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POPULATION AND BREEDING ECOLOGY OF SAGEBRUSH STEPPE SONGBIRDS

By

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Thesis

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Population and breeding ecology of sagebrush steppe songbirds

Chairperson: Dr. Victoria Dreitz

ABSTRACT

Sagebrush steppe is one of the most threatened ecosystems in North America. Domestic livestock grazing is the dominant land use of sagebrush steppe across the west. Rest-rotation grazing systems can be a conservation management tool, most recently, by the Natural Resource Conservation Service - Sage Grouse Initiative (SGI). The goal of SGI is to encourage private landowners to use a livestock grazing regime that maintains or improves habitat for greater sage-grouse (*Centrocercus urophasianus*), as well as improve rangeland productivity. Songbirds are biological indicators that can assess the health of sagebrush steppe. Avian adult density estimates are often used to assess conservation actions, given the relative ease in collecting data to inform these estimates. However, information on how conservation actions influence life histories, such as nest density and nest success are lacking, even though life histories inform abundance. My goal was to understand the relationship between adult abundance, nest density, and nest success, as well as how land management practices, in the form of grazing, influence those patterns. I investigated songbird adult densities, nest densities, and nest success over multiple breeding seasons in central Montana. I concentrate on Brewer's sparrow (*Spizella breweri*), McCown's longspur (*Rhynchophanes mccownii*), and vesper sparrow (*Pooecetes gramineus*). I explore how nest density affects nest survival and whether density dependence was present in nesting sagebrush steppe songbirds. While nest density did not appear to explain nest survival, the distance to the next nearest interspecific nest did explain nest survival for vesper sparrows, which shows some support for the presence of density dependence. Additionally, I examine the relationship between adult density and nest density on the landscape. At a local plot level, adult songbirds are often present on the landscape in higher numbers than nests. The discrepancy between adult density and nest density suggests these songbirds may not be breeding every year, as is often assumed. This study provides knowledge on population demographics of sagebrush songbirds in central Montana, their responses to current land management, and provides information that will aid in developing management strategies for these species.

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Introduction

Successful wildlife management and conservation require a foundational understanding of mechanisms influencing wildlife populations, including population regulation (Turchin 2001). Ecologists have attempted to understand the mechanisms limiting populations for decades (Krebs 1995). Regulatory processes in populations involve a negative feedback mechanism, where demographic rates decrease as population size increases, and the opposite is also true (Rodenhouse et al. 1997). The most commonly observed regulatory process controlling population dynamics is density dependence (Lack 1966, Sinclair 1989, Turchin 1995, Newton 1998, Sibly et al. 2005). Density dependence occurs when the density of individuals affects the growth rate of the population through birth, death, and movement rates (Krebs 1995, Hixon and Johnson 2009).

Density dependence has been studied in wildlife for decades but can be challenging to detect or quantify (McCullough 1990, Stewart et al. 2005). Some argue that density independent processes such as weather and climate are also capable of regulating the population, obscuring density-dependent effects from detection (Andrewartha and Birch 1954, Turchin 1995, Ergon et al. 2011). When density dependence is detected, identifying the mechanisms can be an even more challenging task (Fretwell and Lucas 1969). Previous studies have identified two potential primary mechanisms for density-dependent population regulation (Ferrer et al. 2006, Nevoux et al. 2011). The first hypothesized mechanism is that density dependence is driven by habitat and breeding site selection, and available habitat is heterogeneous in terms of quality (Rodenhouse et al. 1997, Ferrer et al. 2006). Higher quality habitat sites are associated with higher vital rates, including survival and reproduction (Rodenhouse et al. 1997). Therefore, as population size increases past what optimal sites can support, suboptimal sites become occupied out of necessity and result in reduced vital rates. When this happens, per capita growth rates can decrease, regulating the population (Andrewartha and Birch 1954). The second hypothesized mechanism focuses on individual behavior (Ferrer et al. 2006). Increased intraspecific aggression, competition, and interference due to high population densities can decrease vital rates across the entire population, resulting in decreased population growth rates (Lack 1966, Fretwell and Lucas 1969, Sinclair 1989, Turchin 1995, Ferrer et al. 2006, Nevoux et al. 2011).

Density dependence has been studied in a range of taxa. Most density dependence studies focus on plants, invertebrates, and marine fish and conclude competition for resources is often the primary mechanism (Lizaso et al. 2000, Forbes et al. 2001, Wright 2002, Brook and Bradshaw 2006). When investigating density dependence in mammals, studies frequently focus on ungulates (Bonenfant et al. 2009**,** Bowyer et al. 2014), such as red deer (*Cervus elaphus*; e.g., Clutton-Brock et al. 1987, Mysterud et al. 2001), white-tailed deer (*Odocoileus virginianus*; e.g., Keyser et al. 2005) and elk (*Cervus canadensis*; e.g., Stewart et al. 2005). Results from these ungulate studies suggest physical condition, fecundity, and survival can all reflect density-dependent processes (Clutton-Brock et al. 1985, 1987; Singer et al. 1997; Taper and Gogan 2002; Festa-Bianchet et al. 2003; Keyser et al. 2005; Stewart et al. 2005; Bowyer et al. 2014). Alternatively, studies have found demographic parameters, such as neonatal survival, can also be density independent (Clutton-Brock and Coulson 2002, Bonenfant et al. 2009). To a lesser extent, studies have investigated the effects of density dependence in small mammals. Saitoh et al. (1999) found a lagged time response in density dependent effects in multiple mice and vole species. Delayed density dependence takes place when a change in demographic rates, such as decreased birth rates or survival, undergo a lagged time response, delaying the effects of density dependence (Ergon et al. 2011). A study examining arctic ground squirrel populations found density-dependent factors work to regulate the population concurrently (Karels and Boonstra 2000).

While understanding overall abundance and survival in response to density dependence is important for management and conservation, other population parameters should be considered to assess a population. Contingent on the life history characteristics of a species, specific age classes or life stages may drive population demographics. For instance, Vonesh and De la Cruz (2002) demonstrate when survival of tadpoles is density-dependent, reduced egg survival may not necessarily yield fewer emerging into frogs. Rather, an increase in tadpole densities can increase larval competition, resulting in the same number of adult frogs emerging as if there was a lower tadpole density, regulating the following stage’s population. Therefore, density dependence within susceptible age classes or life stages may have stronger consequences for population dynamics (Altwegg 2003). Lack (1966) predicted an increase in density leads to a per capita decrease in the fecundity of a population. For example, Rödel et al. (2004) found population density during reproduction was one of the main factors explaining variation in fecundity in European rabbits (*Oryctolagus cuniculus*). Additionally, hatching success of green turtles (*Chelonia mydas*) and olive ridley sea turtles (*Lepidochelys olivacea*) is affected by nest density (Bustard and Tognetti 1969, Cornelius et al. 1991, Honarvar et al. 2008). These studies and others reflect efforts to rectify the large knowledge gaps in understanding how vital rates may drive density dependence. By investigating multiple vital rates and density dependence, a more comprehensive understanding of population regulation can be reached, leading to more informed management and conservation decisions.

Effects of Density Dependence on Avian Populations

The few studies that have investigated density-dependent effects on avian species primarily focus on survival and population growth of waterfowl (e.g., Vickery and Nudds 1984; Saether et al. 2008; Gunnarsson et al. 2013) and seabirds (e.g., Grünbaum and Veit 2003; Hario and Rintala 2006; Ashbrook et al. 2010). The association between reproductive rates and density dependence is seldom studied, likely because avian species range along a slow to fast continuum in terms of breeding activity (Sæther and Bakke 2000). Short-lived avian species breed and grow quickly (e.g., sparrows; *Passeridae*), resulting in many offspring with a lower probability of survival. While long-lived species breed and grow slowly (e.g., parrots; *Psittacoidea*), resulting in fewer offspring that have a higher probability of survival (Haukioja and Hakala 1979). Shorter-lived species may breed multiple times a year and the number of offspring throughout the season reflects the frequency of breeding attempts in addition to the clutch size. While the number of breeding attempts is limited by resource availability (Nagy and Holmes 2005), Ricklefs (2000) suggests that these avian life history characteristics operate over evolutionary responses to density dependence. For example, Cooper et al. (2009) observed eastern kingbird (*Tyrannus tyrannus*) age of first reproduction increased as population density increased.

Many avian species are of conservation concern. Specifically, in North America, songbirds have shown long-term population declines due, in part, to habitat disturbance and fragmentation (Knick et al. 2003, Brennan and Kuvlesky 2005, NABCI 2014). Breeding density may have important density-dependent influences on populations over time. Thus, knowledge of demographic parameters driving population status and the mechanisms affecting these parameters can lead to efficient management strategies. By gaining an understanding of the factors influencing breeding parameters, population status can be assessed over shorter time scales rather than waiting until the population fluctuates to a noticeable low level years later.

However, some patterns in populations detected only over longer time scales. Because of this, it is important to still consider long-term assessments of a population depending on management goals.

The Importance of Avian Species and Breeding Demographics in Sagebrush Steppe Ecosystems

I examined two ways in which nest density, a less often measured metric due to difficulty, affects songbird populations (Bock and Jones 2004). First, I investigated whether density dependence regulates songbird populations by identifying the impacts of nest density on nest survival. By understanding this relationship, possible nesting density dependence could have been detected. Second, I determined the relationship between nest density and adult density within songbird populations. By looking at the relationship between these two parameters, I was able to determine if monitoring adult density is sufficient in assessing population fluctuations.

To fulfill these two objectives, I studied multiple breeding songbird species in a sagebrush steppe ecosystem. This ecosystem has faced considerable decline with > 50 percent of sagebrush steppe altered or removed for human use (Bock et al. 1993, Krannitz and Rohner 2000, Anderson and Inouye 2001, Ruehmann et al. 2011, Pyke et al. 2015). Sagebrush steppe is characterized as a mix of grasslands and sagebrush (*Artemisia* spp.) in the western United States with hot, dry summers and cold, moist winters (Pyke et al. 2015). The loss of sagebrush steppe is predominantly the result of human-caused landscape changes, such as the spread of invasive species, conversion to croplands, and domestic livestock grazing (Bock et al. 1993, Krannitz and Rohner 2000, Anderson and Inouye 2001, Knick et al. 2003).

Bradford et al. (1998) stated that songbirds in sagebrush steppe ecosystems have the qualities required of indicator species, making them a useful tool in assessing the status of sagebrush steppe systems. Qualities of indicator species or guilds include quick responses to environmental stressors, a wide population range across varying intensities of environmental stressors, and the ability for cost-effective monitoring (Carignan and Villard 2002). Songbirds have been used to assess ecosystem health of sagebrush, forests, grasslands, wetlands, and riparian systems (Morrison 1986, Bradford et al. 1998, Hausner et al. 2003). Furthermore, songbird populations are ecologically important within the sagebrush steppe ecosystem as they are predators, pollinators, and seed dispersers (Murphy and Romanuk 2012). As songbirds are suitable indicator species, management and conservation of sagebrush steppe songbird species can benefit additional native species, such as greater sage-grouse (*Centrocercus urophasianus*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), pygmy rabbits (*Brachylagus idahoensis*), and sagebrush lizard *(Sceloporus graciosus*; Anderson and Inouye 2001, Davies et al. 2011).

Avian species associated with arid landscapes, such as sagebrush steppe, have had population declines for over 40 years (NABCI 2014). Sagebrush-nesting species have had strong population declines and are of high conservation concern (Paige and Ritter 1999, Knick et al. 2003, Ruehmann et al. 2011). Many sagebrush steppe songbird species have a high reliance on the sagebrush and grassland vegetation, two important components of sagebrush steppe ecosystems (Rich et al. 2004, Pyke et al. 2015). These declines in songbird populations have been associated with significant loss through the conversion of sagebrush steppe habitat and associated vegetation to cropland or other means (Paige and Ritter 1999, Knick et al. 2003, NABCI 2014).

The Relationship between Nest Density and Success of Nesting Attempts

In order for density dependence to be present, a resource needs to be limited due to the number of individuals exploiting that resource. Resource limitation has ecological consequences varying from individual performance up to community composition and structure (Wiens 1984, Begon et al. 1996, Pöysä and Pöysä 2002). This limitation results in intraspecific competition (Rodenhouse et al. 2003). For example, food supply may be limited, resulting in competition for adequate energetics for breeding. Measuring competition directly can be difficult, but there are proxy metrics for varying taxa. For instance, breeding site (e.g., dens, nests, egg masses) density, can act as a proxy for competition as breeding sites for some species are a limited resource required for successful reproduction (Pöysä and Pöysä 2002, Jones et al. 2014).

For avian species, reproductive success is usually accessed by examing nest survival, the probability of at least one nestling reaching the fledging stage and leaving the nest (Mayfield 1975, Flaspohler et al. 2001, Pidgeon et al. 2003). For songbirds, higher quality nest sites can help offspring avoid predation and nest failure during the developmental process while being close enough to adequate foraging sites that adults can rear nestlings successfully to fledge. Therefore, nest survival can be density-dependent because suitable nest sites regulate the rate of nest survival (Both et al. 2000, Dunn et al. 2015). When breeding adult songbirds require more high-quality nest sites than available in a heterogeneous habitat, those with nest sites in higher quality areas could have correspondingly higher vital rates (Rodenhouse et al. 1997). Therefore, at high population density, high-quality nest sites are obtained by a portion of the population, resulting in some individuals occupying suboptimal nest sites. These suboptimal nests may experience higher predation risks. Alternatively, individual behavior, such as competition and negative conspecific interactions, may cause a decrease in vital rates across all nest sites, as described by Lack (1966) and Fretwell and Lucas (1970). As breeding adults spend more energy competing for resources, nests and offspring become more energetically expensive, lowering rates of nest success in relation to nest densities.

For many songbird species, nest predation is the dominant factor influencing nest survival (Martin 1988, 1993; Heske et al. 2001). This is especially the case for ground or low shrub nesting birds, such as sagebrush steppe songbirds (Nolan 1963, Ricklefs 1969, Knapton 1979, Vickery et al. 1992, Bock et al. 1993, Fondell and Ball 2004). Predation in most ecosystems is often a mechanism regulating populations. Therefore, predation of ground and low shrub nesting songbirds is likely also a population regulating mechanism. To help avoid predation, adults select nesting sites with adequate surrounding vegetation to help conceal nests (Clark and Nudds 1991, Heske et al. 2001).

I tested whether density dependence was present in sagebrush steppe songbird populations by investigating if nest density affects nest survival. I hypothesized that nest survival was density-dependent, leading to a negative impact of nest density on nest survival. By measuring multiple breeding parameters, ecological traps where nests are unlikely to succeed but cause populations to decrease (Bock and Jones 2004), can be quickly identified and remedied to benefit the population. Ecological traps manifest as a result of a discrepancy between cues and true quality of habitats, resulting in individuals selecting suboptimal habitats for survival and breeding (Dwernychuk and Boag 1972, Gates and Gysel 1978, Kokko and Sutherland 2001).

