egg or nestling remains, damage to nest structure) (Martin and Geupel 1993, Ralph et al. 1993).

Nestling condition. For altricial songbirds, increased physical condition of nestlings can result in increased survival in later life stages (Naef-Daenzer et al. 2001, Naef-Daenzer and Gruebler 2016). Therefore, we measured morphometrics (mass, wing chord length, and tarsus length) of known-age nestlings to determine body mass given skeletal size, an index of body condition (Brown 1996, Jakob et al. 1996). We acknowledge that assessing body condition on the basis of morphometrics offers only a potential index of body condition, absent direct measures of energetic or nutritional state (e.g., fat or protein reserves; Peig and Green 2009, 2010). We weighed each nestling using a digital scale (AWS-100; American Weigh Scales, Cumming, Georgia, USA; accuracy ± 0.02 g) and measured wing chord and tarsus length using a digital caliper (Series 700; Mitutoyo, Kawasaki, Kanagawa, Japan; accuracy ± 0.2 mm). In 2014 we measured only nestling Brewer's Sparrows, but we expanded these efforts to also include nestling Sage Thrashers and Vesper Sparrows in 2015. We included only known-age nests, or nests for which the hatch day was known, and measured each nestling at the age when the primary feathers typically break sheath (pin break; Ralph et al. 1993), which was day

TABLE 1. Model-selection results comparing candidate hierarchical distance-sampling models to estimate Brewer’s Sparrow abundance in relation to mowing treatments implemented for Greater Sage-Grouse in central Wyoming, USA, 2013–2015.^a

Model ^b	Key	ΔAIC ^c	w _i	K
p(observer)	Hazard rate	0.00	0.53	17
p(shrub height + observer)	Hazard rate	0.29	0.46	18
p(observer)	Half-normal	10.59	0.00	16
p(shrub height + observer)	Half-normal	11.94	0.00	17
p(.)	Hazard rate	65.26	0.00	6
p(shrub height)	Hazard rate	66.80	0.00	7
p(.)	Half-normal	77.04	0.00	5
p(shrub height)	Half-normal	78.98	0.00	6

^a Key = key function describing the form of the distance-detection relationship; ΔAIC = difference in AIC between the model and the top-ranked model in the set; w_i = model weight; K = number of parameters.
^b Only the detection portion of the hierarchical model (*p*) is shown. The abundance portion (*λ*) is omitted because it was fixed across all candidate models: *λ*(period + treatment + [period × treatment]).
^c Lowest Akaike’s Information Criterion (AIC) value = 3,989.05.

6 for Brewer’s and Vesper sparrows and day 7 for Sage Thrashers. We avoided handling nestlings in the early morning or during cold or wet weather (Ralph et al. 1993).

Statistical Analysis

We used ArcGIS (ESRI 2014) to create the systematic grid used to site point-count locations and to create map figures. We conducted all statistical analyses using R (R Core Team 2017). We used the “unmarked” package (Fiske and Chandler 2011) for distance-sampling analyses. We used the “raster” (Hijmans 2015), “rgeos” (Bivand and Rundel 2015), “rgdal” (Bivand et al. 2015), and “sp” (Pebesma and Bivand 2005) packages for spatial data handling and analysis. We used the “ecoinfo” (Carlisle and Albeke 2016), “lubridate” (Grolemund and Wickham 2011), “plyr” (Wickham 2011), “RODBC” (Ripley and Lapsley 2016), and “tidyr” (Wickham 2016) packages for general data handling. We used the “ggplot2” (Wickham 2009) and “ggthemes” (Arnold 2017) packages for data visualizations and figures. We present 95% confidence intervals (CI) for estimates of effect size and used an α level of 0.05 for all statistical tests.

Abundance. We used the hierarchical distance-sampling model of Royle et al. (2004) to estimate abundance for each species. This method, based on a hierarchical generalized linear model, provided estimates of abundance (or density) that accounted for imperfect detection of individuals. It was unlikely that the same individual songbird was detected at multiple point-count locations, so we treated each point-count location as an independent site in the hierarchical model (Royle et al. 2004). Therefore, the unit of replication in this analysis was a point-count

TABLE 2. Model-selection results comparing candidate hierarchical distance-sampling models to estimate Sage Thrasher abundance in relation to mowing treatments implemented for Greater Sage-Grouse in central Wyoming, USA, 2013–2015.^a

Model ^b	Key	ΔAIC ^c	w _i	K
p(shrub height)	Hazard rate	0.00	0.62	7
p(shrub height)	Half-normal	2.17	0.21	6
p(.)	Hazard rate	3.04	0.13	6
p(.)	Half-normal	5.44	0.04	5

^a Key = key function describing the form of the distance-detection relationship; ΔAIC = difference in AIC between the model and the top-ranked model in the set; w_i = model weight; K = number of parameters.
^b Only the detection portion of the hierarchical model (*p*) is shown. The abundance portion (*λ*) is omitted because it was fixed across all candidate models: *λ*(period + treatment + [period × treatment]).
^c Lowest Akaike’s Information Criterion (AIC) value = 1,920.88.

survey location (circle with 125 m radius). Differences in site-specific habitat structure and/or observer skill can create heterogeneity in the detectability of animals in the field (White 2005, Kellner and Swihart 2014); therefore, we considered shrub height and observer as covariates in the detection process in our distance-sampling analyses. We calculated shrub height as the mean height of shrubs within 125 m of each point-count location using a spatially explicit dataset of shrub attributes derived from remote sensing (30 m cell size; Homer et al. 2012). Because the mowing treatments were intended to reduce shrub height and cover, we accounted for this reduction when calculating the value of this covariate in posttreatment years. Prior work in the area revealed that shrub height posttreatment was, on average, 61% of the pretreatment height (LeVan et al. 2015; SE = 3.46%, K. T. Smith personal communication), so we multiplied cell values of the shrub height raster that were within mowed patches by 0.61 to estimate shrub height during posttreatment point-count surveys. We prepared the songbird detection data for analysis by truncating records for birds detected >125 m from the observer and binning counts into 5 equally sized distance intervals (Supplemental Material Figure S4).

