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Estimating Avian Populations with Passive Acoustic Technology and Song Behavior

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I am submitting herewith a thesis written by Stephanie C. Prevost entitled "Estimating Avian Populations with Passive Acoustic Technology and Song Behavior." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

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Estimating Avian Populations with Passive Acoustic Technology and Song Behavior

A Thesis Presented for the
Master of Science
Degree
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Stephanie C. Prevost
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ABSTRACT

The need for improvements in avian wildlife monitoring efficiency, accuracy, and scope has led to use of new technologies such as autonomous recording units (ARUs). As a monitoring tool, passive acoustic recording has numerous benefits, but it is still limited to use in human-accessible areas. There is also need for monitoring technologies in areas that are inaccessible. Military installations, which host a disproportionately large number of threatened, endangered, and at-risk species compared to other federal lands, pose the accessibility problem with sizeable impact areas that are too hazardous for humans to access. This thesis introduces the Balloon Aerial Recording System (BARS), a novel technology that fuses acoustic and aerial strategies to address the problem of ground-based land accessibility. The primary objectives of this thesis were to create models that could be used to predict male songbird abundance from song cue-count data and to establish and implement an analytical pathway for bird population estimation from acoustic data recorded with the BARS. ARUs were used to study the song rates/behaviors of Prairie Warbler (*Setophaga discolor*), Bachman's Sparrow (*Peucaea aestivalis*), Field Sparrow (*Spizella pusilla*), Grasshopper Sparrow (*Ammodramous savannarum*), and Henslow's Sparrow (*Ammodramus henslowii*) across 3 military installations. Point-count and line-transect field tests were implemented to directly compare BARS data with that of human-observer techniques in both real-bird communities and simulated-bird communities (with known populations). Both thesis objectives were met for each focal species except Grasshopper Sparrow. Based on negative binomial regression models, song activity was positively related to male abundance and was negatively related to either day of breeding season or time of day. Song activity was also influenced by temperature, wind speed, or atmospheric pressure for some species. The BARS analytical method successfully predicted densities of Prairie Warbler, Bachman’s Sparrow, and Henslow’s Sparrow. Field tests of the BARS with simulated-bird communities revealed that species-specific footprints of detection are needed to further improve density estimates. Through this study, the BARS system has been validated and shown to be useful for documenting presence/absence of rare species, relative abundance of more common species, and in some cases, actual estimation of densities.

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LIST OF ABBREVIATIONS AND SYMBOLS

~	approximately
Δ	change in
AIC_c	corrected Akaike's Information Criterion
ANOVA	analysis of variance
ARU	autonomous recording unit
BARS	Balloon Aerial Recording System, also referred to as “balloon”
BBS	North American Breeding Bird Survey
C	Celsius
CI	confidence interval
dB	decibel
DEM	digital elevation model
Dev	residual deviance
df	degrees of freedom
DoD	Department of Defense
ESA	Endangered Species Act
FF	free flight
GPS	global positioning system
ha	hectare
Hg	mercury
hr	hour
HSD	honest significant difference
Hz	hertz
JPG	Jefferson Proving Ground
K	number of parameters
kg	kilogram
kHz	kilohertz
LT	line transect
m	meter
min	minute
mm	millimeter
n	number of observations
n/a	not applicable
NWR	national wildlife refuge
P	probability of event occurrence given a true null hypothesis
PC	point count
R^2	coefficient of determination
r_s	Spearman rank-order correlation coefficient
s	second
SE	standard error

TER-S	threatened, endangered, and at-risk species
UAV	unmanned aerial vehicle
w_i	Akaike weight
X	covariate value
z	Wilcoxon test statistic
α	alpha
β	covariate coefficient

CHAPTER 1

Introduction

Birds are important wildlife resources as well as valuable indicators of ecological health (Baillie 1991). Because birds are sensitive to environmental changes and are more practical to monitor than many other taxa (Baillie 1991), avian monitoring can provide an important foundation for conservation and natural resources decision-making.

Typical approaches to avian monitoring in large areas include point-count or line-transect surveys (Bibby 2000). These techniques are criticized for being subject to human variability and bias (Faanes and Bystrak 1981). Simons et al. (2007) found that observer variability led to significant variance in abundance estimates, which ranged from 81-132% of actual populations. Even in counts where distance-sampling is not a factor, like those of the North American Breeding Bird Survey (BBS), changes in observers can erroneously influence population trend analysis (Sauer et al. 1994).

The use of passive acoustic technology may bypass many of the widespread concerns about the influence of human observer variability and bias in avian surveys. Autonomous recording units (ARUs) may actually provide more accurate, better quality data. Some of the benefits of using acoustic technology are that expert field observers are not needed, field observer biases are eliminated, permanent records of the data are created, and bird detection rates may increase (Haselmayer and Quinn 2000, Acevedo and Villanueva-Rivera 2006, Tegeler et al. 2012). Furthermore, ARUs greatly increase the amount of data that can be collected, are amenable to automated data collection and processing, and are able to collect data when visibility is poor and/or in environments that are inhospitable to humans (Marques et al. 2013).