Patterns between Adults and Nest Densities

There have been multiple studies on songbirds in sagebrush steppe ecosystems with most focusing on the density of songbirds in the area of interest (e.g., Knight et al. 2016; Duchardt et al. 2018). However, adult populations are directly driven by reproductive success of individuals in the population, especially in short lived species, such as songbirds (Martin 1993, Sæther and Bakke 2000, Nagy et al. 2005). Therefore, understanding the reproductive output of songbird populations, including nest site densities, are crucial to understanding the status of a songbird population.

Obtaining information on nest density can be very time intensive, making it a challenging metric to measure (Péron et al. 2014). Thus, nest density is rarely measured relative to adult abundance, and population assessments are based solely on adult density. As a result, there is an assumption in the scientific community that nest density follows similar patterns as adult density, and therefore will provide the same information on a population (Horne 1983; Bock and Jones 2004; Skagen and Yackel Adams 2011). Van Horne (1983) and Pulliam and Danielson (1991) determined that an area with numerous adults did not always reflect breeding efforts because more adults than nest sites were observed to be present on the landscape.

Effective monitoring and management of any species are crucial, but in order to successfully understand the state of a population, multiple aspects of the population must be considered. In this case, by not considering nest density and primarily focusing on adult density, the existence of non-breeders or late migrants may fail to be acknowledged (Dickie et al. 2014). In essence, it is possible to predict a higher population level in subsequent years due to assumptions that every individual is attempting to breed. Also, assuming every individual is breeding can mask habitat issues, such as ecological traps and sinks that may be taking place.

I tested the assumption that adult density is reflective of nest density by investigating the relationship between sagebrush steppe songbird adult and nest site density. I hypothesized that adult density drives nest density, leading to a positive relationship between the two parameters. If adult density and nest density are positively related, adult estimates may be sufficient in monitoring the status of the population for management purposes. If there is no relationship between the two parameters, another factor or factors may be affecting songbird breeding activity. Thus, it would be important to monitor both nest and adult densities to assess the population.

In this thesis, I examine the relationships between nest density, nest survival, and adult density to gain a better understanding of population dynamics. First, I evaluate the effects of nest density on nest success to detect possible density dependence. Secondly, I examine the direct link between adult and nest density, verifying or disputing assumptions of adult density reflecting breeding densities of songbird populations. With this greater understanding of sagebrush steppe songbird adults, nest density, and nest success, managers and biologists can efficiently evaluate songbird populations by deciding whether multiple parameters should be measured or if adult density is a beneficial monitoring proxy for population status. If adult density is the only parameter measured, it is important for both managers and researchers to understand the possible limitations in only considering this population parameter.

Methods

Study Area

The study area encompassed 89,000 ha of sagebrush (*Artemisia sp.*) steppe in Golden Valley and Musselshell counties, near Roundup, Montana (Figure 1). I located sampling sites on both private and public lands grazed by domestic livestock, primarily cattle (*Bos taurus*). The US Department of Interior Bureau of Land Management (BLM) manages the public land, which is leased to private landowners for grazing. The dominant shrubs in this landscape are Wyoming big sagebrush (*Artemisia tridentate* spp. *wyomingensis*) and silver sagebrush (*Artemisia cana*). Dominant grasses include needle-and-thread grass (*Hesperostipa comata*) and western wheatgrass (*Pascopyrum smithii*). Non-native plants such as cheatgrass (*Bromus tectorum*) and crested wheatgrass (*Agropyron cristatum*) are also present throughout the study area. Additionally, there are isolated patches of ponderosa pines (*Pinus ponderosa*) and riparian areas. Average annual precipitation for the area is roughly 360 mm (National Climatic Data Center 2018, Smith et al. 2018).

A portion of the study area implemented a conservation grazing regime. In 2010, the US Department of Agriculture - Natural Resources Conservation Service (NRCS) introduced the Sage Grouse Initiative (SGI) to conserve greater sage grouse (*Centrocercus urophasianus*) and sagebrush steppe habitat. The conservation effort is based on rest-rotation and deferred grazing strategies in the area, to create and maintain sustainable rangeland that supports both wildlife and domestic livestock (Golding and Dreitz 2017, Smith et al. 2018). In general, rest-rotation grazing includes moving livestock through different paddocks or pastures for shorter grazing periods, varying the annual timing of grazing in each pasture over the years (Hormay 1970, Smith et al. 2018) and giving vegetation an opportunity to recover and reproduce. The SGI grazing regime follows rest-rotation and deferment grazing strategies while creating customized and ranch-specific grazing strategies. Grazing is limited to >45 days of use in any pasture with varying rest and deferment schedules. Approximately 20% of the enrolled ranch is rested over three years of SGI enrollment (Smith et al. 2018). Sample sites that were not enrolled in SGI consisted of a variety of other grazing regimes, with the most common strategy being season-long grazing.

Season-long grazing involves the presence of livestock in an area throughout the growing season over multiple years (Holechek et al. 1999, Briske et al. 2008).

Plot Selection and Size

Each sample site, hereafter referred to as a plot, was as an independent sampling unit for nest and adult songbird surveys. A total of 80 plots used for this study were randomly selected within two grazing regimes following Golding and Dreitz (2017). Forty plots were randomly selected plots enrolled in SGI rest-rotational grazing. The remaining 40 plots were randomly selected plots in pastures not enrolled in SGI grazing. I considered all plots not enrolled in SGI rest-rotational grazing to be classified as "Non-SGI".

Plots were 500 x 500 m (25 ha) following studies conducted by Tipton et al. (2008, 2009) and Golding and Dreitz (2017). Plots overlapping county roads were excluded, as well as plots that were not primarily dominated (≥70%) by grasses or sagebrush in order to maximize our efforts in sampling songbirds associated with each vegetation type. When a plot was excluded, another random plot was selected in order to maintain 40 plots on both pastures with SGI enrollment and pastures that were not enrolled in SGI. Plot sampling for adults and nests did not take place more than once every three days, in order to minimize disturbance.

Songbird Species

The sagebrush steppe system supports a large and diverse avian community of migratory songbirds that are grassland and sagebrush specialists, as well as many generalists. Information from prior efforts in my study area suggests a total of 103 different avian species (Dreitz et al. 2015). In order to focus my efforts, I concentrated on one species from each of the following functional groups: sagebrush obligate (Brewer's sparrow; *Spizella breweri*), grassland obligate

(McCown’s longspur; *Rhynchophanes mccownii*), and generalist (Vesper sparrows; *Pooecetes gramineus*).

The most abundant sagebrush obligate in the study area is Brewer’s sparrows (*Spizella breweri;* Rich 1980, Golding and Dreitz 2016). Brewer’s sparrows require sagebrush dominated landscapes for both nesting and foraging during the breeding season (Rich 1980, Rotenberry and Wiens 1989). This species tends to prefer areas with denser and larger sagebrush shrubs for nesting (Petersen and Best 1985). Brewer’s sparrows also nest later in the breeding season than most other songbird species, usually around late May or early June, in order to take advantage of the warmer weather associated with early summer (Rich 1980).

Grassland obligates such as McCown’s longspurs (*Rhynchophanes mccownii*), chestnut-collared longspurs (*Calcarius ornatus*), and horned larks (*Eremophila alpestris*) are prominent in grass heavy areas (With 1994, Golding and Dreitz 2016). I focused on McCown’s longspurs as my focal grassland obligate. McCown’s longspurs are known to form loose colonies during the breeding season (Mickey 1943). Nests are placed in depressions of bare ground in disturbed areas near patches of grass or forb vegetation in heavily grass dominated areas of the sagebrush steppe system (Mickey 1943, With 1994). McCown’s longspurs are the earliest of the three species to begin nesting, typically laying eggs by early May (With 2010).

Vesper sparrows (*Pooecetes gramineus*) are one of the most prominent generalist songbirds in the study area that exploit both shrub and grassland areas for nesting and foraging activities (Jones and Cornely 2002). Vesper sparrows represented my focal generalist species on the landscape. While vesper sparrows use both grassland and sagebrush heavy areas for nesting, they do require a nesting site that is well-concealed by vegetation to avoid predation (Harrison et al. 2010). Vesper sparrows are also one of the earlier migrants to arrive and begin nesting, beginning in late April or early May (Jones and Cornely 2002).

Field Methods

Locating and Monitoring Nests

Nest Sites—I surveyed sampling plots for nests based on distance sampling field protocols to estimate nest site density at the plot level. For each sampling plot, I established multiple 500 m long transects in which the distance from the transect to a nest allows for an estimate of detection probability (Buckland et al. 2001). These transect lines were dispersed every 100 m across the plot and shifted east 25 m on consecutive sampling visits. This resulted in four or five 500 m long transects for a nest search on the sampling plot. I recorded the distance from the transect line to a detected nest for distance analysis. I also recorded observed details about the nest, including whether the nest was active, if an adult flushed, and how many eggs or nestlings were present in the nest. If I checked the nest three times without any flush or change in contents in the nest, I considered it inactive.

Nest searches took place between May 1 and July 15 to observe the maximum number of nests during the 2016-2018 breeding seasons for our target species. For each sampling plot, I conducted one to four nest searches each breeding season, depending on conditions and logistical constraints. Plots were sampled between one and four separate times, dependent on the availability of time each season. I did not conduct nest searches during precipitation or when air temperatures were extremely high (>90 ^{O}F) or low (<40 ^{O}F), when flushing the adult may have affected nest survival.

The field methods for performing the nest searches depended on if grass or sagebrush shrubs were the dominant type of vegetation on the plot. Nest surveys on sagebrush dominated plots were conducted by two observers walking ~10 m apart with wooden dowels tapping the tops of the shrubs to flush nesting birds (Ruehmann et al. 2011). In grass dominated plots, two observers held a 10 m long chain that brushed the ground to flush ground nesting adults (Higgins et al. 1969, Martin and Geupel 1993, Winter et al. 2003). In mixed plots, we used a combination of both methods.

Nest Survival—I monitored nests located using distance sampling field methods and opportunistically (e.g., when performing adult surveys or monitoring the status of other nests) in sampling plots for nest survival. When I located a nest, and on subsequent visits, I recorded the species, nesting stage, presence of nest parasites, and the number of eggs or nestlings. I also took a photo for stage confirmation, aging nestlings, and determining nest fate. Additionally, I noted nest tending adult behavioral observations. I monitored nests approximately every three days, weather permitting; until there was either evidence of failure or success. A nest was considered "successful" if at least one nestling fledged (Mayfield 1975, Flaspohler et al. 2001, Pidgeon et al. 2003). Fledging occurred when the nest cup was empty near the expected fledging date without signs of disturbance, a provisioning adult was seen close by, or fecal matter was found around the edge of the nest cup (Martin and Geupel 1993, Williams and Wood 2002). I determined the cause of nest failure (e.g., predation, abandonment, weather) based on any evidence around the nest. I inferred depredation from indicators such as the disappearance of eggs and nestlings prior to the anticipated fledge date, disturbed nest cup or surroundings, or broken eggs (Martin and Geupel 1993, Pietz and Granfors 2000, Shitikov et al. 2018). If the fate could not be determined, the nest fate was marked "unknown".

Adult Surveys

Avian abundance transects were conducted using a dependent double-observer (DDO) method developed by Nichols et al. (2000). This method is commonly used in open space environments such as grasslands and prairies (Tipton et al. 2008, 2009). Golding and Dreitz (2016) showed an increase in detection rates and precision with the DDO method in comparison to point counts in sagebrush steppe.

Two observers, a primary and secondary observer, were present for each sampling period for the DDO method. The primary observer started at the southeast corner walking north 375 m, roughly 10 m ahead of the secondary observer along the transect line, communicating any visual observations of avian individuals (Figure 2). The secondary observer recorded the primary observer's observations and recorded their observations of birds the primary observer did not observe. The observers continued along the transect, turning to walk west 250 m and then south 375 m until they reached the southern edge of the plot. By walking this transect line, observers were never more than 125 m from the edge of the plot. This distance was chosen because ≥95% of visual songbird detections occur within 125 m of the observer (Ralph et al. 1995). Auditory observations required visual confirmation by at least one observer. Each observer alternated between being primary and secondary observer during subsequent surveys. Adult surveys took place between sunrise (approximately 530 MST) and 1100 MST. Surveys were not conducted during high amounts of precipitation or when winds were stronger than 15 mph. Surveys were no longer conducted once juvenile songbirds began to resemble adults.

Covariates Measured

Multiple biotic and abiotic covariates were considered for models estimating nest density, nest survival, and adult density (Table 1). Nest density was analyzed in groups based on year or SGI enrollment. Julian date was considered a covariate for nest survival as the target songbird species nest during a small period of time during the spring and summer (Rich 1980, Jones and Cornely 2002, With 2010). I expected decreased survival for early and late initiated nests and therefore included an additional quadratic term for Julian date. When assigning Julian dates, I used January 1 as the initial start date, giving it a Julian date value of 1. In order to investigate the effects of nest density on nest survival, estimated intra- and interspecific nest densities were included as covariates. Furthermore, the distance (m) to the nearest intra- and interspecific neighboring nest were also included as covariates as an additional measurement proxy to nest density. SGI enrollment was considered binary in nest survival models, where plots were either categorized as being enrolled in SGI implemented grazing strategies for any portion of time between 2011 and 2018, or never having been enrolled. Because range quality varies across private and public lands, a range quality covariate encompassing regional and local productivity metrics was included in the adult density model (Golding 2015). Rangeland productivity is defined by the NRCS as the amount of vegetation expected to grow annually in a well managed area and is measured in pounds per acre of dry vegetation (NRCS 2011). Annual variation was considered for all three types of model estimates, as annual variation in observers, precipitation, and temperature varied by year.

Analytical Methods

Nest Density

I calculated nest density for each of the three years per plot using line transect samples and distance sampling techniques (Buckland et al. 2001, Thomas et al. 2010) in program R (ver.

3.5.1; R Core team 2016) using the package ‘Distance’ (ver. 0.9.7; Miller 2017). Distance sampling along a line transect generates a detection function in order to understand how the probability of detection varies with distance from the transect line (Buckland et al. 2001; Figure 3). Nest density estimates using distance sampling required at least two nests to be found at the plot for the sampling year and for the majority of nest searches to result in one new nest being found. Therefore, the number of plots used in each species nest density estimates varied from year to year but remained similar in value. Due to the limited number of McCown’s longspur nests detected, only Brewer’s sparrow and vesper sparrow nest densities were estimated (Table 2).

Three key function models were considered for this analysis (half-normal, uniform, and hazard-rate), as well as adjustment terms (cosine, simple polynomial and Hermite polynomial) in order to improve model fit (Buckland et al. 2001). Model selection was determined across the key function models using Akaike Information Criterion (AIC; Akaike 1973; Akaike 1987, Table 3), as well as visual inspection of data.