We analyzed data for each songbird species separately. We used an information-theoretic model-selection approach to compare candidate models to find the best-fitting combination of key function (i.e. the form of the relationship between detection probability and distance; half-normal or hazard rate) and covariates on detection. There were 8 models in the candidate model set for Brewer’s and Vesper sparrows, including models that allowed for heterogeneity in detection probability (*p*) due to habitat structure and/or observer, and models that assumed that *p* was constant (Tables 1 and 3). Not all observers had sufficient numbers of detections of Sage

TABLE 3. Model-selection results comparing candidate hierarchical distance-sampling models to estimate Vesper Sparrow abundance in relation to mowing treatments implemented for Greater Sage-Grouse in central Wyoming, USA, 2013–2015.^a

Model ^b	Key	ΔAIC ^c	w_i	K
p(observer)	Half-normal	0.00	0.72	16
p(shrub height + observer)	Half-normal	1.97	0.27	17
p(observer)	Hazard rate	9.75	0.01	17
p(shrub height + observer)	Hazard rate	11.58	0.00	18
p(.)	Half-normal	11.95	0.00	5
p(shrub height)	Half-normal	13.81	0.00	6
p(.)	Hazard rate	19.29	0.00	6
p(shrub height)	Hazard rate	20.59	0.00	7

^a Key = key function describing the form of the distance-detection relationship; ΔAIC = difference in AIC between the model and the top-ranked model in the set; w_i = model weight; K = number of parameters.

^b Only the detection portion of the hierarchical model (p) is shown. The abundance portion (λ) is omitted because it was fixed across all candidate models: $\lambda(\text{period} + \text{treatment} + [\text{period} \times \text{treatment}])$.

^c Lowest Akaike's Information Criterion (AIC) value = 2,840.39.

Thrashers, the least abundant species, to investigate heterogeneity in p due to observer. Therefore, we limited the candidate model set for Sage Thrashers to 4 models, including models that allowed for heterogeneity in p due to habitat structure and models that assumed that p was constant (Table 2). Because of our BACI experimental design, we were particularly interested in an interaction between the study period (pretreatment or posttreatment) and treatment group (reference or mowed), which would indicate a change in songbird abundance due to habitat treatments. Thus, the abundance portion of each model (λ) was structured the same way: $\lambda \sim \text{period} + \text{treatment} + (\text{period} \times \text{treatment})$. We ranked models using Akaike's Information Criterion (AIC; Akaike 1974, Burnham and Anderson 2002) and used the highest-ranked model for each species to test for an effect of the mowing treatment on songbird abundance.

We conducted a secondary abundance analysis to determine whether the finer-scale exposure to mowed areas was associated with abundance. This analysis was restricted to point-count surveys located where the mowing treatment was applied and included data only from the years after the mowing treatment. Here, we used the proportion of the area that was mowed within 125 m of the point-count location as the single predictor variable for the abundance portion of the model: $\lambda \sim \text{proportion mowed}$. The detection portion of the model (p) included the same key function and predictor variable(s) from the highest-ranked model selected in the primary BACI analysis of abundance. The unit of replication in this secondary abundance analysis was also a point-count survey location (circle with 125 m radius).

Nest-site selection. We analyzed nest placement in relation to the nearest edge of a mowed patch as a measure of nest-site selection in relation to the mowing. We included only nests from the 4 nest-searching plots that received the mowing treatment, and we used data from both the pretreatment and posttreatment periods. The unit of replication in this analysis was a nest. We recorded the location of the perimeter of each mowed patch using a handheld GPS unit. For data from posttreatment years, we calculated the distance from each nest to the nearest edge of a mowed patch using a GIS. Negative distances represented nests located inside the mowed footprint, and positive distances represented nests located in unmowed areas. For data from the pretreatment year, we calculated the distance from each nest to the nearest edge of where the mowed footprint would be once the treatment was implemented. These pretreatment data provided the baseline of what the distribution of distances to the mowed patches would be under unmanipulated conditions, given the shape and size of the nest-searching plots and the spatial arrangements of mowing patches. For each species, we used a 2-sample t -test (Hayter 2002) to determine whether the mean distance from a nest to the edge of the nearest mowed patch was different between pretreatment and posttreatment periods. To gain insights on potential mowing effects not captured by the mean distance, we created violin plots (Hintze and Nelson 1998) as a graphic representation of the distribution of distances from nests to the mowed edge.