ARUs have already shown benefits over other survey methods in side-by-side comparisons. For example, acoustic recording devices detected more species than traditional survey techniques in California montane meadows (Tegeler et al. 2012), in Puerto Rico wetland forests (Acevedo and Villanueva-Rivera 2006), and in tropical grasslands and forests in Thailand (Chimchome 2004). Haselmayer and Quinn (2000) found that sound recordings were preferable to point counts when species richness was high, such as during the dawn chorus. Analysis of recordings made from a stereo microphone configuration by Hobson et al. (2002) produced abundance estimates similar to those from point counts for most species.

JUSTIFICATION

The United States federal government owns 29% of the nation's land area (Stein et al. 2008). Much of this land is undeveloped, thus natural resource management and conservation are important priorities for federal land policy. Various federal legislative acts (e.g., Endangered Species Act (ESA), Sikes Act, and Migratory Bird Rule) require federal land managers to monitor and reduce impact on threatened, endangered, and at-risk species (TER-S), as well as all migratory birds. The Department of Defense (DoD) is one federal agency that is challenged with meeting these legislative mandates.

DoD landholdings include 12 million ha (Boice 2006). Although this area comprises only 3% of federal landholdings, DoD lands contain ~3 times as many imperiled and ESA status species per unit area than any other federal landowner (Stein et al. 2008). This concentration of listed species on DoD lands reflects the ecological uniqueness of DoD installations among federal landowners. DoD installations are maintained and used for a range of military readiness activities, which exposes the land to frequent disturbance, often in the form of fire (Fischer et al. 2011). These disturbance regimes create and maintain habitat for a diversity of TER-S, leading to a disproportionately large number of TER-S on DoD lands, relative to acreages of other federal land management agencies (Stein et al. 2008, Fischer et al. 2011). DoD installations also contain highly threatened ecosystems that typically have been lost from the surrounding region because of development activities. DoD installations, in some cases, support the only remnant populations of TER-S in the region (Fischer et al. 2011). These factors make avian monitoring on DoD lands extremely important.

Traditional human-based avian monitoring methods are particularly unsuitable for DoD lands for several reasons. The DoD holds very large parcels of remote, undeveloped land with limited infrastructure and road access. To adequately sample these lands, additional time and capital are required because of access difficulty. On DoD lands, time is a resource that is not readily available without obstructing the DoD's main objective of maintaining military readiness.

In addition to these vast tracts of DoD lands posing logistical constraints because of scope and accessibility, large parcels of DoD lands set aside as impact areas further complicate these constraints. Decades of military training and testing weapon platforms have littered these areas with potentially unexploded ordnance. Human safety concerns associated with impact areas typically preclude human access on the ground. Existing avian monitoring techniques all require on-the-ground access to the areas being studied. This unmet need for remote monitoring of wildlife populations has recently catalyzed the development of a new technology: the Balloon Aerial Recording System (BARS, or "balloon").

The BARS is a novel technology that fuses acoustic and aerial monitoring strategies. The technology addresses many of the criticisms associated with traditional observer-based survey techniques by employing a custom ARU design. The BARS also addresses the needs for inventorying and monitoring on DoD lands because it is a remotely-operated aerial device.

Proper deployment of this technology allows acoustic sampling of large areas in short periods of time and collects data without requiring on-the-ground access. The BARS is designed to fly, with the wind, over large areas while recording bird song and transmitting real-time global positioning system (GPS) data to an operator on the ground (Hockman in prep.). The current model of this payload was developed based on a system first designed by the Cornell Laboratory of Ornithology (Fristrup and Clark 2009). Since the initiation of the BARS project at the University of Tennessee, Knoxville in 2010, significant improvements to the payload have been made by personnel in the Environmental Sensors Lab in the Department of Biosystems Engineering and Soil Science.

RESEARCH

As with any new technology, the BARS must be validated to determine the appropriate conditions under which it is able to collect useful avian monitoring data. The fieldwork for my Master's project was designed to demonstrate the applicability and functionality of BARS use for monitoring songbirds on military installations. To do this, I focused on the following 5 species, which exhibit a range of vocal qualities and are of conservation concern: Prairie Warbler (*Setophaga discolor*), Bachman's Sparrow (*Peucaea aestivalis*), Field Sparrow (*Spizella pusilla*), Grasshopper Sparrow (*Ammodramous savannarum*), and Henslow's Sparrow (*Ammodramus henslowii*). Northern Bobwhite (*Colinus virginianus*) was also included in part of the study. The field tests were also designed so that BARS data collection results could be directly compared to results obtained from traditional bird monitoring methods (i.e. human observer point-count and line-transect surveys). Additional study methods were implemented to investigate focal species song behavior. The study of song behavior was used to inform our development of population estimation procedures. The major challenge addressed by the following chapters is the estimation of avian population densities from acoustic recordings collected with the BARS. Acoustic recordings collected by the balloon are unique because they are recorded with a single microphone that is mobile and at a potentially great vertical distance from the sources of the acoustic signals. Unlike the large majority of acoustic population analysis procedures (McGregor et al. 1997, Marques et al. 2013, Stevenson et al. 2014), we cannot estimate the direction/distance of the acoustic signals. Therefore, we used a cue-count approach (Hiby 1985) and developed an analytical pathway for estimating populations without being able to distinguish between individuals or groups of individuals.