Nest Survival

I analyzed nest survival using a logistic exposure method (Shaffer 2004, Shaffer and Thompson 2007). This is a generalized linear model, where daily nest survival is modeled as a logistic function of any explanatory variables over exposure days (i.e., time between nest checks). This approach was developed with the awareness that nests are often found based on adult birds flushing from the nest and are therefore less likely to locate nests that fail early in the nesting stage (Shaffer 2004). As a result, nests survival parameters can be positively biased (Klett and Johnson 1982, Rotella et al. 2004, Lusk and Koper 2013). The logistic exposure method avoids this bias by only accounting for periods where the nest is monitored, not the period prior to detection (Rotella et al. 2004). Model assumptions for logistic exposure include homogeneity in daily survival rates, correctly determined fate outcomes, no effect of nest discovery or monitoring, and nest fates are independent (Rotella et al. 2004). This method is often used across avian taxa, including waterfowl (e.g., Koper and Schmiegelow 2007; Pieron and Rohwer 2010), shorebirds (e.g., Kwon et al. 2018), and songbirds (e.g., Winter et al. 2005; Benson et al. 2010; Roach et al. 2018).

Two explanatory covariates were included in the “null” model: stage and year. Multiple studies have shown that daily survival rates (DSR) vary between different stages of the nesting process (i.e., incubation and nestling stage; Mayfield 1961, 1975, Johnson 1979, Klett and Johnson 1982). Year was included as an effect on DSR because abiotic factors such as precipitation, temperature, and observers vary greatly between years (Major 1990, Morrison and Bolger 2002, Weatherhead 2005). A random effect for site was included in all models to account for any unexplained variation (Rotella et al. 2004, Shaffer 2004). Additional covariates for nest survival included SGI enrollment, Julian date, conspecific nest density, nest density of all three focal species, distance (m) to nearest conspecific nest, and distance (m) to nearest nest of all three species. Interactions between covariates were also considered. DSR estimates were calculated in program R (ver. 3.5.1; R Core team 2016) using the ‘lme4’ package (ver. 1.1-21; Bates et al. 2015). Top models were selected using Akaike Information Criterion (AIC; Akaike 1973; Akaike 1987).

Adult Density Estimates

Adult density was estimated using a multispecies dependent double observer abundance model (MDAM) developed by Golding et al. (2017). This model is an extension of a multispecies N-mixture model and the first to incorporate data collected from the DDO method.

The MDAM uses a hierarchical framework and accounts for biological (density) and observational (detection) processes (Golding et al. 2017). Species density was modeled as a function of a site-specific intercept and a fixed-effect for SGI enrollment. Fixed-effects for both rangeland quality and year were also included, as well as a random effect to account for site-level variations not captured by covariates. Detection was modeled as a function of observer, species, and year (Golding et al. 2017).

Analyzing Adult Density and Nest Density

From plot-level estimates, I compared adult densities to nest densities in plots by considering adult pairs on a plot. I note that there is no documented sex-ratio data for the three study species; therefore, a 1:1 sex ratio was assumed. Brewer's sparrow, McCown's longspur, and vesper sparrow are all observed to be socially monogamous (Berger 1968, Rotenberry et al. 1999, Meddle et al. 2003). Assuming each pair is breeding, adult pair density and nest density should have a 1:1 relationship. I tested for a linear relationship between adult density and nest density using Pearson's correlation test. I compared these two metrics for each species, across all plots. I also compared these metrics within year and SGI enrollment for each species. These correlations were used to better understand the relationship between adult density and nest density at the plot-level.

Results

Of the plots sampled, 32 were grass dominated (>60% grass), 34 were sagebrush dominated (>60% sagebrush), and 14 were a mix of equal grass and sagebrush. A total of 438 nest searches took place from 2016-2018 (Table 4). The frequency of nest searches averaged 146 nest searches per year, or 1.825 nest searches per plot per year, but varied each year due to logistical constraints. The number of nests monitored each year totaled 125 in 2016, 143 in 2017, and 111 in 2018 (Table 5). This averaged to 1.56 nests per plot in 2016, 1.79 nests per plot in 2017, and 1.39 nests per plot in 2018. Nests across all species and years were monitored over 5,124 exposure days, with 1,783 monitor visits. Average clutch size for Brewer's sparrow, McCown's longspur, and vesper sparrow were 3.33, 3.49, and 3.61 respectively. Covariate values are listed in Table 6.

Nest Survival and Covariates

A total of 379 nests from 2016 to 2018 were used to estimate nest survival. The number of nests for Brewer's sparrow was 128 nests, McCown's longspur was 84 nests, and vesper sparrow was 167 nests (Table 2 and 7). Of the 379 nests, 186 (0.49) nests survived to fledge at least one offspring. Predation was the most common reason for nest failure with evidence of predation observed in 147 of 198 (0.74) nests. Observed nest parasitism by brown-headed cowbirds (*Molothrus ater*) was uncommon. Only 5 Brewer's sparrow nests and 12 vesper sparrow nests were observed to be parasitized, in which one Brewer's and two vesper sparrow nests successfully fledged at least one non-parasite offspring.

Nest survival was highest for all three species and across all three years during the nestling stage (Figures 4a and 4b). Some variation among years was also observed within each species. In total, 205 nests did not have any detected conspecific nests found within the plot and were the only nests of that species on the plot. A total of 65 nests did not have any recorded nests found nearby, as they were the only nests found on the plot. A year effect for daily survival rates (DSR) of nests was present for all three species (Figure 5).

Brewer’s sparrow nest survival was explained by Julian date. There was a negative effect of Julian date on nest survival for Brewer’s sparrows (Figure 6, Tables 9 and 10). McCown’s longspur nest survival was explained by the distance to the next nearest nest of any species. The distance to the next nearest nest had a negative effect on McCown’s longspur (Figure 7, Table 8 and 9). Vesper sparrow nest survival was explained by the distance to the next nearest nest of any species as well as SGI enrollment of the pasture the nest was in (Tables 9 and 10, Figures 8 and 9). The distance to the next nearest nest had a negative effect on Vesper sparrow nest success, while SGI enrollment had a positive effect(Figures 8 and 9, Tables 8 and 9).

Nest Density

Nearly 33% (124 of 379) of nests for target species were found during nest transect surveys (using either the dowel or drag chain) and found on plots at high enough frequencies (at least two nests) to estimate nest density using distance sampling (Table 2). In total, 21 plots across all three years had sufficient nest samples sizes to estimate nest density for Brewer’s sparrows and 24 plots across all years had high enough nest sample sizes to estimate nest density for vesper sparrows (Table 10). The raw number of nests found varied between species, years, and SGI enrollment (Table 10). Nests were comprised of 59 Brewer’s sparrow nests and 65 vesper sparrow nests. McCown’s longspur nests were not included due to insufficient sample size. The average detection probability using distance sampling from 2016 – 2018 for Brewer’s sparrow nests was 0.375 (SE: ±0.066), and for vesper sparrow nests was 0.384 (SE: ±0.057; Figure 10; Table 11).

A total of 36.08 (95% CI: 17.77, 88.18) of Brewer’s sparrow nests were estimated to be present across the six sampled sites in 2016. The average number of nests estimated per sampled plot was 6.01 (4.20, 7.82). A total of 46.97 (27.38, 116.41) Brewer’s sparrow nests were estimated across ten plots in 2017. On average, 4.20 (3.96, 5.43) nests were estimated per plot in 2018 for Brewer's sparrows. The estimated total of nests found across five sampled plots in 2018 was 24.50 (11.61, 82.63), averaging 4.90 (3.62, 6.18) nests per sampled plot. No plots were used in 2016 that were enrolled in SGI due to too few Brewer's sparrow nests. Average nest densities between SGI and Non-SGI plots in 2017 were not statistically different as confidence intervals overlapped between estimates, but were statistically different in 2018, with more nests being estimated per plot on Non-SGI enrolled plots.

In 2016, vesper sparrow nests were found at high enough frequencies on seven plots. A total of 38.97 (25.04, 52.13) nests were estimated to be present across those seven plots, averaging 5.57 (4.20, 6.93) nests per plot. In 2017, vesper sparrow nests were found at nine plots, totaling an estimated 47.95 (35.43, 66.32). This resulted in an estimated average of 5.99 (5.78, 6.21) nests per plot. Lastly, in 2018, vesper sparrow nests were found on nine plots with an estimated total of 64.09 (45.31, 90.76) nests. On average, across the nine sites, 7.12 (6.75, 7.49) nests per plot were estimated. Nest density estimates across Non-SGI and SGI plots were not significantly different for any of the three sample years (Table 11).

Adult Density

Adult DDO surveys were conducted three times per plot for each of the three seasons, totaling 240 sampling occasions per year (Table 4). In 2018, nine of 80 plots were sampled two times due to weather conditions and logistical constraints. Over the three study years, a total of 15,263 observations were made on McCown's (*n* = 6,107 observations), vesper sparrows (*n* = 5,037 observations) and Brewer's sparrows (*n* = 4,119 observations). Average detection of Brewer's sparrows across all years and observers was 0.48 (0.42, 0.54; Figure 11). McCown's longspurs were detected at the highest rate, averaging 0.61 (0.43, 0.69) across all years and observers. Vesper sparrows were detected at an average rate of 0.47 (0.41, 0.54) across all years and observers.

Adult density estimates per plot fluctuated each year for each of the three species (Figure 12 and Table 12). For all three species, estimated densities per plot were highest in 2016, while in 2018 each species had their lowest estimated densities per plot. Brewer's sparrow adult densities in 2016 were 16.11 (13.19, 20.05) adults per plot. McCown's longspurs estimated density in 2016 per plot was 23.19 (21.45, 25.80). Vesper sparrow adult density was estimated to was 17.04 (14.17, 20.76) per plot in 2016. Brewer's sparrow and vesper sparrow adult density estimates were similar between Non-SGI and SGI plots in all three years, with 95% confidence intervals overlapping (Table 14 and Figures 13a and 13c). In all three years, McCown's longspur adult density estimates were higher in SGI enrolled plots in comparison to plots not enrolled in SGI (Table 14 and Figure 13b).

Adult Density and Nest Density

In addition to understanding adult density in a population, understanding reproductive output, in this case, in the form of nest densities, is also important to evaluate the status of a population. Typically, it is assumed that all pairs of adults are breeding, which should result in a 1:1 relationship between the number of adult pairs and number of nests on the landscape (depicted by the dotted line in Figures 14a and 14b). Nest density estimates for each plot but one were lower than estimated adult pair density for Brewer's sparrows. The correlation value calculated from the Pearson's correlation test between the densities of Brewer's sparrow nests and adult pairs across all three years was -0.279, suggesting a very weak negative relationship. With a *P*-value of 0.186, this correlation is non-significant, suggesting no confidence in the relationship and that adult density and nest density are likely unrelated. As with Brewer's sparrows, nest density estimates in each plot except one were lower than estimated adult pair density for vesper sparrows. Vesper sparrow adult pair density and nest density across all three years showed no relationship through a calculated correlation value of 0.064 (*P* = 0.782). This relationship did not appear to change based on year or grazing enrollment.

When plot-level estimates of nest density and adult pair density were averaged across all plots, rather than at each plot level, the average estimated number of adult pairs of vesper sparrows was similar to the average estimated number of nests for all three years (Figure 15). Brewer's sparrow average estimates across all sampled plots for adult pairs were 1.5-2 times higher all three years than average estimated nest densities (Figure 16).

Discussion

Effects on Nest Survival

Daily nest survival models for the three species experienced differences in annual variation, likely due to environmental conditions between years. McCown's longspur and vesper sparrow both had higher nest survival probabilities in 2017, while that year showed the lowest nest survival probabilities for Brewer's sparrow. This suggests that these species require different environmental conditions, such as rainfall and temperature, that may vary annually. Rainfall totals for May 2017 were about 2.5 centimeters, while in 2016 and 2018 rainfall totals were 8.66 and 7.82 centimeters respectively (U.S.ClimateData 2018). It is possible that Brewer's sparrow nests benefit from increased rainfall, through vegetation growth or soil moisture, nests during the breeding season than vesper sparrow and McCown's longspur nests.

Nesting stage also showed a strong effect on daily nest survival for all three species. The nestling stage had the highest daily survival rate for all three species across all three years, followed by the laying stage and then incubation. No nests were found during the laying stage for McCown's longspur. Therefore, no daily survival rates were estimated for the laying stage of that species.

Estimated daily survival rates derived from the top nest survival model for Brewer's sparrows ranged from 0.41 to 0.96, and annual average daily survival estimates ranged from 0.55 to 0.88. DSR from 2017 were lower than estimates reported in the literature, which range from 0.75 to 0.98 (Rotenberry and Wiens 1989, Matthew Vander Haegen et al. 2002, Ruehmann et al. 2011), averaging a daily survival rate of 0.45 over the breeding season. Vesper sparrow estimated daily survival rates derived from the top nest survival model for this project ranged from 0.56 to 0.93, similar to other studies investigating nest survival for this species (Grant et al. 2006, Lusk and Koper 2013). McCown's longspur estimated daily survival rates derived from the top nest survival model ranged from 0.51 to 0.97. I found no studies reported estimated daily survival rates for McCown's longspur, studies on chestnut-collared longspur, a similar species, report similar daily survival estimates to our study (Davis 2005, Lusk and Koper 2013).

Brewer's sparrow nest success was best explained by Julian date. As Julian date increases, DSR for Brewer's sparrows decreased at varying levels, depending on the year, throughout the season. The Julian dates ranged from May 30 to July 1. Brewer's sparrows in Montana are known to nest later in the breeding season (Rich 1980). This is due to the fact that Brewer's sparrows arrive on their breeding regions later than other species and are often not sighted in Montana until mid to late May (eBird 2012).

Lower DSR as Julian date increases may suggest that Brewer's sparrow nests are predated at higher rates as the season continues. Increasing predation as the breeding season continues has been observed in multiple nest survival studies on numerous songbird species (Schaub et al. 1992, Grant et al. 2005, Peak 2007). Grant et al. (2005) suggest early nesting is an adaptation for some songbird species to avoid higher predation rates associated with later in the breeding season. Predator composition may also change throughout the breeding season, possibly explaining successful early nesting, as suggested by Peak (2007).

Precipitation may also explain annual variation in DSR of Brewer's sparrows as well as decreasing survival as Julian date increases. As 2017 had the lowest amount of rain in the months of May and June (U.S.ClimateData 2018) and also reflected the lowest Brewer's sparrow nest survival rates, higher amounts of precipitation may be beneficial to nest survival. There is decreased precipitation as the Julian date increases, which may be associated with nutritional needs of nestlings. As the landscape dries out, reducing insect biomass, nutritional needs for nestlings may be harder to meet (Rotenberry and Wiens 1989).