Nestling condition. We estimated nestling body condition using a residual index based on a multiple regression of body mass on measures of body size or length (Jakob et al. 1996). Whether residual-based body condition indices serve as accurate proxies for direct measures of energetic or nutritional state (e.g., fat or protein reserves) is uncertain (Peig and Green 2009, 2010); however, body condition indices that account for multiple measures of body size and for nonlinearity in the relationship between body mass and size generally perform better than traditional methods that do not (Schulte-Hostedde et al. 2005, Peig and Green 2010, Labocha et al. 2014). We first fit a multiple regression model for each species: $\text{mass} \sim \text{wing} + \text{tarsus} + \text{wing}^2 + \text{tarsus}^2$. The inclusion of a quadratic term for each measure of body size (i.e. wing chord length and tarsus length) in our multiple regression accommodated nonlinearity in the mass–size relationship. Data for Brewer's Sparrows spanned 2 yr (2014 and 2015), so we included an additional additive term for year in the Brewer's Sparrow model to accommodate any potential year effect. The residual value for each nestling from the multiple regression was treated as an index of its body condition index (Jakob et al. 1996).

Preliminary analysis revealed that nestling condition was negatively correlated with brood size (number of nestlings

in the nest); however, because brood size did not differ between treatment groups for any species ($P \geq 0.44$ for all species), we did not directly control for brood size in calculating the body condition index. Because the conditions of multiple siblings within the same nest are likely not independent, we summarized body condition at the nest level as the mean of the body condition indices of the nestlings within the nest. Therefore, the unit of replication in this analysis was a nest. Then, for each species, we used a weighted linear regression model (Kutner et al. 2004) to test whether the mean body condition index at nests was different between treatment groups, with the number of nestlings within the nest as the weight. This approach was equivalent to a 2-sample t -test, but it treated nests with more nestlings as more informative in the test for a treatment effect.

Nest survival. Because nests that fail early in the nesting cycle are less likely to be discovered by observers, apparent nest survival (the proportion of observed nests that survive to fledge young) overestimates actual nest survival (Mayfield 1975, Shaffer 2004, Johnson 2007). We thus used a generalized linear model that accounts for this bias (the logistic-exposure model of Shaffer 2004), to estimate daily nest survival rates and test for an effect of mowing on songbird nest survival. The unit of replication in this analysis was a nest-check interval (typically 1–2 days). We analyzed the data for each songbird species separately. Because of our BACI experimental design, we were particularly interested in an interaction between the study period (pretreatment or posttreatment) and treatment group (reference or mowed), which would test for a change in songbird nest survival rates due to the mowing treatments. Thus, each model was structured in the same way: survival \sim period + treatment + (period \times treatment).

We conducted a secondary survival analysis to determine whether the finer-scale proximity to mowed patches was associated with nest survival. This analysis was restricted to nests found in the posttreatment period at nest-searching plots where the mowing treatment was applied. Here, we used the distance to the edge of the nearest mowed patch, with negative values indicating nests inside the mowed patch, as the single predictor variable: survival \sim distance to mow. The unit of replication in this secondary nest-survival analysis was also a nest-check interval (typically 1–2 days).

RESULTS

The mowing treatment was applied as 149 disjunct patches, resulting in 488.87 ha mowed within the study area (Figure 1). The average (\pm SD) mowed patch was 3.28 ± 2.27 ha (range: 0.34–12.36; [Supplemental Material Figure S5](#)). Across the 4 nest-searching plots where the

mowing treatment was applied, an average of $32.40 \pm 5.83\%$ of the plot area was mowed (range: 27.23–38.06%). Across the 40 point-count locations at the 4 nest-searching plots where the mowing treatment was applied, an average of $26.08 \pm 16.71\%$ of the area within the 125-m-radius point-count circles was mowed (range: 0.00–61.00%; [Supplemental Material Figure S6](#)). When summarized across the 80 point-count locations included in the secondary abundance analysis ($n = 40$ at mowed nest-searching plots; $n = 40$ in mowed areas outside nest-searching plots), an average of $28.23 \pm 19.20\%$ of the area within the 125-m-radius point-count circles was mowed (range: 0.00–86.00%; [Supplemental Material Figure S6](#)).

Abundance

We conducted 560 point-count surveys across 120 point-count locations. We detected 3,643 individuals (prior to truncation of distant individuals): 1,829 Brewer's Sparrows (50.2%), 973 Vesper Sparrows (26.7%), and 841 Sage Thrashers (23.1%). The highest-ranked distance-sampling model for Brewer's Sparrows (Table 1) used a hazard-rate key function and included observer-specific variation in the detection process: $\lambda(\text{period} + \text{treatment} + [\text{period} \times \text{treatment}]) p(\text{observer})$. The highest-ranked model for Sage Thrashers (Table 2) used a hazard-rate key function and included habitat-specific variation in the detection process: $\lambda(\text{period} + \text{treatment} + [\text{period} \times \text{treatment}]) p(\text{shrub height})$. The highest-ranked model for Vesper Sparrows (Table 3) used a half-normal key function and included observer-specific variation in the detection process: $\lambda(\text{period} + \text{treatment} + [\text{period} \times \text{treatment}]) p(\text{observer})$.

The BACI comparison of point-count locations between the reference and the mowing treatment group indicated that mowing treatment did not influence the abundance of Brewer's ($P = 0.22$) or Vesper ($P = 0.87$) sparrows (Figure 3). By contrast, Sage Thrasher abundance decreased by a relative 48.08% (95% CI: 16.40–67.75%) in response to mowing ($P = 0.007$; Figure 3). The secondary, finer-scale analysis (using only the 320 point-count surveys conducted in mowed areas during the posttreatment period) of abundance in relation to the proportion of the point-count survey area that was mowed revealed different effects by species. For every incremental 10% increase in the amount of the point-count circle that was mowed, the abundance of Brewer's Sparrows decreased by a relative 7.42% (95% CI: 4.06–10.67%; $P < 0.001$; Figure 4). Abundance did not vary by the amount of mowing in the point-count circle for Sage Thrashers ($P = 0.63$; Figure 4), although the precision of this estimate was poor. By contrast, the abundance of Vesper Sparrows increased by a relative 5.38% (95% CI: 0.73–10.23%; $P = 0.02$) for every incremental 10% increase in the amount of the point-count circle that was mowed (Figure 4).