Chapter 2 describes the process and results of the song behavior investigation of 5 focal species. The primary objectives for this chapter were to (1) document avian song activity at various male abundances and relate it to temporal and weather-related conditions, and (2) build models that can be used to predict male abundance from song cue counts and temporal and weather-related covariates. Chapter 2 also addresses how availability for detection and alternative song types may be relevant to acoustic monitoring.

The primary objective of Chapter 3 was to describe and evaluate a novel acoustic approach for estimating densities of breeding songbirds from mobile, aerial, single-microphone recordings. The secondary objective of Chapter 3 was to compare acoustic-based density estimates with estimates derived from typical human-based avian population monitoring methods, including point-count and line-transect distance-sampling techniques. To accurately validate BARS performance, we used both real- and simulated-bird communities. The simulated communities allowed us to compare the balloon-based population estimates to actual known populations.

The final chapter summarizes the most important results from chapters 2 and 3. It also reiterates our recommendations for future balloon research and cue-based acoustic monitoring.

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CHAPTER 2

Effects of Conspecific Abundance, Weather, and Time on Song Activity: Applications for Acoustic Population Monitoring

ABSTRACT

The use of automated audio recording technology for documenting avian song behavior and monitoring populations has increased greatly as recording devices have become highly portable and more affordable. This technology affords many benefits, including extensive documentation of song behavior, elimination of observer bias, and data collection efficiency. We used automated recording devices to document breeding season song behavior for 5 passerine species: Prairie Warbler (*Setophaga discolor*), Bachman's Sparrow (*Peucaea aestivalis*), Field Sparrow (*Spizella pusilla*), Grasshopper Sparrow (*Ammodramous savannarum*), and Henslow's Sparrow (*Ammodramus henslowii*). We collected field data during the breeding seasons of 2012-2013 at study areas in Indiana, Kansas, and North Carolina. We employed automated recording units, observer-based song counts, and territory mapping to measure and validate song activity and to estimate abundance. We documented variability in species song activity based on various temporal and weather-related parameters. Negative binomial regression models showed linear relationships between the total numbers of songs recorded per unit time and the estimated male abundances for most species. Species song activity was also related either to the day of the breeding season or to the time of day. Occasionally, weather variables were influential in the song activity models. In addition to providing new information on vocal behavior for our focal species, the modeled relationships can be used to predict male abundances based on the total counts of songs per unit time. This simple approach to population estimation has a growing number of applications for passive acoustic monitoring.

INTRODUCTION

Typical approaches for fulfilling avian monitoring requirements in large areas include sampling techniques such as avian point-count or line-transect surveys (Bibby 2000). These techniques have generated concerns associated with observer biases and errors (Faanes and Bystrak 1981, Bart and Schoultz 1984, Diefenbach et al. 2003). Problems with avian monitoring techniques include observer variability in skill, experience, and/or hearing ability; species misidentification; inaccurate distance estimation; and/or other distance-sampling assumption violations (Franzreb 1981, Ramsey and Scott 1981, Bart 1985, Sauer et al. 1994b). Playback experiments in a forested setting showed that these types of problems may lead to abundance estimates that range from 81-132% of the actual populations (Simons et al. 2007). The use of autonomous recording units (ARUs) is one potential means to address problems associated with observer bias.

Use of ARUs has already shown benefits against other survey techniques in side-by-side comparisons. For example, Chimchome (2004) found that ARUs in tropical grasslands and forests in Thailand detected more species than unlimited-distance point counts or spot mapping in most habitat types. Likewise, a recording system in wetland forests of Puerto Rico, detected more avian species than 10-min fixed-radius point counts and more amphibian species than traditional amphibian aural/visual transect methods (Acevedo and Villanueva-Rivera 2006). In addition to better data collection, ARUs preclude the need for expert field observers and create permanent data records.

A potential flaw of ARUs is that they lack the ability to detect individuals visually, whereas human observers can include visual detections while sampling. However, in breeding-bird point-count surveys, 70-94% of observations are typically aural detections (Scott et al. 1981, Dejong and Emlen 1985, Sauer et al. 1994a). In fact, some studies reported that point counts were based solely on aural detections, without observers seeing any birds at all (Wiens 1969, Scott et al. 1981). Thus, ARUs may be a powerful tool in conditions where observer biases are strong and auditory detections are the most frequent form of detection. By replacing field observations with permanent acoustic recordings, researchers may have the opportunity to eliminate error and bias, and to estimate avian populations with greater precision and accuracy.