Additionally, my results suggest that daily nest survival rates of vesper sparrows were slightly higher on SGI enrolled sites compared to sites not enrolled in SGI. Confidence intervals did overlap for these estimates, suggesting a very slight or negligible difference in nest survival. The associated *p*-value of 0.6 for the SGI beta coefficient also suggests no significance. This may be due to range quality discrepancy between SGI enrolled sites than sites not enrolled in SGI, as suggested by Golding (2015). It is also possible that different environmental variables, such as differences in the predator community or insect biomass between the two grazing systems, may explain the slightly higher survival rates of vesper nests on SGI plots.

Evidence for Density Dependence in Nests

My prediction that nest survival would decrease as nest density increases through density dependence was not supported, as nest density was not present in any top models for nest success. Brewer's sparrow and vesper sparrow nest survival did not appear to be strongly predicted by nest density of conspecifics or nest density of all species. This indicates no detectable density-dependent effects in either breeding populations during sampling. Vesper sparrow nest survival was explained by the distance to the next nearest nest, however, which may show slight responses to nest density at a highly localized level.

My results suggest that vesper sparrow and McCown's longspur nest survival was negatively influenced by the distance to the nearest neighboring nest of any species, which may support positive density dependence. As the distance to the nearest neighboring nest increased, DSR decreased, suggesting that nests that are closer together have higher survival probabilities. This may suggest a strategy of reducing predation risk by increasing the number of other similar prey species nearby. McCown's longspurs are known to nest near one another and are gregarious nesters, which may suggest nesting near one another is beneficial to nest survival (Mickey 1943). Davis (2005) found songbirds in grassland systems displayed non-random nesting patterns. Aggregating nests can help breeding adults detect and defend against predators (Anderson and Hodum 1993, Oro 1996). With multiple adults of the same or similar species breeding near others, predators are more likely to be detected by at least one individual, and therefore, defense against predators can allow each individual to be less vigilant than if they were more solitary (Roberts 1995, Terhune and Brillant 1996). Additionally, nest synchrony can minimize predation risks for nests by narrowing the nesting and/or hatching period to a short period in time, such as 3-6 weeks in late spring (Emlen and Demong 1975, Robinson and Bider 1988). Together, these strategies can minimize the predation risk for individual nests, as predators will become satiated before a large proportion of the nests are predated (Nisbet 1975, Findlay and Cooke 1982, Hernández-Matías et al. 2003). This predator saturation reduces the probability of predation for each individual nest (Robinson and Bider 1988, Eckrich and Owens 1995, Spencer 2002, Doody et al. 2003).

The benefits of having neighboring nests may be outweighed by resource limitations and density dependence in some cases or trigger inverse density dependence, where survival increases with density. For example, Shitkov et al. (2018) demonstrated a positive relationship between DSR of booted warbler (*Iduna caligata*) and whinchat (*Saxicola rubetra*) and distance to the nearest neighboring nest of any species. Multiple studies have shown positive, negative, and neutral effects of closer neighboring nests and increased numbers of nests nearby (Bayne and Hobson 1997, Larivière et al. 1998, Hernández-Matías et al. 2003, Shitikov et al. 2018). This discrepancy may be due to variations in spatial scales, predator communities, life history characteristics, and habitat (Burger and Gochfeld 1991, Martin 1995, Brunton 1999, Gehring and Swihart 2003, Ackerman et al. 2004, Ringelman et al. 2012).

Nest Site Density

Nest site density for both Brewer’s sparrows and vesper sparrows did not vary across years and was similar between the two species, ranging from about four to eight nests per plot. Additionally, nest density did not vary between Non-SGI and SGI enrolled plots. This suggests that neither species is selecting either type of plot more strongly for nesting sites. Brewer’s sparrows are primarily sagebrush obligates, nesting in the sagebrush, off the ground and away from the grasses (Rich 1980, Rotenberry and Wiens 1989). Their lack of interaction with the ground and grasses during the nesting period may suggest why Brewer’s sparrow nest density is not affected by grazing regimes implemented on the plot, which primarily affect the grass and ground vegetation structure (Smith et al. 2018).

Vesper sparrows are considered generalists (Jones and Cornely 2002). It is possible that their nest densities did not vary across Non-SGI and SGI enrolled plots due to their ability to thrive in a variety of conditions (Jones and Cornely 2002, Begon et al. 2014). Vesper sparrow nests require some vegetation to conceal the nest from predators (Harrison et al. 2010). While nest survival did appear to be higher in SGI enrolled areas in comparison to Non-SGI areas, the variation was minimal, which suggests suitable nesting sites in both types of plots. A majority of vesper sparrow nests detected during 2016-2018 were situated at the base of sagebrush. Because of this, the nest is partial concealed by sagebrush rather than just perennial grasses. This may explain why nest density did not vary for vesper sparrows.

Adult Density

Average adult densities of Brewer's sparrows, vesper sparrows, and McCown's longspurs were similar to previous studies (Golding and Dreitz 2017). Average adult densities decreased as year increased for all three species, which may reflect species-wide declines in the region (NABCI 2014). The continual declines in these population trends are limited in scope when only looking at three years. These trends may also suggest an annual effect, such as precipitation which can be highly variable and directly influence vegetation structure (Lipsey and Naugle 2016) and the densities of songbirds. For example, monthly rainfall in April 2016 was about average (3.80 cm), whereas in 2017 April rainfall was 2.40 cm. In 2018, rainfall was 7.0 cm (U.S.ClimateData 2018).

Adult density for Brewer's sparrows and vesper sparrows did not vary between Non-SGI and SGI enrolled plots. Brewer's sparrows are sagebrush steppe obligates, depending on sagebrush shrubs both for foraging and nesting (Rich 1980, Rotenberry and Wiens 1989). This may explain why Brewer's sparrows do not show a response to different grazing regimes during the breeding season. Additionally, vesper sparrows are considered generalists that exploit a variety to habitat conditions (Jones and Cornely 2002). Additionally, vesper sparrows are considered generalists on the landscape. Generalists are known for being able to exploit a variety of habitat conditions (Jones and Cornely 2002), which may explain why vesper sparrows did not respond to grazing variations.

Adult density was consistently higher on SGI enrolled plots than Non-SGI plots for McCown's longspurs all three years. McCown's longspurs have been observed to form loose colonies (With 2010). Social benefits or conspecific attraction may explain the strong difference between densities on Non-SGI plots and SGI plot. Slight differences in vegetation have been observed between Non-SGI and SGI plots (Smith et al. 2018). Therefore, slightly higher senesced and live grass, as well as a modest increase in litter in SGI plots may suit McCown's longspur foraging or nesting requirements more than the Non-SGI plots. This may explain the dramatic increase in adult densities. Alternatively, there may be a different metric that has not been observed or measured that McCown's longspurs are cueing into on SGI enrolled plots.

Nest Density as it Relates to Adult Density

My hypothesis of a positive relationship between adult density and nest density at a plot level was not supported for either Brewer's sparrows or vesper sparrows. Van Horne (1983) suggested that adult densities may not indicate breeding densities and that proper habitat quality assessments should consider more than just adult densities in order to successfully manage a species. While some studies have investigated the relationship between adult density and nest survival, very few studies on songbirds have examined whether adult density is reflective of breeding densities (Van Horne 1983, Bock and Jones 2004, Winter et al. 2005). However, by understanding how adult density and breeding density are related, biologists and managers can forecast whether a population is fluctuating or stable years in advance. Nesting density, in addition to adult density and nest survival, should be considered when evaluating songbird species for management purposes.

There was some support for my hypothesis when considering the vesper sparrow adult density and nest density across plots, rather than plot-specific estimates. It is possible that vesper sparrows may be foraging in different sites than nests are detected in, but across the study area, the majority of pairs are breeding. Vesper sparrows have been known to have expanded territories and foraging areas in areas with lower insect and food abundance (Rodenhouse and Best 1983), which may explain why I observed no correlation in nest density and adult density at a plot level.

Brewer's sparrow pairs were estimated at higher densities than estimated nest densities at both a plot level and across the study area. This difference in densities suggests that not every adult Brewer's sparrow is initiating a nest in an attempt to breed. Reynolds (1981) observed that only 23% of Brewer's sparrow males initiated nests, while the remaining proportion of males were either unsuccessful in defending territories or relocated to a different location. Additionally, this may indicate that the population estimates may be inflated by migrants, suggesting a possible sink habitat.

The lack of relationship between nest density and adult density at a plot level did not differ across SGI enrolled lands in comparison to Non-SGI enrolled lands for either species.

This, as well as the fact that nest density, adult density, nest success, did not differ across the grazing regimes, indicates that these songbirds did not respond strongly to different grazing regimes. It is possible that grazing differences were not dramatic enough to see a change in Brewer's sparrow or vesper sparrow parameters. Additionally, the time scale analyzed was not long enough to detect strong responses. However, these species may also be assessing their nest sites and selecting habitat based on other factors.

Our work suggests that future studies focus on addressing knowledge gaps in the relationships between vital rates of sagebrush steppe songbirds. Sagebrush steppe habitat is the most altered habitat in North America, specifically through agricultural means such as croplands and livestock grazing (Bock et al. 1993, Krannitz and Rohner 2000, Anderson and Inouye 2001, Knick et al. 2003). By understanding how songbirds are responding to grazing pressures, managers can implement less impactful grazing strategies. Furthermore, by understanding how population parameters relate to each other, managers can tailor land management to improve or maintain overall breeding habitat for songbirds.

Management Implications

Successful management and conservation begin with a strong understanding of the community or population of focus. Therefore, evaluating the status of a population requires comprehension of what parameters are driving a population, rather than simply measuring adult density. Detecting possible population regulation mechanisms across demographic parameters can allow for more informed management decisions. For example, monitoring of vesper sparrow populations through adult density can be effective in sagebrush steppe areas, as nesting numbers are similar to adult pair densities. Brewer's sparrow adult density, in contrast, did not reflect nesting density in this sagebrush steppe habitat, indicating that the population may be sustained primarily through migrants or may even be declining due to a lack of nesting adults. By monitoring nesting parameters, such as the density of nests and nest success, biologists and managers may be able to forecast possible future declines in a population, allowing them to adjust management plans accordingly.

Grazing regimes in this study area did not elicit strong responses in any of the three species overall. McCown’s longspur adult density showed a stronger preference towards SGI enrolled pastures, vesper sparrow nest survival was slightly higher on SGI enrolled pastures, and Brewer’s sparrows did not show differences in any measured parameters in response to grazing. This suggests that conservation driven grazing regimes may not be a “one size fits all” conservation solution for all songbirds on the landscape. Rather, life history characteristics, such as what vegetation they depend on or social behavior, may drive their responses.

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Tables and Figures:

Figures

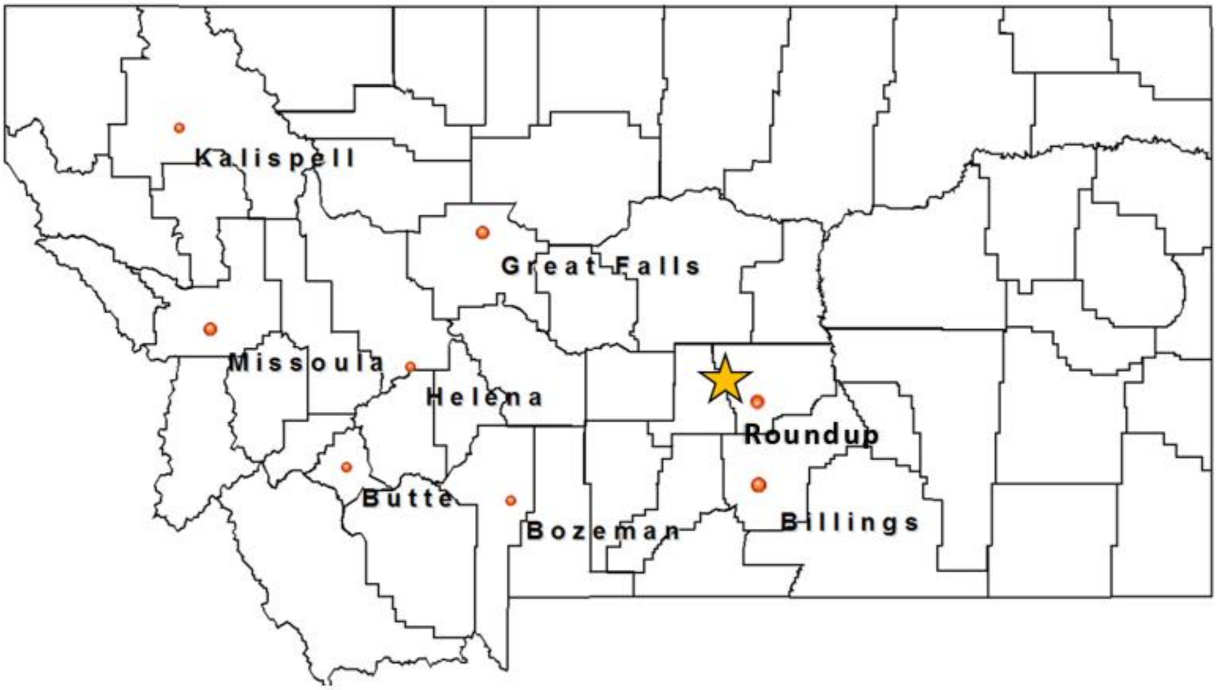

Figure 1. The study site (represented by the star) located in central Montana (MT) in Golden Valley and Musselshell counties near the town of Roundup, MT.

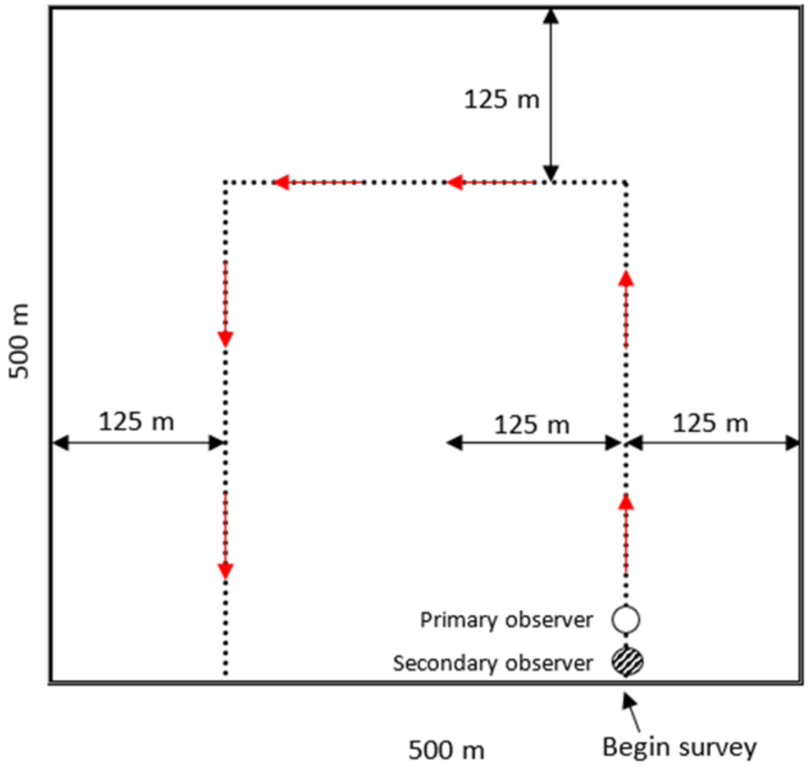

Figure 2. Schematic illustrating the dependent double-observer method used to estimate adult density. The primary (open circle) and secondary observer (dashed circle) walk along the transect (dotted line). Observers record observations up to 125 m on either side of the transect. All surveys start at the southeast corner of the sample plot. Red arrows indicate the direction of travel.