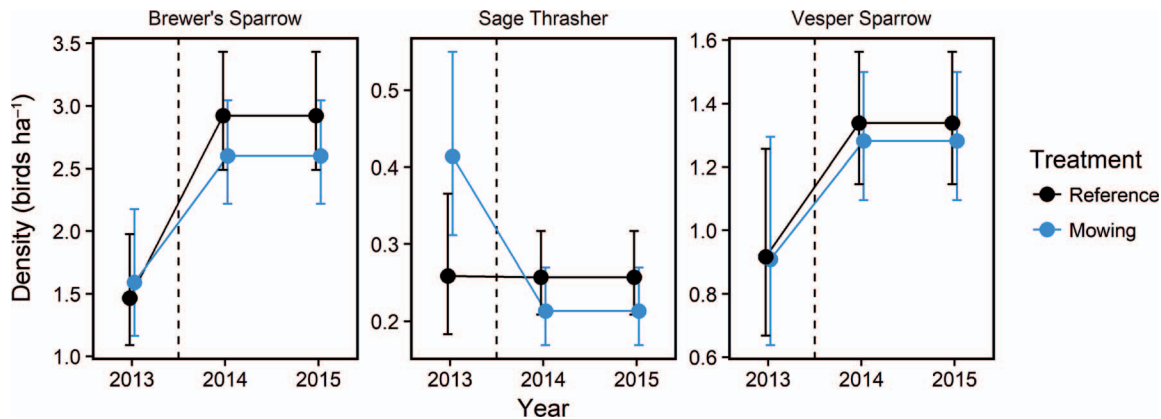


FIGURE 3. Abundance of songbirds (\pm 95% confidence interval) in relation to mowing treatments implemented for Greater Sage-Grouse in central Wyoming, USA, 2013–2015. Dashed line indicates when mowing treatments were applied.

Nest-Site Selection

We located and monitored 812 nests. The nest-site selection analysis was restricted to the 396 nests found at plots in the mowing treatment group. These included 218 Brewer's Sparrow, 106 Sage Thrasher, and 72 Vesper Sparrow nests. Approximately 1/4 of songbird nests found in the pretreatment period were located in what would become mowed patches, including 22.45% (95% CI: 12.24–34.69%) of Brewer's Sparrow, 23.53% (95% CI: 5.88–47.06%) of Sage Thrasher, and 30.77% (95% CI: 7.69–53.85%) of Vesper Sparrow nests. For Brewer's Sparrows and Sage Thrashers, there was marginal evidence that the mean distance from nests to the nearest mowed patch tended to be greater during the posttreatment period than the baseline distance (from the pretreatment period) to where the nearest mowed patch would be ($P = 0.06$ for Brewer's Sparrow, $P = 0.07$ for Sage Thrasher; Figure 5).

Moreover, no Brewer's Sparrow or Sage Thrasher nests were found within the mowed footprint during the posttreatment period (Figure 5). By contrast, 54.24% (95% CI: 40.68–66.10%) of Vesper Sparrow nests at plots subjected to the mowing treatment were located within the mowed footprint during the posttreatment period (Figure 5 and [Supplemental Material Figure S7](#)). Vesper Sparrow nest-site selection in relation to the nearest edge of the mowed footprint differed between the pretreatment and posttreatment periods ($P = 0.03$; Figure 5). On average, Vesper Sparrow nests were located 20.87 m (95% CI: 2.24–39.50) closer to or farther into the mowed patches during the posttreatment period.

Nestling Condition

We estimated the body condition index of 441 nestlings: 252 Brewer's Sparrows (106 in 2014 and 146 in 2015), 128

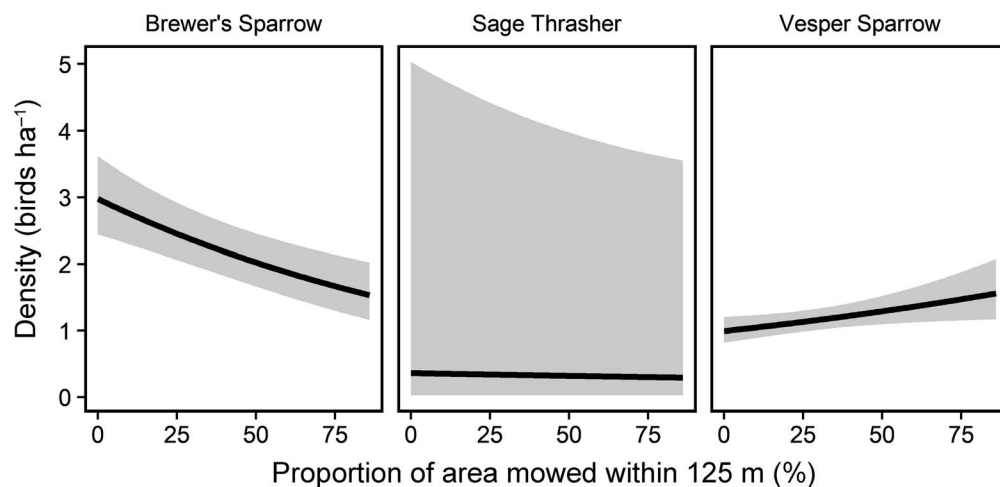


FIGURE 4. Abundance of songbirds (\pm 95% confidence interval) in relation to the proportion of the surveyed area (125-m-radius circle) that was mowed as part of treatments implemented for Greater Sage-Grouse in central Wyoming, USA, 2014–2015. Only posttreatment surveys of point-count locations in mowed areas are included.