The ability to estimate abundance/density for avian populations remains a large challenge in the use of acoustic monitoring approaches. A simple way to fuse acoustic monitoring techniques and abundance estimation is to bring the point count to the laboratory. A high-quality 2-microphone stereo configuration was used to make field recordings and then observers listened to the recordings with headphones, estimating distance and direction of bird songs as they would have in the field (Hobson et al. 2002). However, both equipment and observer-time costs can be high in these situations (Hobson et al. 2002, Hutto and Stutzman 2009). Furthermore, this technique did not eliminate observer bias in distance and direction estimation, and as such did not improve population estimates (Hobson et al. 2002). Nor did this technique increase the amount or regional scope of data collected in comparison to traditional point-count methods because the ARUs were still limited to monitoring one area at a time, defined by the detection distance of the microphone.

Automated computer analysis of acoustic data would both eliminate observer biases and greatly increase the ability to process large amounts of data. The field is already moving in this direction (Marques et al. 2013) and several software packages have become available for this purpose (Specht 2004, Figueroa 2011). Software can also potentially be used to spatially distinguish individuals with microphone-array recording systems (Blumstein et al. 2011).

Researchers are also interested in the use of autonomous aerial recording devices (Fristrup and Clark 2009), where movement of the recording systems would complicate, if not preclude, the use of distance and direction as means of abundance estimation. For these applications, methods that require only one acoustic input channel are desirable. A viable method under these circumstances may be cue counting, where a known cue rate is applied to a count of the number of cues detected per unit of time and area (Buckland 2006). Cue counting was originally introduced as a method for estimating densities of great whales (Hiby 1985) but has also been applied to bird surveys (Buckland 2006) and, more recently, acoustic bird surveys (Lambert and McDonald 2014). The primary issue for cue-based population estimation is obtaining a known cue-rate for species of interest under survey conditions (Marques et al. 2013). This is a problem when cue-rate is influenced by the density of individuals, which may be expected for vocalizations used for social communication (Marques et al. 2013). Several studies have confirmed a link between bird abundance and song rate, indicating that a bird's likelihood of detection increases with density (McShea and Rappole 1997, Sexton et al. 2007, Laiolo and Tella 2008, Warren et al. 2013).

We propose the use of density-dependent variation in song activity (total number of songs observed per unit of time) as a potential predictor of abundance, as opposed to a problem for abundance estimation. This method would enable researchers to use stationary or mobile single-microphone audio recordings to estimate populations of vocal species.

Study Objectives

This chapter’s study objectives were to (1) document avian song activity at various male abundances and relate it to temporal and weather-related conditions, (2) build models that can be used to predict male abundance from song cue counts and temporal and weather-related covariates, and (3) investigate how availability for detection and alternative song types may be relevant to acoustic monitoring. We modeled the song behavior of 5 songbird species and the song-rate relationships with factors that could influence song activity. We hypothesized that song activity during the breeding season would (1) increase proportionately with abundance at low densities and then gradually level-out at high abundances (because of signal saturation in the environment) and (2) would be related to one or more temporal or weather covariates.

Study Species and Song Characteristics

We selected 5 passerine species for study based on the desire to evaluate the song-rate-abundance relationship for species that occupy different habitats and exhibit different song types and acoustic characteristics. The individual species song characteristics are reviewed below.

Prairie Warbler (*Setophaga discolor*). A Neotropical migrant, the Prairie Warbler breeds in old fields and young forests throughout the eastern United States and southern Ontario. Prairie Warbler is a species of conservation concern because of population declines in parts of its breeding range since 1966 (Nolan Jr. et al. 1999).

Song behavior and characterization. Male Prairie Warblers have been described to have 2 main song types (A and B), both of which can vary considerably. The classification of A and B songs is mostly agreed upon in the literature but there are some slight disagreements regarding some of the variants within each category. We reviewed the classifications by Nolan Jr. (1978)

and Nolan Jr. et al. (1999), but we adopted the discrete A and B classification types from Houlihan (2000), the most recent classification.

Type A songs (Figure 2.1A) are mostly associated with mate attraction and male-female communication (Nolan Jr. 1978, Houlihan 2000). The typical A song, lasts 1-2.5 s, and consists of a rising series of short, buzzy notes (Nolan Jr. et al. 1999, Houlihan 2000). Type A songs are often loud and may be heard up to 185-200 m under optimal conditions, although there is a continuous graduation of song volume down to being barely audible from 4-5 m (Nolan Jr. 1978).

Type B songs (Figure 2.1B) are associated with male-male communication and territory disputes but the evidence for this is not as strong as the evidence for type A songs being related to male-female interactions (Nolan Jr. 1978, Houlihan 2000). B songs are more complex and more variable than A songs in both time and frequency and they contain whistles, buzzy notes, or combinations of both (Houlihan 2000). One type B variant consists of several long, ringing, and sometimes raspy notes that rise in pitch [Figure 2.1C; described as "Sing-song," a type A variant, in Nolan Jr. (1978)]. Some versions of this variant end in a short series of quicker notes that rise in pitch more rapidly. Another type B song (Figure 2.1D) is remarkably similar to a simple Field Sparrow song but it terminates in a buzzy, up-slurred note that is uncharacteristic of Field Sparrows (F. H. Allen quoted in Bent 1953, Nolan Jr. 1978, S. C. Prevost personal observation).