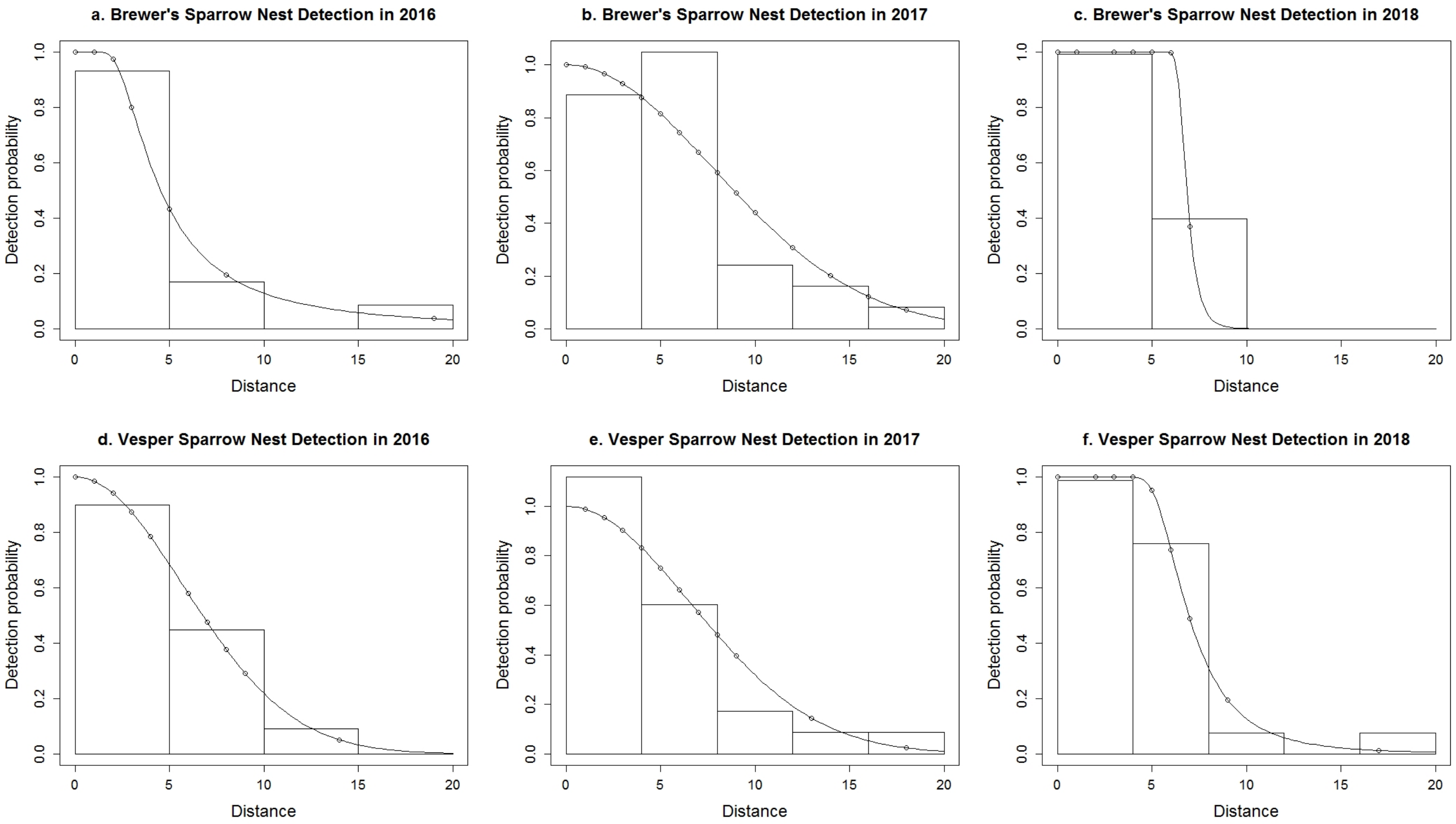

Figure 3. Detection functions of Brewer's sparrow and vesper sparrow nest densities based on distance sampling methods from 2016 - 2018 near Roundup, MT. Half-normal key functions were used for Brewer's sparrow nest density estimates in 2016 and 2018 and for vesper sparrow nest density in 2016 and 2017. Hazard rate key functions were used for Brewer's sparrow nest density estimates in 2017 and for vesper sparrow nest density estimates in 2018.

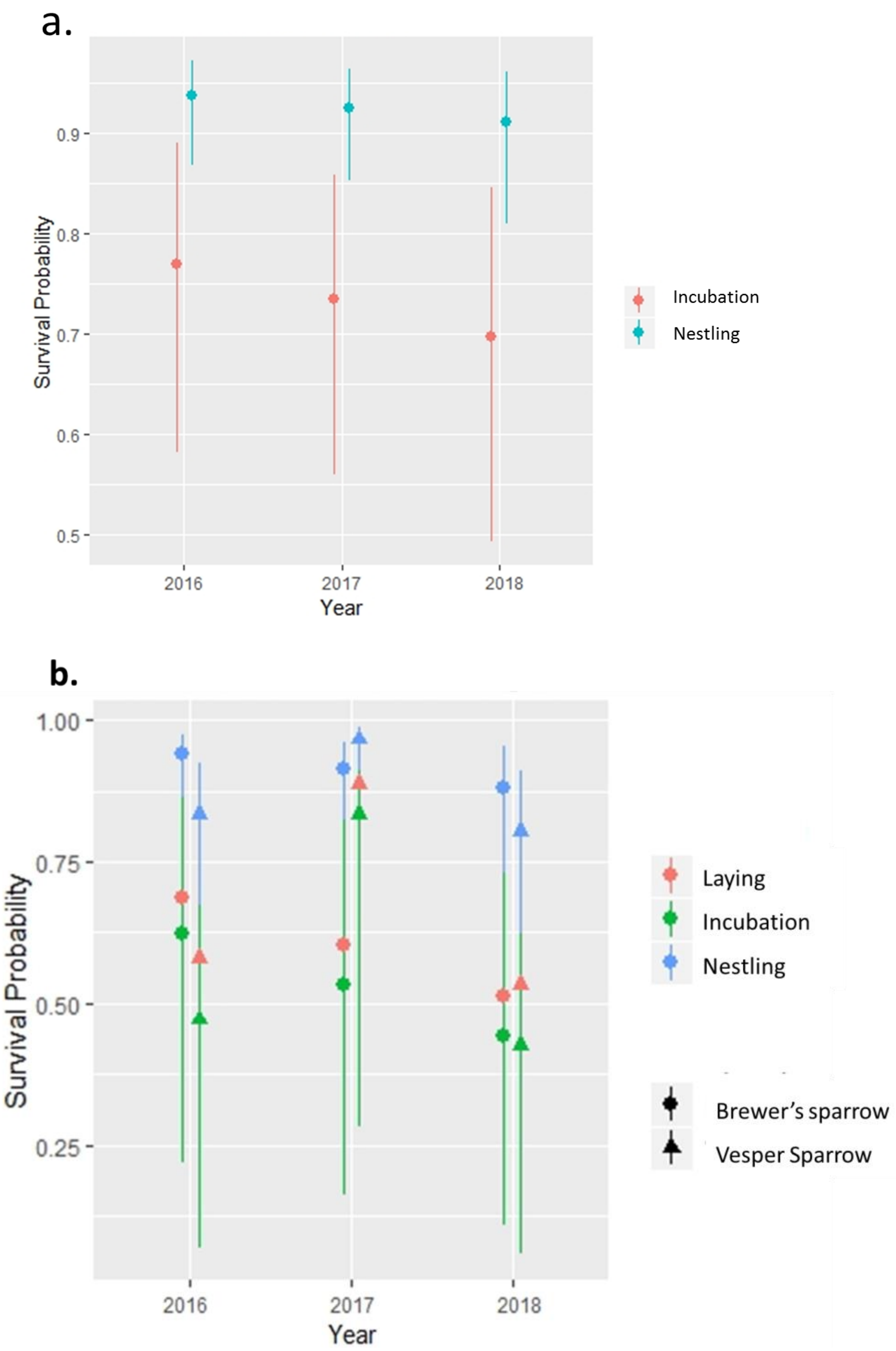

Figure 4. Nest survival probabilities for (a.) McCown’s longspur and (b) Brewer’s sparrow (BRSP) and vesper sparrow (VESP) with 95% confidence intervals estimated using logistic exposure method for samples near Roundup, MT based on year, species, and stage. McCown’s longspur nests were not observed during the laying stage; therefore laying stage survival could not be estimated.

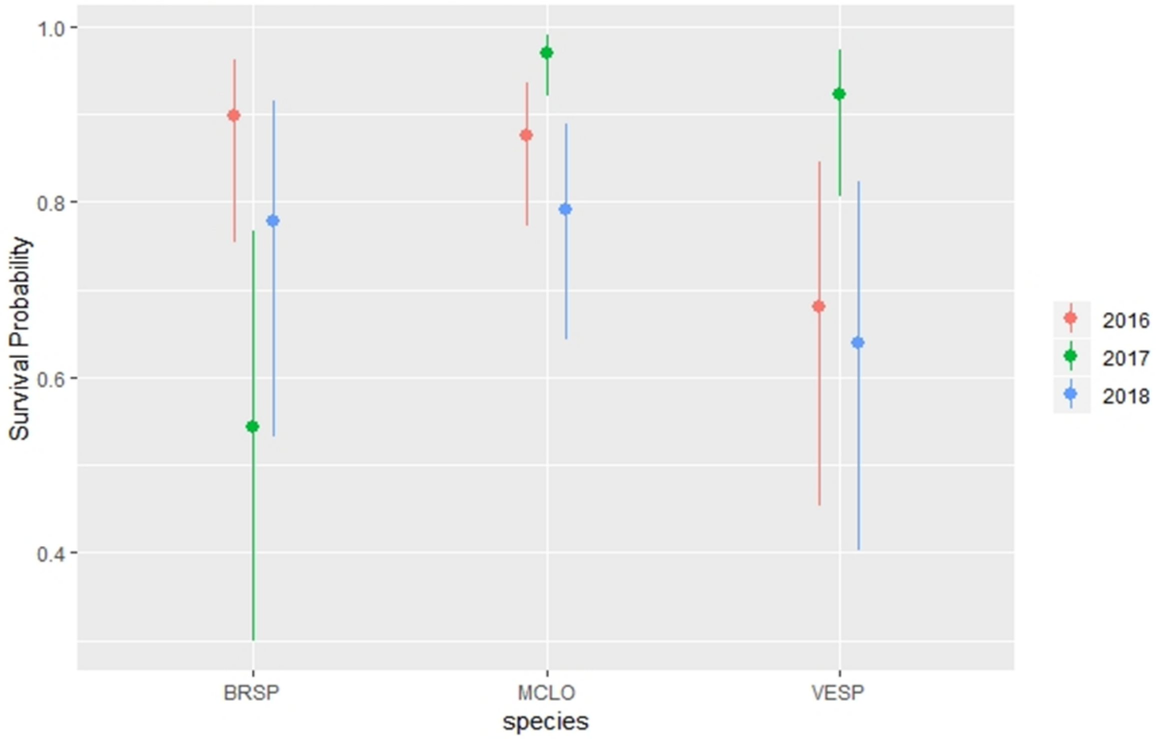

Figure 5. Average daily survival rate at the average mid-date through the breeding season for Brewer's sparrow (BRSP), McCown's longspur (MCLO), and vesper sparrow (VESP) with 95% confidence intervals.

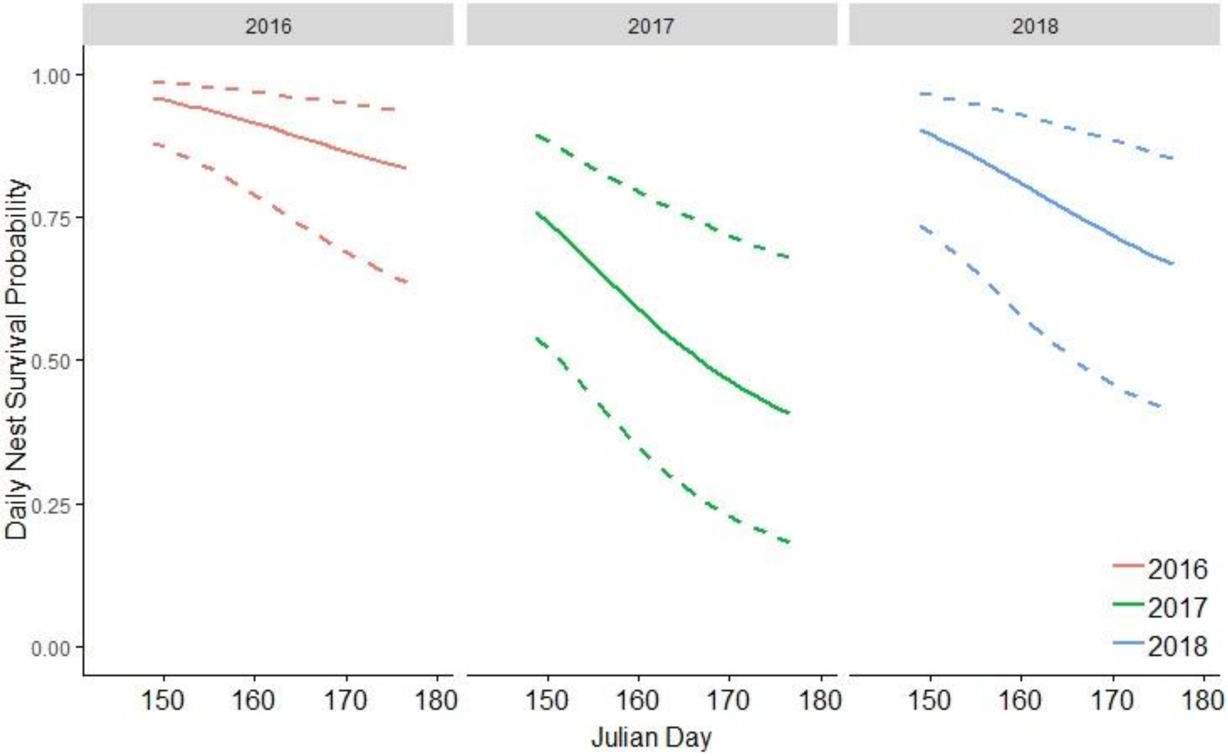

Figure 6. Daily nest survival probabilities with 95% confidence intervals for Brewer’s sparrow nests based on Julian date from 2016 - 2018.