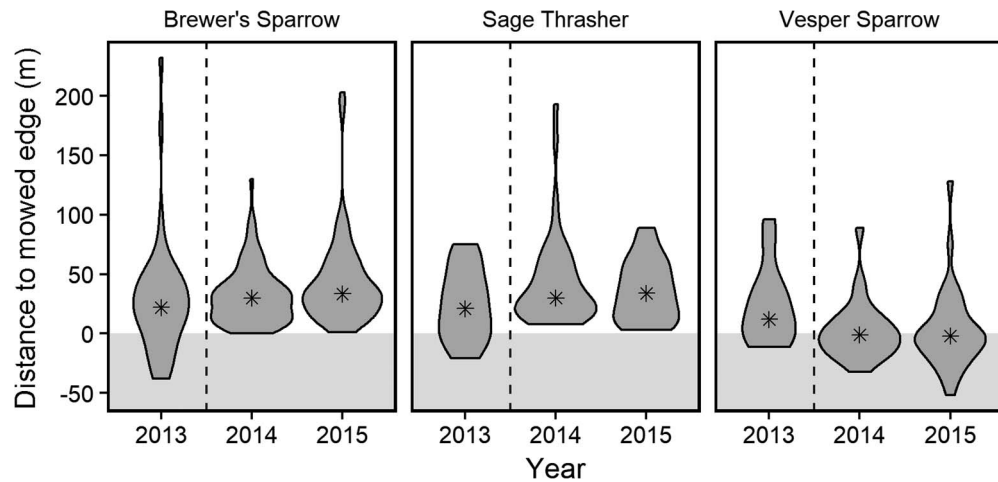


FIGURE 5. The distribution of distances from nests to the nearest edge of mowing treatments implemented for Greater Sage-Grouse in central Wyoming, USA, 2014–2015. Only nests at plots where the mowing treatment was applied are included. Dashed line indicates when mowing treatments were applied. Year 2013 was prior to the treatment, so distances are from nests to where the nearest edge of a mowed patch would be posttreatment (2014 and 2015). Negative distances (gray-shaded region) are within a mowed patch, and asterisks indicate medians.

Sage Thrashers, and 61 Vesper Sparrows. These nestlings came from 144 nests: 84 Brewer's Sparrow (29 in 2014 and 55 in 2015), 36 Sage Thrasher, and 24 Vesper Sparrow. Nestling condition did not differ between treatment groups for Brewer's Sparrows ($P = 0.77$) or Sage Thrashers ($P = 0.97$) (Figure 6). Vesper Sparrows reared at plots where the mowing treatment was applied had higher body condition indices than those reared at reference plots ($P < 0.01$; Figure 6). Holding wing and tarsus size constant, the average nestling Vesper Sparrow within a nest located at a nest-searching plot where the mowing treatment was applied was 1.16 g heavier (95% CI: 0.39–1.93) than one reared at a reference plot. Given that the average nestling Vesper Sparrow in our study

weighed 13.51 g, the observed effect size equates to an 8.59% difference in body mass.

Nest Survival

We monitored the survival of 812 nests: 466 Brewer's Sparrow, 218 Sage Thrasher, and 128 Vesper Sparrow. Our sample totaled 11,170 nest-days of monitoring. We found no evidence in the BACI comparison of a plot-level effect of mowing treatment on nest survival rates of Brewer's Sparrows ($P = 0.34$), Sage Thrashers ($P = 0.53$), or Vesper Sparrows ($P = 0.52$) (Figure 7).

The secondary, finer-scale analysis (using only the 317 nests at mowed plots during the posttreatment period) of nest survival in relation to the distance to the nearest

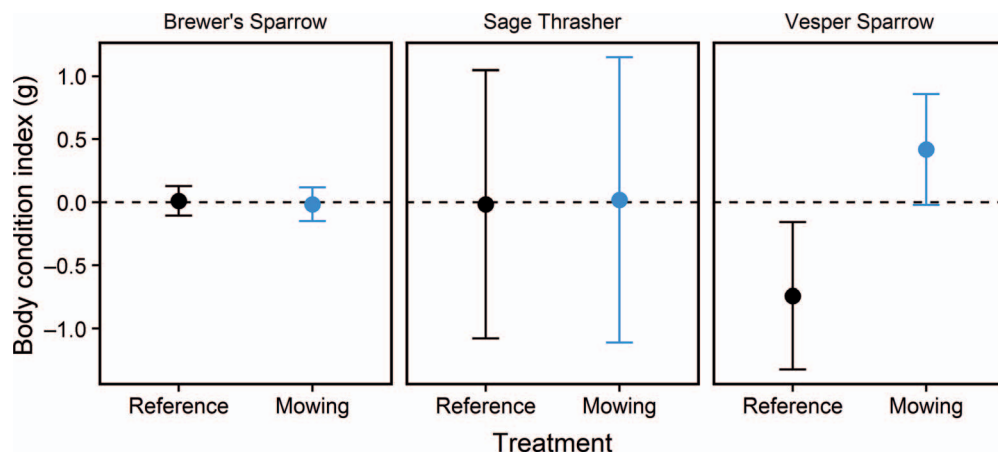


FIGURE 6. Body condition, estimated as residual mass given wing chord and tarsus length, of nestling songbirds (\pm 95% confidence interval) in relation to mowing treatments implemented for Greater Sage-Grouse in central Wyoming, USA, 2014–2015. Nestling condition was assessed only during posttreatment years. Dashed line indicates the mean body condition for each species.