Song rates. Prairie Warbler song rate declines through the breeding season but rate, as well as song type, can be significantly related to stages in the breeding cycle (Houlihan 2000). Males start singing at low rates before arriving on breeding grounds (Nolan Jr. 1978). Average song rates are greatest during territory establishment before females arrive (3.2 songs per min between 0530 and 1230) and during pair formation (2.8 songs per min between 0530 and 1230) and rates seem to be lowest during the last day of active nest-building (0.3 songs per min between 0500 and 1230) (tables 11 and 12 in Nolan Jr. 1978). Males that lost females between May and July 10 increased their song rates to levels comparable to the pair-formation stage (tables 11 and 12 in Nolan Jr. 1978). Song rates may increase slightly during incubation and perhaps after fledging (tables 11 and 12 in Nolan Jr. 1978).

Song rate within a singing bout (time between first notes of consecutive songs ≤45 s apart) varies both within and between males (Nolan Jr. 1978). Rate does not seem to be affected continuously by time of morning but rate is more likely to be greater earlier than later in the day (Nolan Jr. 1978, Houlihan 2000). Song activity and male aggressiveness generally decrease in windy conditions and during cold rain but are not affected by high temperature or humidity (Nolan Jr. 1978).

Bachman's Sparrow (*Peucaea aestivalis*). Bachman's Sparrow is a resident of mature pine forests and open habitats of the southeastern United States. Loss of mature, open pine forests has caused Bachman's Sparrows to shift their habitat use to open grasslands created by clear-cuts or utility rights-of-way. Over the last century, contraction in Bachman's Sparrow range and decreasing populations have caused management concern for this species (Dunning 2006).

Song behavior and characterization. Bachman's Sparrows have 3 song types described as (1) primary song, (2) whisper song, and (3) excited song (Dunning 2006). The primary song (Figure 2.2) is used for territory defense and counter-singing (Borror 1971, Dunning 2006) and it is typically described as a long, clear introductory whistle followed by 1-2 long trills of different pitch. Another variation is similar but the introductory note is buzzy. There also may be a second introductory note before the trill (Meanley 1990). Bachman's Sparrow songs sometimes may be heard from as far away as 213 m (Meanley 1990).

The whisper song is similar to the primary song except that it is barely audible. Dunning (2006) suggested that while whisper song seems to be directed at mate and nestlings, it might also function as part of a distraction display. Whisper song is sung during all stages of the nesting cycle.

The excited song, which has had various names in the literature, is described as a "bubbling, exuberant combination of slurs, whistles and trills" (Dunning 2006). The context may vary but Bachman's Sparrows seem to use this song only when agitated (Dunning 2006, E. V. Hockman personal communication).

Bachman's Sparrows have extensive song repertoires. Birds (n = 13) sang 244 different song patterns among 820 songs recorded in Ohio and Florida (tables 1 and 2 in Borror 1971). Most of these Bachman's Sparrows sang 20 or more different song patterns, with some individuals singing close to 40. Birds typically sang one particular pattern 1-4 times before switching to another song pattern (Borror 1971). Several song patterns were common to different individuals within the same geographic area but no patterns were common between Ohio and Florida Bachman's Sparrows (Borror 1961, 1971).

Song rates. Bachman's Sparrows in the Southeast may start singing as early as late February (Dorsey 1976, Meanley 1990). Whisper songs were not observed in an 8-week study of 8 individual males but low rates of excited songs (<5% of all songs) were observed (Sirman and

Cox 2010). Wind speed and sky condition (standard North American Breeding Bird Survey codes) were not related to Bachman's Sparrow song rates (Sirman and Cox 2010).

Bachman's Sparrow song rates may be related to male breeding status. In Georgia, observed song rates of unpaired males (3.1 songs per min) were greater than that of paired males (0.2 per min); but paired male song rates before and after hatching did not differ (Sirman and Cox 2010). In between the onset of singing, but before nesting activities, a male Bachman's Sparrow in Louisiana sang 52 times in 15 min (3.5 songs per min) (Meanley 1959). A male in North Carolina sang 99 times in 40 min (2.5 songs per min) during a morning on an unspecified date (Meanley 1990).

Field Sparrow (*Spizella pusilla*). The Field Sparrow is a common passerine of eastern North America, inhabiting undeveloped, brushy fields and young forests. Though relatively abundant, the Field Sparrow is still a species of concern because of declining populations associated with loss of breeding habitat (Carey et al. 2008).

Song behavior and characterization. Field Sparrow males sing 2 song types, a "simple" type and a "complex" type (Nelson and Croner 1991). Simple songs are used in long-distance counter-singing among neighboring males (Nelson and Croner 1991). These songs are assumed to have the dual purpose of defending the territory and attracting females because complex song use has not been associated with male-female interactions (Morrison-Parker 1977). A typical simple song (Figure 2.3A) begins with long (potentially down-slurred) notes with slow or little frequency modulation, and ends with one or more rapid trills (Carey et al. 2008). The notes in the song do not vary much in frequency but they become shorter and faster in duration as the song progresses into a trill.