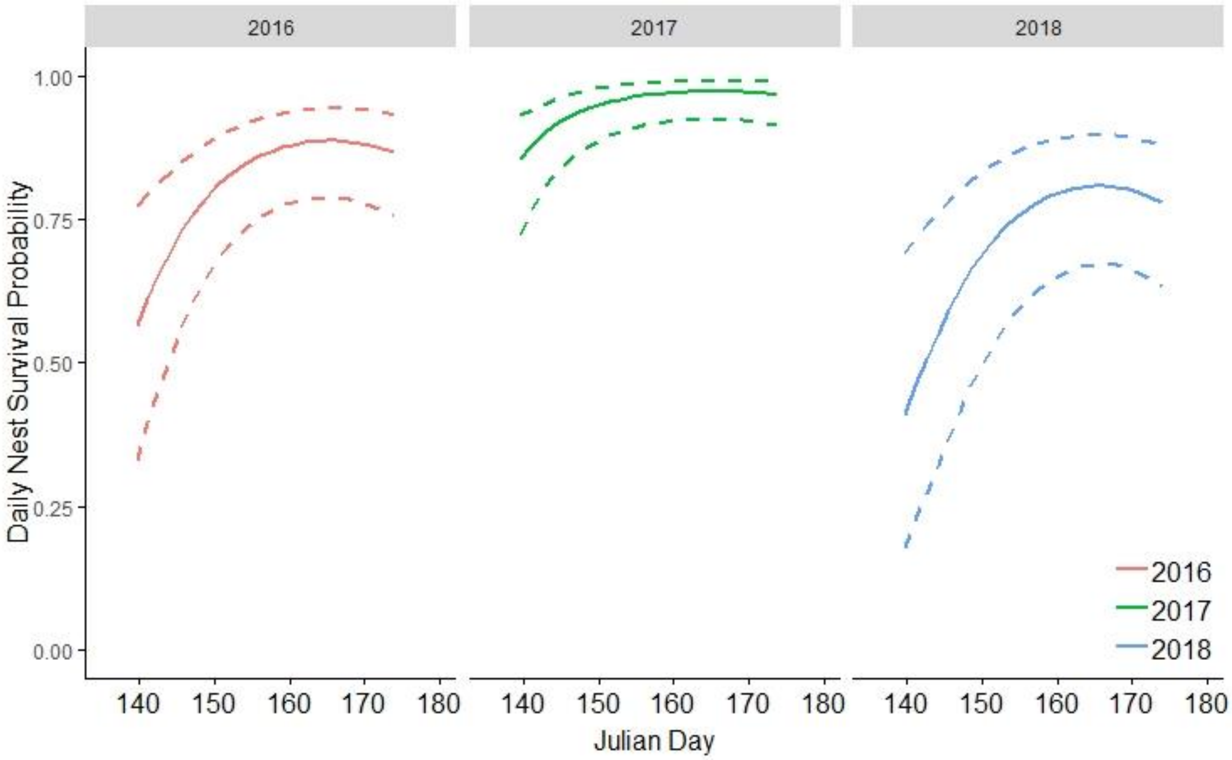

Figure 7. Daily nest survival probabilities with 95% confidence intervals for McCown's longspur nests based on Julian date from 2016 - 2018.

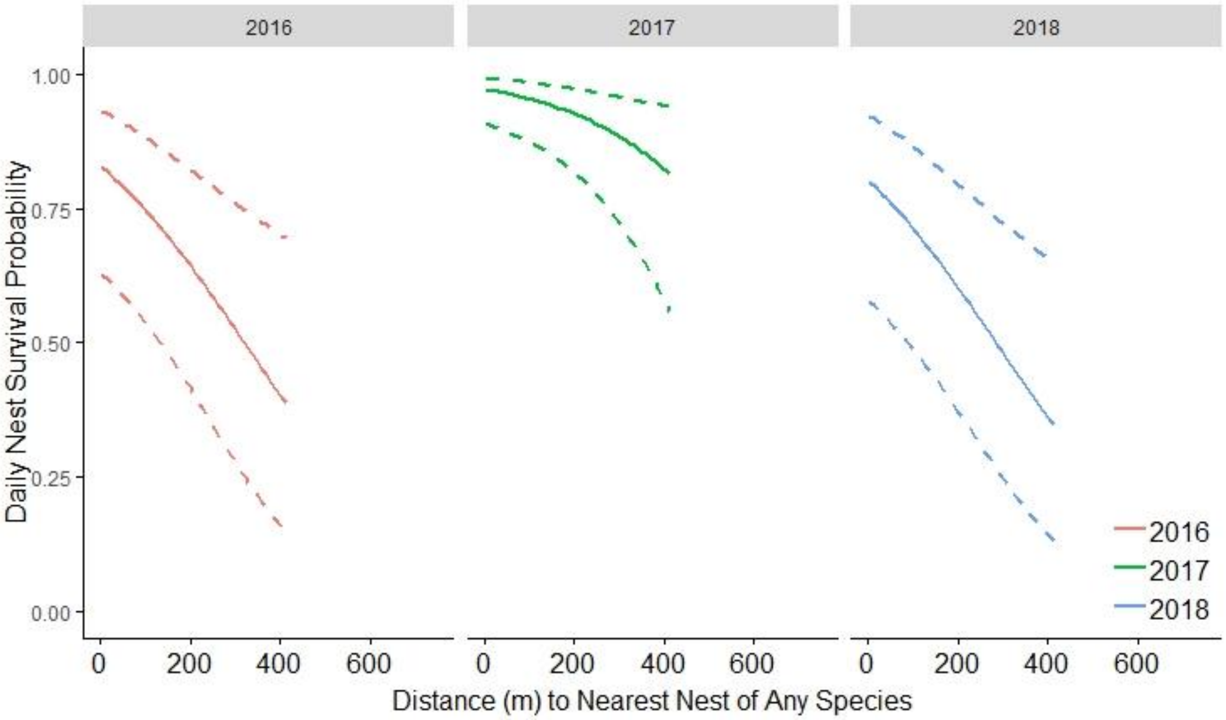

Figure 8. Daily nest survival probabilities with 95% confidence intervals for vesper sparrow nests as a function of distance to the nearest neighboring nest of any species from 2016 - 2018.

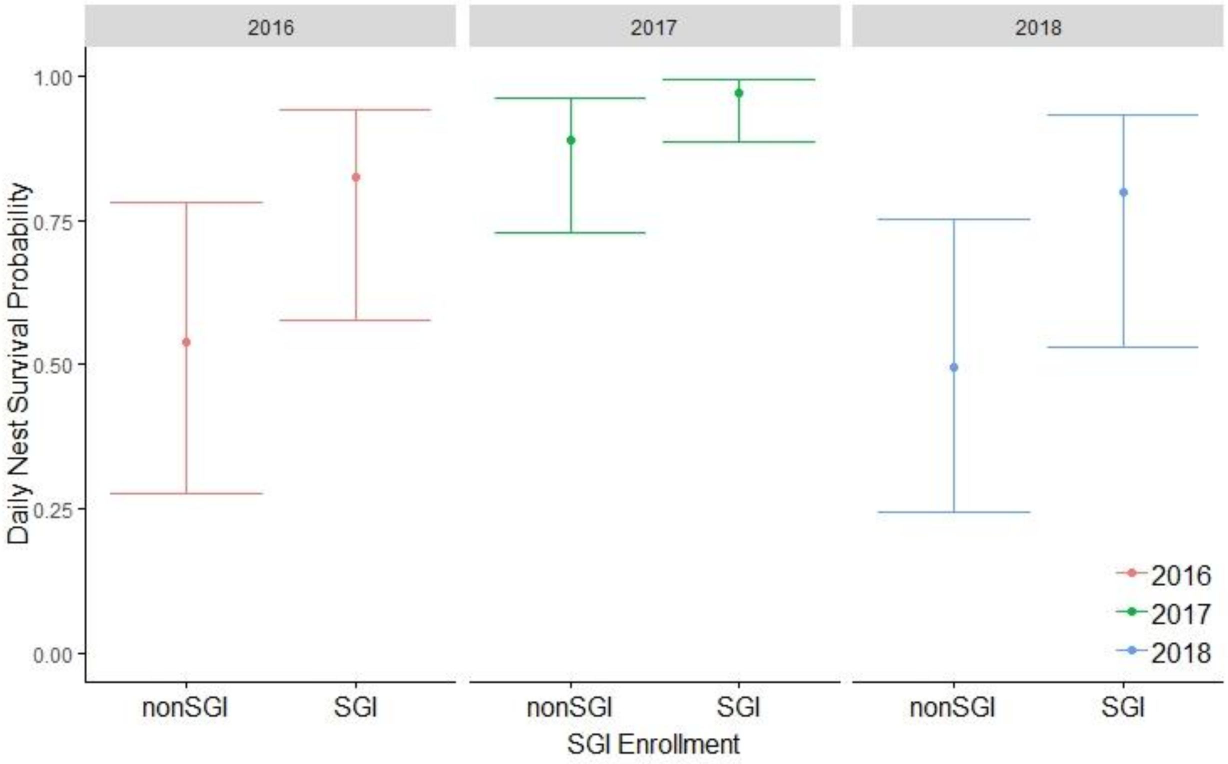

Figure 9. Daily nest survival probabilities with 95% confidence intervals for vesper sparrow nests on SGI enrolled lands or lands not enrolled in SGI (Non-SGI) from 2016 - 2018.

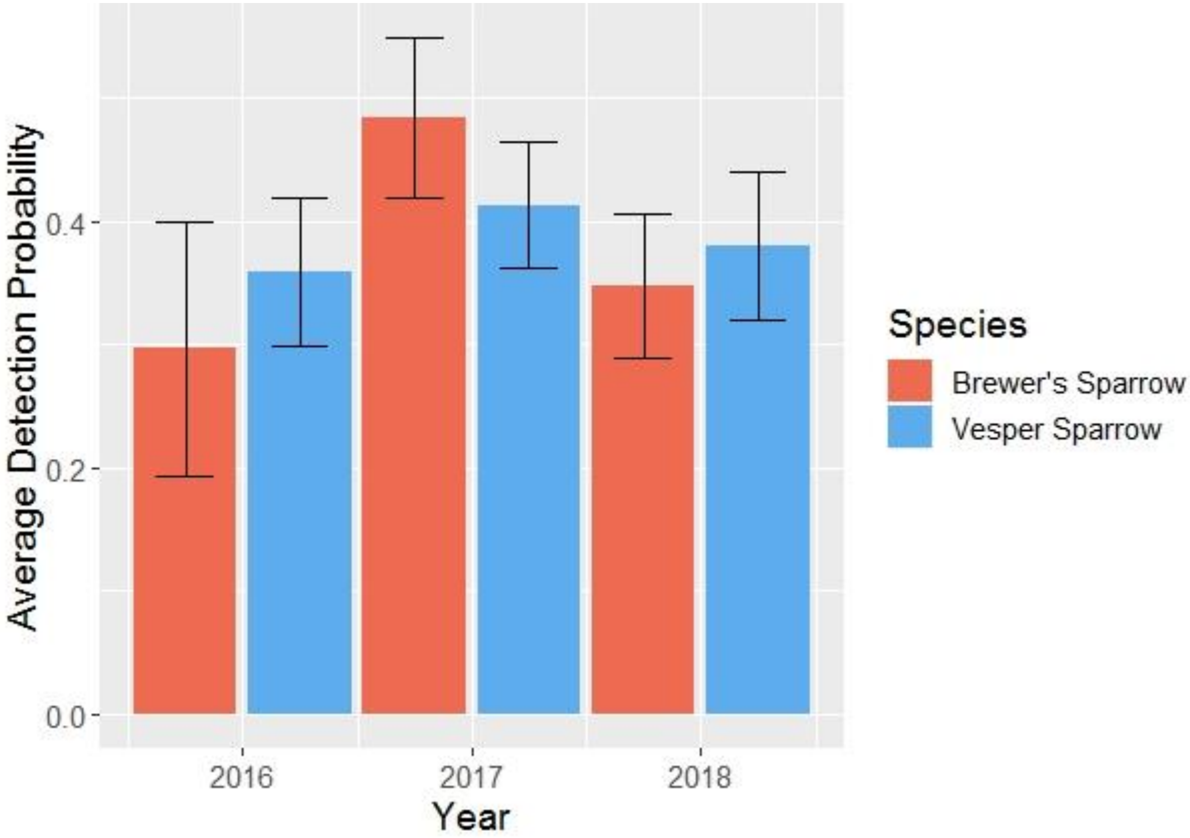

Figure 10. Estimates of average detection of nests using distance sampling with standard errors for Brewer's sparrow and vesper sparrow nests from 2016 – 2018.

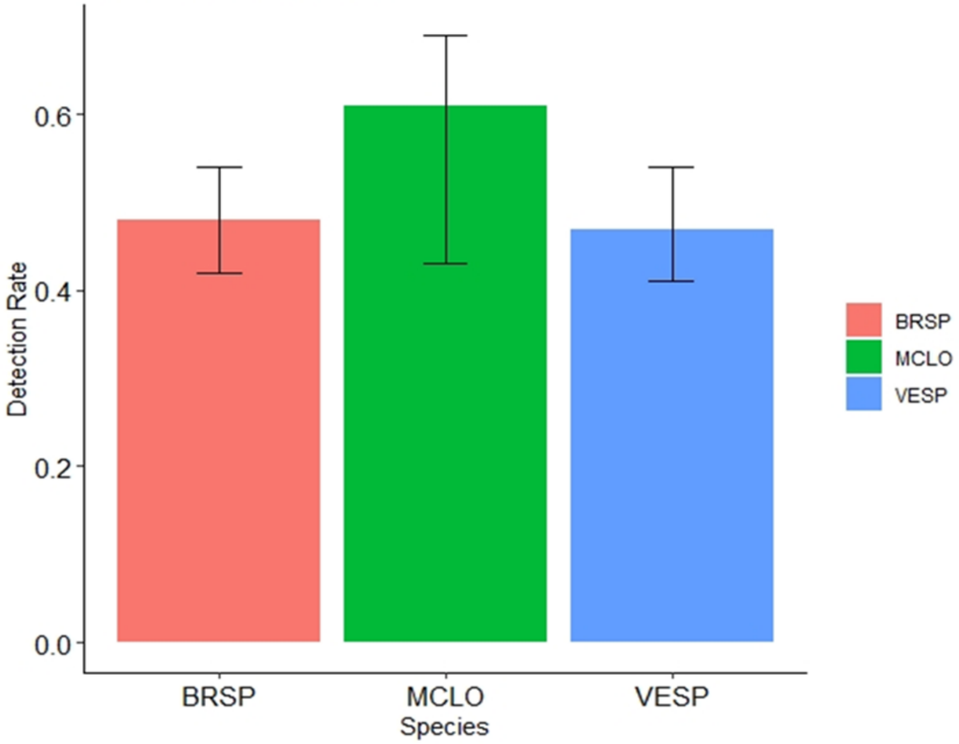

Figure 11. Estimates of average detection of adults with 95% confidence intervals per 25 ha sample plot for Brewer's sparrow (BRSP), McCown's longspur (MCLO), and vesper sparrow (VESP) observed during avian count transect surveys.