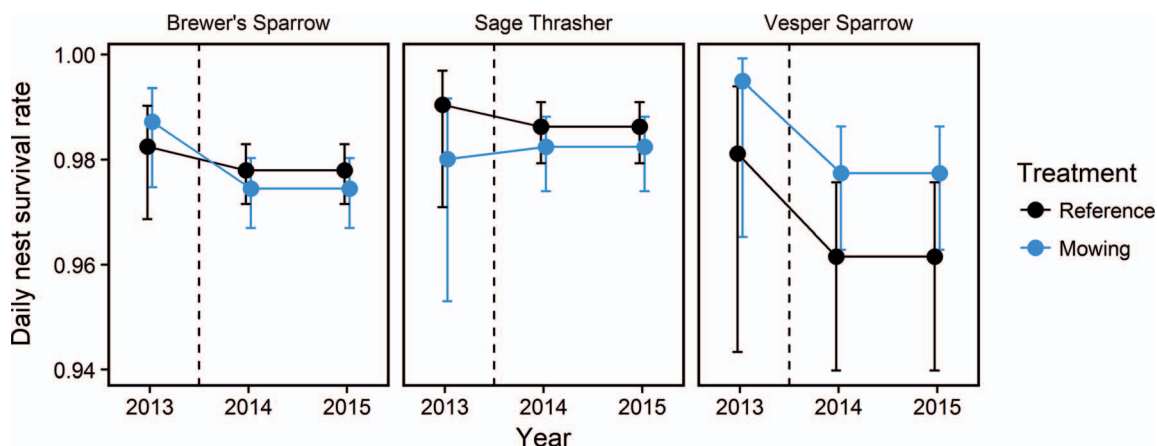


FIGURE 7. Daily nest survival rates of songbirds (\pm 95% confidence interval) in relation to mowing treatments implemented for Greater Sage-Grouse in central Wyoming, USA, 2013–2015. Dashed line indicates when mowing treatments were applied.

mowed patch revealed different effects by species. Brewer's Sparrows nesting in unmowed shrubs near a mowed patch had marginally higher survival rates ($P = 0.06$), but nest survival did not vary by distance to the nearest mowed patch for Sage Thrashers ($P = 0.51$) (Figure 8). Vesper Sparrow nests located closer to, or farther within, mowed patches had higher survival rates ($P = 0.03$; Figure 8). For every additional 10 m in distance that a Vesper Sparrow nest was located closer to the edge of a mowed patch (for nests outside the mowed footprint) or farther into the interior of a mowed patch (for nests inside the mowed footprint), the odds of daily nest survival increased by a relative 17.57% (95% CI for odds ratio: 1.00–1.35). Assuming a 25-day nesting period (i.e. number of days from the laying of the first egg until the fledging of young),

our model estimated that a Vesper Sparrow nest located at the mowed edge (distance = 0 m; Figure 8) had a 59.58% chance of surviving to fledge young. The Vesper Sparrow nest that we found farthest into the interior of a mowed patch during the posttreatment period was 52 m inside the mowed patch (distance = –52 m; Figure 8), and our model estimated that a nest located at this distance had a 79.90% chance of surviving to fledge young. The Vesper Sparrow nest that we found farthest from the nearest mowed patch during the posttreatment period (but still within the nest-searching plots where the mowing treatment was applied) was 128 m away from the nearest mowed patch (distance = 128 m; Figure 8). Our model estimated that a nest located at this distance had a 2.14% chance of surviving to fledge young.

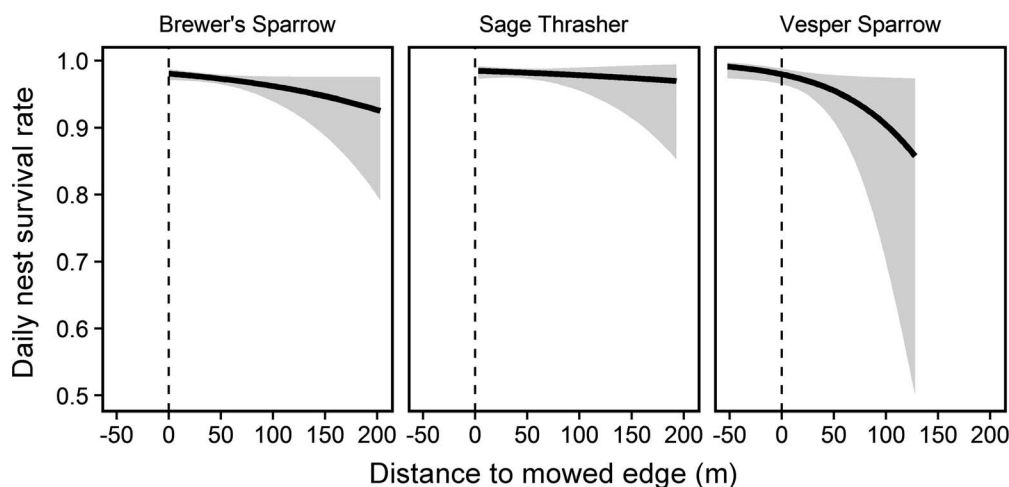


FIGURE 8. Daily nest survival rates (\pm 95% confidence interval) in relation to the distance of songbird nests to the nearest edge of mowing treatments implemented for Greater Sage-Grouse in central Wyoming, USA, 2014–2015 (including only nests posttreatment at plots where the mowing treatments were applied). Dashed line indicates the edge of a mowed patch, and negative distances are within a mowed patch.