The less common, complex song (Figure 2.3B) is usually restricted to dawn chorus singing and aggressive territorial interactions (Nelson and Croner 1991). Typically longer, complex songs begin with a trill of short notes followed by longer down-slurred notes, and the song often alternates between phrases of these 2 types (Carey et al. 2008).

Field Sparrows apparently are able to recognize individual conspecifics by their song attributes (Goldman 1973, Morrison-Parker 1977, Nelson 1989), but song-sharing between neighboring males also occurs (Saunders 1922, Cross 1951, Nelson 1992). Nelson (1992) found that males acquiring particular territories for the first time often sing 2 or more simple song types but retained only the simple song that “best matches the most vocally active neighboring male.” This led to localized groups of neighboring males that all shared the same simple song as the only song in their repertoires (Nelson 1992). If song-sharing was not common, then individual differentiation could be obtained from recordings.

Song rates. Field Sparrow singing begins upon male arrival on breeding grounds and becomes less common after pair formation. Males may resume singing at lesser rates once incubation begins or upon nest failure (Carey et al. 2008). In spite of the relationship between song activity and stages of the breeding cycle, the mean interval between songs during singing bouts remains fairly constant until August where the time lag increases to 26 s from an interval of 16-19 s in March-July (Morrison-Parker 1977).

When Field Sparrows sing, the mean interval between successive songs does not change by time of day (Morrison-Parker 1977) but overall song rate is greater during the dawn chorus than during mid-morning (Nelson and Croner 1991). Average song rate of 11-12 New York males was 3.1 (±0.49) songs per min during the dawn chorus and 1.7 (±0.39) songs per min during mid-morning.

Grasshopper Sparrow (*Ammodramous savannarum*). The Grasshopper Sparrow typically breeds in dry grasslands throughout much of the lower 48 states. Although its range encompasses a large area, this sparrow is uncommon to rare throughout much of it. Loss of prairies and agricultural grasslands are likely linked to the population declines that began early in the 20th Century (Vickery 1996).

Song behavior and characterization. Grasshopper Sparrows are one of few North American sparrows that sing 2 completely different songs. Primary songs (Figure 2.4A) are used during territory establishment and during male-male interactions (Smith 1959). The primary song is ~1.5-2 s in duration and begins with 1-3 short, high-pitched, staccato notes that are followed by a long, dry, insect-like buzz (Vickery 1996). The sustained song (Figure 2.4B) is used for mate attraction and may also be important for maintaining the pair bond (Smith 1959). The sustained song is typically a 5- to 15-s series of short, buzzy notes varying slightly in pitch (Vickery 1996). The primary song is often interspersed between sustained songs. Acoustically, primary songs have limited variability across the breeding range but sustained songs are quite variable (figure 2 in Vickery 1996). Grasshopper Sparrows also have a third song type that is sung both by males and females and seems to be exclusively used for intra-pair communication (Smith 1959).

Song rates. Patterns of singing and song type use in Grasshopper Sparrows are influenced both by the time of season/breeding cycle and by weather conditions (Smith 1959). Although male Grasshopper Sparrows primarily sing in the morning, there is no pronounced predawn song period and they commonly sing in the evening after dusk (Smith 1959, Vickery 1996). Singing may lessen during pairing but is fully resumed during laying/incubation (Smith 1959, Vickery 1996). Singing also becomes less frequent while feeding young (Smith 1959). Beyond the regional differences in temporal patterns and song use, the sustained song is common 2-3 weeks after territory establishment (Smith 1959) and during July and August (Vickery 1996). The use of the primary song appears to be greater for unpaired than for paired males in Maine and Florida (Vickery 1996).

Wisconsin Grasshopper Sparrows spent ~60% of their daily time budget singing (including perched time while singing) (figure 24 in Wiens 1969). Pennsylvania male song rates ranged from 5-150 songs per day (before dawn till dark) over the course of the breeding season (figure 1 in Smith 1959). During territory establishment, Grasshopper Sparrows may sing up to 220 songs per hr (3.7 songs per min) (Smith 1959).

Henslow's Sparrow (*Ammodramus henslowii*). The Henslow's Sparrow winters in the southeastern United States and breeds mainly in the Midwest. Henslow's Sparrows are grassland obligates and prefer wet prairie with tall, dense vegetation and thick litter. Loss of this specific cover type has likely led to the population declines observed since the initiation of the North American Breeding Bird Survey (BBS) in 1966 (Cooper 2007). Sharp annual population declines have created extra concern for the status of this species. Although not federally listed in the United States, the Henslow's Sparrow is listed as Endangered in 7 states and in Canada, as Threatened in 5 states, and as a species of Special Concern in 4 states (Herkert et al. 2002).