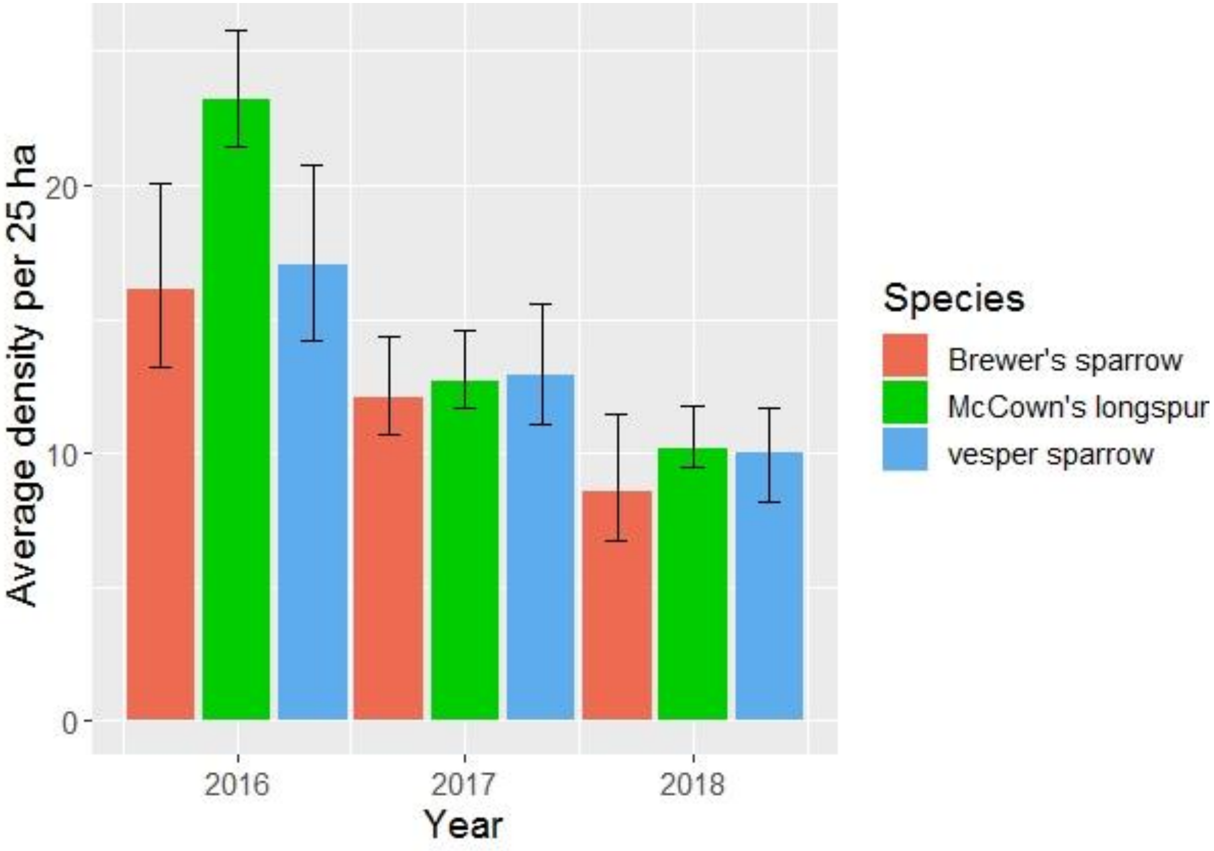

Figure 12. Estimates of detection of adults with 95% confidence intervals per 25 ha sample plot for Brewer’s sparrow, McCown’s longspur, and vesper sparrow observed during avian count transect surveys.

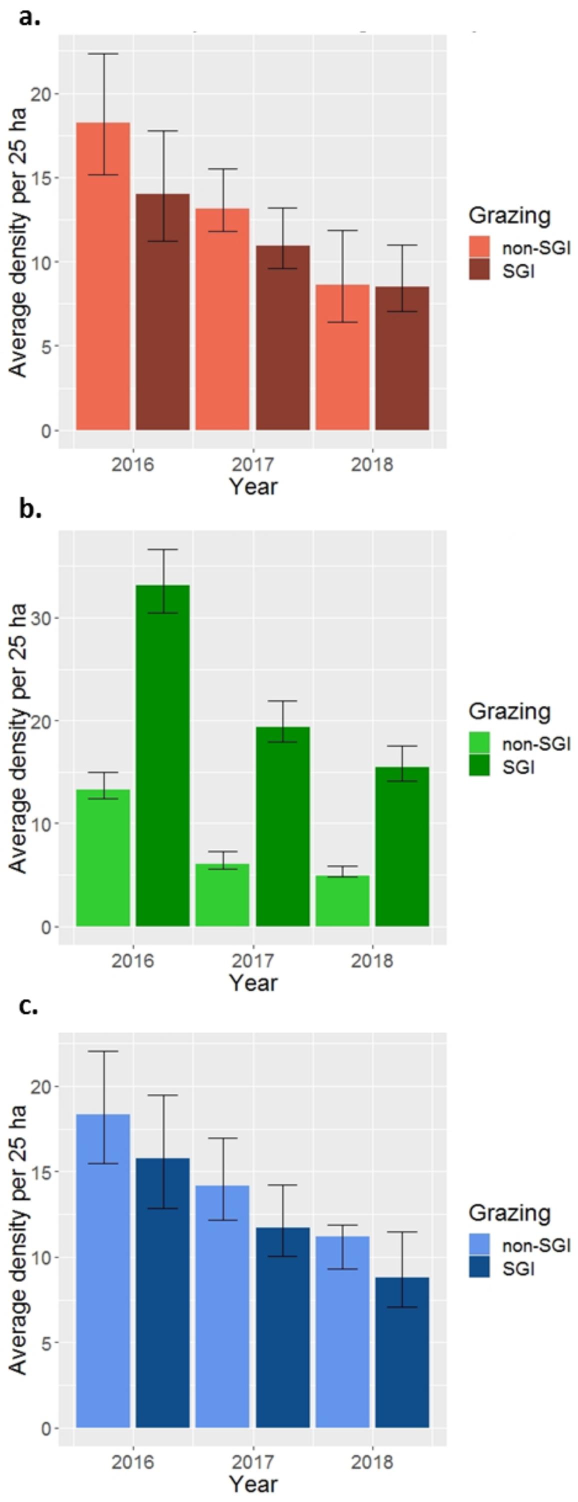

Figure 13. Average estimated adult abundance with 95% confidence intervals per 25 ha plot from 2016-2018 on Non-SGI and SGI plots for (a.) Brewer's sparrows, (b.) McCown's longspurs, and (c.) vesper sparrows.

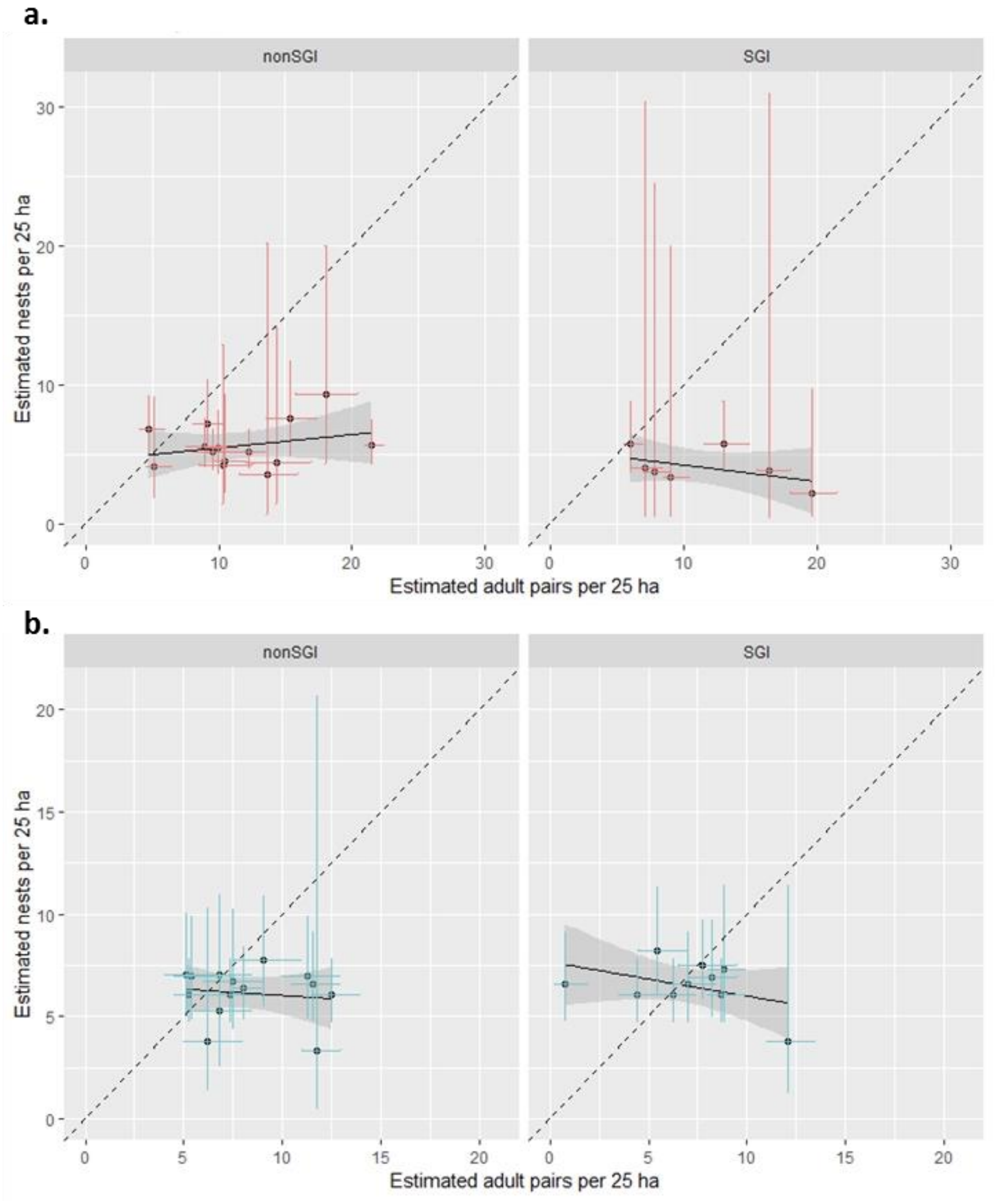

Figure 14. Plot-specific adult density and nest density estimates for (a.) Brewer's sparrows (red) and (b.) vesper sparrows (blue) across all three years (2016-2018). Colored lines show 95% confidence intervals. The black dotted line represents the expected 1:1 relationship between adult pairs and nests. The solid dark line represents the estimated linear relationship with 95% confidence intervals in gray.

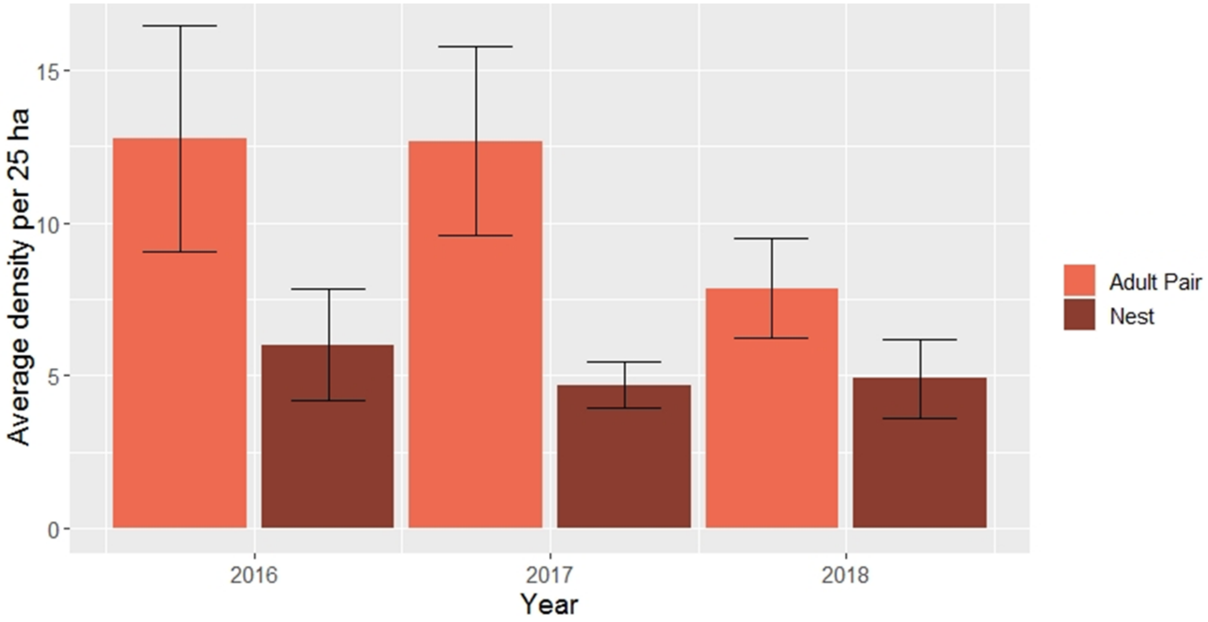

Figure 15. Average estimated adult pair density and nest density with 95% confidence intervals for vesper sparrows from 2016-2018

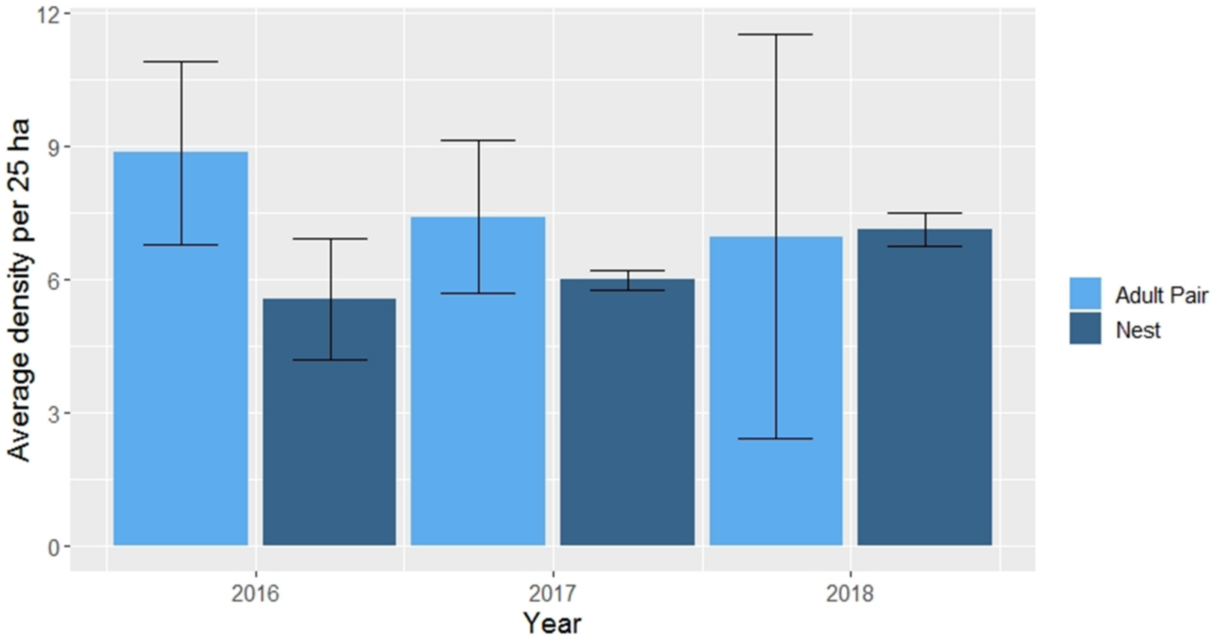

Figure 16. Average estimated adult pair density and nest density with 95% confidence intervals for Brewer's sparrows from 2016-2018.