DISCUSSION

The umbrella species concept and other surrogate-species approaches are potentially useful tools in the conservation of biodiversity; however, for these approaches to be effective, management actions implemented on behalf of the umbrella species should not be detrimental to sympatric taxa of concern. Using a controlled field experiment, we found that habitat manipulations intended to benefit Greater Sage-Grouse, a high-profile umbrella species, had mixed effects on the abundance, habitat use, nestling condition, and nest survival of 3 background songbird species of conservation interest. Given the broad conservation concern for sagebrush-obligate songbirds, the complete loss of nesting habitat for Brewer's Sparrows and Sage Thrashers in areas within the mowed footprint and the reduced abundances of these species in association with mowing are particularly concerning.

Implications for Greater Sage-Grouse as an Umbrella Species

The mowing treatment had either neutral or negative effects on Brewer's Sparrows and Sage Thrashers, the 2 sagebrush-obligate songbirds of conservation concern that we studied. We found no nests of Brewer's Sparrows or Sage Thrashers within the mowed footprint, which suggests that the treatment resulted in the complete loss of nesting habitat for these sagebrush-obligate songbird species for at least the 2 yr following mowing. Because sagebrush plants are slow to reestablish following disturbance (Baker 2006), it may be decades until there are shrubs in the mowed patches that are sizable enough to be used by Brewer's Sparrows or Sage Thrashers as nesting substrates. Despite the lack of evidence that mowing reduced nest survival or the condition of nestlings (which can influence postfledging survival and recruitment; Naef-Daenzer et al. 2001) during the 2 yr following mowing, the mowing treatment reduced the abundance of Sage Thrashers. And although Brewer's Sparrows were equally abundant between the mowing and reference groupings of point-count locations, within areas that experienced some mowing Brewer's Sparrows were less abundant where the mowing was more extensive.

The loss of Brewer's Sparrow and Sage Thrasher nesting habitat applied only to the areas directly mowed ($\sim 1/3$ of the area within plots where the mowing treatment was applied). Both sagebrush-obligate species continued to nest within intact sagebrush patches that remained after mowing, even continuing to nest in such intact patches within plots subjected to the mowing treatment. Indeed, there was only equivocal evidence that the mean distance of nests in relation to the mowed edge was altered by the mowing treatment, meaning that birds apparently side-stepped the mowed patches and nested in unmowed areas

adjacent to the mowed edge (Figure 5). Small-scale displacement of Brewer's Sparrow and Sage Thrasher nests has also been observed in response to shrub-reducing treatments elsewhere (Norvell 2008).

The effects of the mowing treatment were largely beneficial for the more generalist and ground-nesting Vesper Sparrow. Vesper Sparrows were equally abundant between the mowing and reference groupings of point-count locations; however, within areas that experienced some mowing, Vesper Sparrows were more abundant where the mowing was more extensive. Additionally, the mowing treatments remained suitable as nesting habitat or even created more-suitable nesting habitat for Vesper Sparrows, and nests closer to or within the mowed footprint had higher rates of survival. Moreover, Vesper Sparrow nests located within plots where the mowing treatment was applied produced nestlings of higher body condition than nests within reference plots. Our findings corroborate and expand upon other work showing that generalist and grassland-associated species respond more favorably than sagebrush-obligate species to sagebrush treatments (Wiens and Rotenberry 1985). Our study of only 3 species suggested that the response of each species to the shrub-removing treatment could be predicted on the basis of the habitat association and nesting substrate requirements of each species; however, we caution that species with similar habitat associations may not always respond in like manner to habitat alterations (Norvell et al. 2014).

The mechanisms underlying songbird responses to the mowing treatment remain uncertain, but our observations suggest that the direct reduction in sagebrush shrubs was likely more important than indirect trophic effects. The redistribution of nests within landscapes that experience habitat loss and fragmentation could affect competition for food or other resources; however, the abundances of key songbird food resources such as insects were not substantially altered by the mowing treatment (Smith 2016). We have not profiled the species that depredate songbird nests in our study area, so we cannot explain why Vesper Sparrow nests had higher survival rates closer to or within mowed patches.

We emphasize that the mowing treatments evaluated here were patchily distributed, even within "treatment" sites, and that our findings are not applicable to forms of high-intensity, uniform disturbance that result in wholesale conversion of large areas of sagebrush-steppe, including some forms of agricultural, exurban, and energy development. The proportion of area mowed within 125 m (1.23 ha) of the 80 point-count locations in mowed areas ranged from 0.00% to 86.00% (mean = 28.23%; [Supplemental Material Figure S6](#)), and the proportion of area mowed within the 24 ha nest-searching plots was more consistent, ranging from 27.23% to 38.06% (mean =

32.40%). Given that our treatments covered only $\sim 1/3$ or less of the area in any given study plot, our treatments were similar, but generally lighter than other mechanical treatments implemented for sage-grouse elsewhere (Dahlgren et al. 2006, Norvell et al. 2014, Lukacs et al. 2015, Baxter et al. 2017).