Song behavior and characterization. The Henslow's Sparrow has only one type of song, very short, non-musical, and insect-like, which functions both for mate attraction/pair formation and territory defense (Herkert et al. 2002). Despite the apparent simplicity and brevity of the song, audio-spectrographic analysis showed that it is composed of 4 to 6 complex groups of notes that vary in frequency and intensity (Borror and Reese 1954; Figure 2.5). Song variation exists among different individuals but song variation may not necessarily be related to geographic location (Borror and Reese 1954).

Song rates. Henslow's Sparrow males sing immediately upon arrival on the breeding grounds. Song activity increases until approximately mid-May and may remain relatively constant into August (Hyde 1939) or even mid-September (Robins 1971). Song activity may also be linked to the breeding stage. Daily time budget accounts for Henslow's Sparrow documented ~65% of observed time singing (including perched time while singing) for 4 males in Wisconsin (figure 24 in Wiens 1969) and 15% of observed time singing during incubation in Michigan (Hyde 1939).

Song rates vary considerably for Henslow's Sparrow. Song totals for 3 males in Michigan ranged from 223 to 4,962 songs per day (0.2 to 3.4 songs per min) during 24-hr counts (Robins 1971). Song rate may decrease during the breeding season, as linkages between song activity and breeding stage would suggest. The mean time intervals between 73 songs of 3 males in Ohio were 3.04 s (range: 1.9-5.9; 0830 on April 18), 1.21 s (range: 0.8-1.8; 0930 on April 26), and 5.22 s (range: 3.5-7.5; 0740 on May 16) (Borror and Reese 1954). These data give average rates of ~10-40 songs per min (based on small sample size) but it is unclear whether this variation could be attributed to a decreasing seasonal trend or to individual differences. Henslow's Sparrows in Michigan showed a decreasing trend in song rate between mid-June (13-14 songs per min) and early-August (~7-9 songs per min) (table 1 in Hyde 1939).

METHODS

Study Areas

We selected 3 study areas from eastern Department of Defense (DoD) installations for this research based on their ability to represent (1) a range in cover types that occur on eastern United States DoD installations (i.e. grasslands, forests, savannas), (2) a range in climate (e.g., wind conditions, temperature, relative humidity), and (3) avian species of interest to land managers for acoustic monitoring (Fischer et al. 2011). DoD installation willingness to host our research, as well as the practicality of fulfilling our objectives without interfering with DoD training activities, were also critical factors in the selection process.

Big Oaks National Wildlife Refuge (NWR), Indiana. The northern-most installation, previously known as Jefferson Proving Ground (JPG), is a deciduous forest intermixed with open grasslands and oak savannahs. JPG is representative of other midwestern installations, such as forts Campbell, KY, Knox, KY, Leonard Wood, MO, and McCoy, WI. The climate is warm with intermediate humidity and moderate winds. Prairie Warbler, Field Sparrow, and Henslow's Sparrow were the focal species at this study area. We collected data at this study area during May-July 2012.

Fort Riley, Kansas. Fort Riley is located in an open grassland/scrub/agricultural landscape. It is representative of the open landscapes found in many Great Plains (e.g., Fort Sill, OK) and southwestern (e.g., Fort Bliss, TX) installations. Climatic conditions are hot, semi-arid, and windy. The focal species for this study area were Field Sparrow, Grasshopper Sparrow, and Henslow's Sparrow. We collected data at this study area during May-July 2013.

Fort Bragg, North Carolina. Fort Bragg is located within a Longleaf (*Pinus palustris*) and Loblolly (*Pinus taeda*) pine-dominated landscape. The Fort Bragg landscape is representative of many other southeastern coastal plain installations, such as Eglin Air Force Base, FL, Camp Lejeune, NC, Fort Benning, GA, and Fort Stewart, GA. The climate is hot and humid with generally light winds. The focal species for study at Fort Bragg were Prairie Warbler and Bachman's Sparrow. We collected data at this study area during May-July, 2012 and 2013.

Field Methods

Territory mapping and acoustic recording. During early May, we mapped territories for 9 males of each focal species at 3 sites within a given study area and logged the individual male locations with global positioning system (GPS) units (Garmin models eTrex 10 and GPSMAP 60, Olathe, KS). In 2012, we conducted these methods at Big Oaks NWR and Fort Bragg, and in 2013, at Fort Riley and Fort Bragg. The 9 males were spread across 3 sites (3 males per site) with at least 4 km between sites. We continued territory mapping the selected territories 1-2 times per week, at various times of day, throughout the breeding season. Field technicians at Big Oaks NWR and Fort Riley also recorded the number and direction of neighboring conspecific territories when additional males were detected.