Tables

Table 1. Covariates considered for nest density, nest survival, and adult density models.

Covariate	Nest Density	Nest Survival	Adult Density
Conspecific Nest Density		X	
Distance (m) to nearest nest		X	
Interspecific nest density		X	
Julian Date		X	
Nesting Stage	X	X	
Range quality			X
SGI Enrollment	X	X	
Year	X	X	X

Table 2. Nest sample sizes of nests used in nest density estimates and nest survival estimates.

Nest Sample Size		**Brewer's sparrow**	**McCown's longspur**	**Vesper sparrow**
Nest Density	**Total**	**59**	**0**	**65**
	2016	14	0	16
	2017	30	0	24
	2018	15	0	25
Nest Survival	**Total**	**128**	**84**	**167**
	2016	40	30	56
	2017	55	31	56
	2018	33	23	55

Table 3. Model selection tables for key functions used in distance sampling estimations. All years and species had a cosine adjustment term used.

Species and Year	**Key Function**	**AIC**	**Delta AIC**
Brewer’s sparrow 2016	Hazard-rate	73.1257	0
	Half-normal	73.5139	0.3881
	Uniform	74.1458	1.0201
Brewer’s sparrow 2017	Half-normal	166.553	0
	Uniform	165.883	0.5188
	Hazard-rate	166.402	0.6699
Brewer’s sparrow 2018	Hazard-rate	60.2456	0
	Half-normal	63.5967	3.3511
	Uniform	67.0603	6.8146
Vesper sparrow 2016	Half-normal	83.3177	0
	Uniform	81.0019	2.1181
	Hazard-rate	83.12	2.3158
Vesper sparrow 2017	Half-normal	127.373	0
	Hazard-rate	126.762	0.6115
	Uniform	166.402	0.7775
Vesper sparrow 2018	Hazard-rate	122.576	0
	Half-normal	124.058	1.4825
	Uniform	125.916	3.3396

Table 4. The number of adult surveys and nest searches conducted on 500 m X 500 m sample plots during 2016 – 2018.

Year	Sampling Occasion	Date	Transect Survey	Nest Search
2016	1	May 7-Jun 14	80	80
	2	May 22-Jul 1	80	66
	3	Jun 16-Jul 5	80	23
	4	Jun 23-Jul 8	-	19
	Total		**240**	**188**
2017	1	Apr 29- Jun 16	80	62
	2	May 11- Jul 5	80	43
	3	Jun 18- Jul 12	80	19
	4	Jun 24- Jul 12	-	6
	Total		**240**	**130**
2018	1	May 3- Jun 3	76	60
	2	May 24 - Jun 21	80	44
	3	Jun 21- Jul 8	75	15
	4	1-Jul	-	1
	Total		**231**	**120**
	Overall Total		**711**	**438**

Table 5. Number of Brewer's sparrow, vesper sparrow, and McCown's longspur nests detected during nest search efforts during 2016 – 2018 with apparent nest survival (# of nests with at least one fledgling / total) and calculated nest survival for the entire nesting period (Shaffer 2004).

Year	Common Name	Number of Nests	Apparent Nest Survival	Calculated Nest Survival
2016	Brewer's sparrow	40	0.675	0.1160
	McCown's longspur	29	0.482	0.0001
	Vesper sparrow	56	0.607	0.0065
	Total	125		
2017	Brewer's sparrow	55	0.691	0.0533
	McCown's longspur	32	0.719	0.5119
	Vesper sparrow	56	0.590	0.0057
	Total	143		
2018	Brewer's sparrow	32	0.625	0.0001
	McCown's longspur	25	0.680	0.1596
	Vesper sparrow	54	0.592	0.0001
	Total	111		
Total		379		

Table 6. Mean, minimums, and maximums of covariates measured for adult density, nest density, and nest survival models

Covariate	Mean	Minimum	Maximum
Julian Date	164	126	199
Date	13-Jun	6-May	19-Jul
Intra specific Nearest Neighbor Distance (m)	181.72	24.3	573.4
Interspecific Nearest Neighbor Distance (m)	148.4	4.2	553.1
Intraspecific Density (number of nests per 25 ha)	7.06	1.75	18.65
Interspecific Density (number of nests per 25 ha)	4.95	1.75	10.77
Rangeland Productivity (pounds per acre of dry vegetation)	1169.485	1121.38	1281.86

Table 7. Average daily survival rates (DSR) with 95% confidence intervals for three species of songbirds from 2016 – 2018.

	DSR	**Lower CI**	**Upper CI**
Brewer's sparrow			
2016	0.88	0.75	0.96
2017	0.54	0.3	0.76
2018	0.78	0.53	0.91
McCown's longspur			
2016	0.88	0.77	0.93
2017	0.97	0.92	0.98
2018	0.79	0.64	0.88
Vesper sparrow			
2016	0.68	0.45	0.84
2017	0.92	0.81	0.97
2018	0.64	0.4	0.82

Table 8. Top nest survival models selected using AIC for Brewer's sparrow, McCown's longspur, and vesper sparrow.

Species	Model	Intercept	Log-likelihood	df	AICc	ΔAIC	Weight
Brewer's Sparrow	Year + lay + inc + Julian date	3.63	-165.25	8	346.93	0.00	0.99
	Year + lay + inc	3.46	-173.23	6	358.70	11.77	0.00
	Year + lay + inc + DensityAll	3.83	-172.80	7	359.92	12.99	0.00
	Year + lay + inc + DensitySp	3.34	-173.22	7	360.77	13.84	0.00
	Year + lay + inc + SGI	3.47	-173.23	7	360.78	13.85	0.00
	Year + lay + inc + SGI + DensityAll	3.83	-172.80	8	362.01	15.08	0.00
	Year + lay + inc + SGI + NNsp	3.49	-172.97	8	362.37	15.44	0.00
	Year + lay + inc + SGI + NNall	3.49	-173.04	8	362.51	15.58	0.00
	Year + lay + inc + SGI + DensitySp	3.35	-173.22	8	362.86	15.93	0.00
	lay + inc	2.47	-178.13	4	364.38	17.45	0.00
	Year	2.52	-198.47	4	405.05	58.12	0.00
	NULL	1.63	-203.44	2	410.92	63.99	0.00
	Julian date	1.74	-201.63	4	411.38	64.45	0.00
McCown's Longspur	Year + lay + inc + Julian date	2.51	-129.05	7	272.55	0.00	0.72
	Year + lay + inc + SGI + NNall	1.93	-130.16	7	274.76	2.21	0.24
	Year + lay + inc + SGI + NNsp	1.93	-132.09	7	278.62	6.07	0.03
	Year + lay + inc	2.13	-135.78	5	281.79	9.24	0.01
	Year + lay + inc + SGI	1.98	-135.72	6	283.77	11.22	0.00
	lay + inc	2.32	-140.89	3	287.87	15.32	0.00
	Year	1.41	-154.37	4	316.89	44.34	0.00
	Julian date	1.97	-155.33	4	318.81	46.26	0.00
	NULL	1.53	-160.88	2	325.81	53.26	0.00
Vesper Sparrow	Year + lay + inc + SGI + NNall	0.93	-235.89	8	488.10	0.00	0.74
	Year + lay + inc + SGI + DensityAll	0.10	-238.19	8	492.69	4.59	0.07
	Year + lay + inc + DensityAll	0.70	-239.58	7	493.40	5.30	0.05
	Year + lay + inc + Julian date	1.60	-238.87	8	494.06	5.96	0.04
	Year + lay + inc + SGI + NNsp	1.00	-239.12	8	494.56	6.46	0.03

	Year + lay + inc	1.48	-241.34	6	494.86	6.76	0.03
	Year + lay + inc + SGI	1.10	-240.49	7	495.22	7.12	0.02
	Year + lay + inc + DensitySp	1.29	-241.27	7	496.79	8.69	0.01
	Year + lay + inc + SGI + DensitySp	0.85	-240.39	8	497.09	8.99	0.01
	lay + inc	1.97	-256.31	4	520.70	32.60	0.00
	Year	0.92	-257.93	4	523.95	35.85	0.00
	Julian date	1.56	-270.02	4	548.13	60.03	0.00
	NULL	1.41	-273.60	2	551.22	63.12	0.00

* Where ‘lay’ refers to the laying stage, ‘inc’ refers to the incubation stage, ‘SGI’ refers to SGI enrollment, ‘DensityAll’ refers to intraspecific nest density, ‘DensitySp’ refers to conspecific nest density, ‘NNall’ refers to intraspecific nearest nest (m), and ‘NNsp’ refers to conspecific nearest nest.

Table 9. Top model covariates for nest survival models selected using AIC for Brewer's sparrow, McCown's longspur, and vesper sparrow.

	Predictor	**Coefficient**	**SE**	**P**
Brewer's Sparrow				
	Intercept (Year 2016, Nestling Stage)	3.63	0.56	1.55E-10
	Laying Stage	-2.67	0.87	0.002
	Incubation Stage	-2.14	0.309	3.69E-12
	Year 2017	-2.00	0.56	0.00044
	Year 2018	-0.92	0.56	9.80E-02
	Julian Date	-0.71	0.19	0.00017
	Julian Date^2	0.16	0.15	2.86E-01
McCown's Longspur				
	Intercept (Year 2016, Nestling Stage)	2.51	0.38	6.76E-11
	Laying Stage	-1.22	0.3	4.25E-05
	Year 2017	1.50	0.45	0.000699
	Year 2018	-0.61	0.38	0.103053
	Julian Date	0.53	0.21	0.0114
	Julian Date^2	-0.59	0.17	0.00069
Vesper Sparrow				
	Intercept (Year 2016, Nestling Stage)	0.93	0.54	0.087774
	Laying Stage	-1.33	1.16	0.252646
	Incubation Stage	-1.15	0.22	5.36E-08
	Year 2017	1.94	0.52	0.000173
	Year 2018	-0.17	0.38	0.654234
	SGI Enrollment	1.39	0.75	0.065731
	Distance to Interspecific Nearest Neighbor	10.44	0.15	0.004163

Table 10. Plot sample size for nest density estimates by year and SGI enrollment and average number of nests estimated per nest sampled plot for Brewer's sparrows and vesper sparrow with 95% confidence intervals in parentheses.

Year and SGI enrollment	**Plots used for nest density estimates**		**Average number of nests estimated**	
	Brewer's sparrow	Vesper sparrow	Brewer's sparrow	Vesper sparrow
2016 Non-SGI	6	5	6.01 (4.20, 7.82)	5.54 (3.94, 7.14)
2016 SGI	0	2	N/A	5.64 (1.95, 9.32)
2017 Non-SGI	5	5	5.205 (4.80, 5.61)	5.96 (5.59, 6.32)
2017 SGI	5	3	4.19 (2.84, 5.53)	6.05 (5.94, 6.16)
2018 Non-SGI	3	4	5.59 (4.80, 5.60)	7.11 (6.64, 7.57)
2018 SGI	2	5	3.86 (3.58, 4.14)	7.13 (6.53, 7.73)

Table 11. Estimates of average detection of nests using distance sampling with standard errors for Brewer's sparrow and vesper sparrow nests from 2016 – 2018.

Species	**Year**	**Average**	**Standard Error**
Brewer's Sparrow	2016	0.29682	0.10290
Brewer's Sparrow	2017	0.48404	0.06476
Brewer's Sparrow	2018	0.34703	0.05847
Vesper Sparrow	2016	0.35925	0.05981
Vesper Sparrow	2017	0.41308	0.05159
Vesper Sparrow	2018	0.37969	0.05956

Table 12. Estimates of detection and abundance per 25 ha sample plot for Brewer's sparrow, vesper sparrow, and McCown's longspur observed during avian count transect surveys during 2015 – 2018 in Golden Valley and Musselshell Counties, MT. Values in parentheses represent the 95% Bayesian credible intervals.

Common Name	**Detection Probability**	**2016**		**2017**		**2018**	
		Non-SGI	**SGI**	**Non-SGI**	**SGI**	**Non-SGI**	**SGI**
Brewer's sparrow	0.48	18.23	13.99	13.16	10.92	8.611	8.53
	(0.42-0.54)	(15.15-22.33)	(11.23-17.78)	(11.78-15.53)	(9.60-13.18)	(6.41-11.89)	(7.08-11.01)
McCown's longspur	0.61	13.25	33.12	6.02	19.37	4.91	15.43
	(0.43-0.69)	(12.43-15.00)	(30.48-36.60)	(5.55-7.33)	(17.88-21.88)	(4.78-5.90)	(14.13-17.55)
vesper sparrow	0.47	18.34	15.74	14.15	11.68	11.17	8.788
	(0.41-0.54)	(15.50-22.03)	(12.83-19.5)	(12.18-16.95)	(10.03-14.20)	(9.33-11.90)	(7.05-11.48)