Compatibility of Active Management with the Umbrella-Species Concept

Because of the interconnectedness of ecological systems, management actions designed to benefit an umbrella species can affect nontarget species in varied and perhaps nonideal ways, as shown here. Because habitat protections undertaken for umbrella species typically span broad spatial extents (Caro 2003, 2010), however, and targeted management actions such as habitat treatments are typically restricted in spatial extent, we encourage the interpretation of any nontarget effects documented at fine scales to be considered within the context of broader conservation efforts undertaken for the umbrella species.

Priority areas for sage-grouse conservation encompass $\sim 310,000$ km² across the western United States (USFWS 2013, 2014). Management across these semi-protected areas is not uniform or guaranteed into perpetuity; however, the general approach has been to limit the amount of habitat loss and fragmentation due to threats such as energy development, invasive plant invasion, and wildfire. Although the mowing treatments we evaluated likely resulted in the temporary loss of ~ 5 km² of nesting habitat for 2 nontarget species, the cost and logistics of such treatments generally prohibit their broad-scale application. Moreover, in Wyoming, the local extent of such treatments implemented for sage-grouse is subject to the same regulations that prohibit other forms of surface disturbance in core areas of sage-grouse habitat (State of Wyoming 2011). The amount of area exposed to shrub-removing treatments each year is difficult to assess but is likely orders of magnitude smaller than the amount of area withheld from activities that can lead to habitat loss and/or fragmentation. For example, the Wyoming state government created a large (61,777 km²), semi-protected reserve to encompass core areas of the state's sage-grouse populations as a means to conserve the species (State of Wyoming 2008, 2010, 2011). Habitat loss caused by energy development is regulated within these reserves (State of Wyoming 2011); consequently, the rate of oil and gas development within them has been substantially lower than that in non-reserve areas (Gamo and Beck 2017). Sagebrush-obligate songbirds tend to be less abundant (Gilbert and Chalfoun 2011) and experience lower nest survival (Hethcoat and Chalfoun 2015) in areas with oil and gas development, and a large portion of the habitat predicted to be suitable for sagebrush-obligate songbirds in Wyoming is within sage-grouse reserves where energy

development is limited (36% of Brewer's Sparrow, 41% of Sage Thrasher, and 47% Sagebrush Sparrow habitat; Gamo et al. 2013). Moreover, the management history of a large section of these reserve areas (50,957 km²) indicates that $<3\%$ (1,511 km²) was treated to reduce shrubs between 1994 and 2012, including areas treated with herbicide, prescribed fire, and mechanical means such as mowing (Smith and Beck 2018). Therefore, the negative effects that nontarget species incur as a result of habitat manipulations for sage-grouse at relatively small scales have the potential to be offset by positive effects resulting from broad-scale conservation efforts also taken on behalf of sage-grouse.

We followed the terminology of Caro (2003, 2010) to refer to the species that live in the same geographic area as an "umbrella species" and, therefore, the species expected to benefit from the conservation of the umbrella species as "background species." The latter term implies that co-occurrence with the umbrella species is the only prerequisite for another species to receive indirect conservation benefits via conservation of the umbrella species. Our work suggests that a more nuanced classification of so-called background species may be warranted. We demonstrated that 3 species sympatric with sage-grouse, and therefore considered background species, had varied responses to management actions taken for the umbrella species; of note, 2 of the 3 species demonstrated negative responses to management actions for the umbrella species, which calls into question the suitability of sage-grouse habitat manipulation as a tool to conserve these species. There is no clear definition of how well covered a background species must be to be considered "covered" under the umbrella of another species' conservation. Furthermore, how many species need to qualify as well-covered background species in order for the umbrella species to be considered a successful one? Such questions about the definition and qualifications of an umbrella species are not new (Andelman and Fagan 2000, Roberge and Angelstam 2004, Seddon and Leech 2008, Branton and Richardson 2011, 2014). In our study, however, even with a limited focus on a single taxonomic group, 1/3 of species benefitted from umbrella species management, whereas 2/3 were either unaffected or potentially harmed by umbrella species management. Does this mean that the sage-grouse is a good umbrella species for sympatric songbirds or not? Moreover, assessments of the sage-grouse as an umbrella species have traditionally focused on vertebrates (Carlisle et al. 2017), but sage-grouse conservation must benefit more than just vertebrates for the sage-grouse to serve as an effective surrogate for entire sagebrush-associated ecosystems (Rich and Altman 2001, Carlisle et al. 2017).

The umbrella species concept hinges on securing the long-term viability of populations of the umbrella and

background species; however, the demographic consequences of managing background species under an umbrella-species strategy are very rarely assessed (Wilcox 1984, Caro 2003, Roberge and Angelstam 2004). Moreover, the effects of habitat changes may not become manifest over short time scales such as those studied here (Wiens 1984, Petersen and Best 1999), especially if the use of altered areas is maintained by site fidelity and/or conspecific attraction (Knick and Rotenberry 2000, Stodola and Ward 2017). We suggest that experimental studies such as ours, but especially those that monitor the demography of background species over longer time scales, will be essential for understanding the ultimate effect of umbrella-species management on the viability and persistence of nontarget species.

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Ethics statement: This research was conducted in accordance with protocols approved by the Wyoming Game and Fish Department (no. 33-952) and University of Wyoming (nos. 20120518JC00200-01, 20140425AC00096-0, and 20140425AC00096-02).

Author contributions: All authors conceived and designed the experiment. J.D.C. and K.T.S. conducted the research. J.D.C. analyzed the data. All authors contributed to the writing of the paper, led by J.D.C.

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