Song Meter SM2 units (Wildlife Acoustics, Maynard, MA), with 2 SMX-II omnidirectional microphones, were mounted on posts (~1.25 m above ground) in the approximate center of each mapped territory. Every 2-8 days, the SM2 units were rotated between individual male territories. Recordings were made between May 15 and July 23, from 1 half-hr before sunrise to 4 hr after sunrise (units at Fort Bragg recorded from sunrise to 4 hr after sunrise). Audio files were saved in 16-bit PCM uncompressed WAV format with 24-32 kHz sampling frequency. Each WAV file was 4-4.5 hr in duration. If a focal male's territory changed or shifted during the season, we adjusted the center point of the territory and the location of the SM2 unit. If the SM2 needed to be moved more than 25 m, the new location was considered a new territory. During the early half of the breeding season, some focal males abandoned their territories and SM2 units were moved to new territories. Recordings made on abandoned territories or territories with fewer than 3 song counts were excluded from analysis.

Song counts. During each rotation of the SM2 units (~1-2 times per week), song counts were performed at each unit. During a song count, a trained observer stood beside the SM2 unit for 10 min, recorded the number of singing males of the focal species, and tallied the number of songs sung per min by each individual. The observer also estimated the distance and direction of each detected individual in reference to the survey point by sketching a map of the singing individuals' relative locations. Song counts were always performed between 1 half-hr before sunrise and 4 hr after sunrise.

Estimating male abundance. We estimated male abundance as the maximum number of singing males detected from each SM2 location during human-observer visits. Most abundance estimates were based on detections during human-observer song counts but we also considered the maximum number of singing males recorded at an SM2 location during territory-mapping sessions. The greater of the 2 maxima was used for male abundance (only song counts were considered for Fort Bragg because maximum male data were not recorded during territory mapping at this study area).

Sampling of Acoustic Files and Acoustic Data Processing

We used a stratified random sampling to select 5-min portions of audio files to be analyzed for songs of focal species. The sampling technique was applied for each dataset (Table 2.1). We define "dataset" as all the sampled recordings for a specific species, study area, and year (e.g., one dataset = all Prairie Warbler samples from Fort Bragg in 2012). Prior to sampling, we excluded all audio data that fell into one or more of the following categories: (a) audio collected from abandoned territories, (b) audio collected from territories with fewer than 3 song counts, (c) audio compromised by human or equipment error (e.g., incorrect time settings, microphone failure), and/or (d) audio with spectrogram quality severely compromised by background noise (e.g., insect chorus covering frequency range of focal species, medium to heavy rain, strong wind). We made one exception to these audio file exclusion criteria for Bachman's Sparrow. Most of the Bachman's Sparrow recordings had only one channel (due to microphone failure) so we only processed one channel for all of this species' recordings. This likely reduced the detection area of the SM2 but the same decrease in detection distance was applied to all Bachman's Sparrow recordings.

To prepare audio data for stratified sampling, we divided the data for each species into 5 equal date intervals (period 1 = May 15-28, period 2 = May 29-June 11, period 3 = June 12-25, period 4 = June 26-July 9, and period 5 = July 10-23). We randomly selected 5 audio files in each date interval while stratifying the sampling across estimated abundances and different territories. Because we were particularly interested in the relationship between song and conspecific abundance, our stratified sampling had relatively equal sample sizes across abundance estimates.

We divided recording time into 5 equal time intervals (270 min / 5 = 54 min each for Big Oaks NWR and Fort Riley, 240 min/5 = 48 min each for Fort Bragg) and randomly selected one min (as a start time) to sample across the 5 time intervals in each file. This sampling strategy selected 125 5-min samples (5 samples in each date/time period) for each species, site, and year. In some cases, sample sizes were >125 in a dataset (Table 2.1) because we opportunistically added 5-min audio segments that had been previously analyzed for a separate study but were not part of the stratified sample. Fewer than 125 samples in a dataset resulted from limited audio data from which to sample because of recording equipment malfunction and/or audio exclusion criteria.

We handled missing audio data in several ways. The dataset for Prairie Warbler at Fort Bragg in 2012 did not include any audio files during the 1st date interval and only 2 files during the 4th date interval. Similarly, the Fort Bragg Prairie Warbler dataset for 2013 had limited data during the 5th date interval. We compensated for these data sampling limitations by increasing the number of samples in the neighboring date periods. Bachman's Sparrow data also had a limited number of samples in some of the date intervals but we did not add samples from neighboring date intervals because we believed, in this case, it would have unduly inflated the influence of the abundance estimates during those intervals. The Grasshopper Sparrow dataset (Fort Riley, 2013) had a total of only 2 samples (10 min total) among time intervals 3, 4, and 5 for the 1st and 2nd date intervals. Where possible, missing audio data were replaced with data from observer song counts at SM2 locations and sample type was added to the analysis as a covariate.

A spectrogram for each 5-min sample was created and annotated with Raven Pro software, Version 1.5 (Bioacoustics Research Program 2014). Spectrogram settings were Blackman window function with 1,125 samples, time grid hop size of 360 with 68% overlap, and frequency grid spacing at 21.5 Hz. I visually and aurally scanned each spectrogram for songs of the specified species. Each audio clip was scanned only for the species associated with the mapped territory where the audio was recorded. Songs were selected and annotated directly on the Raven Pro spectrogram. This approach created a customizable, annotated data table based on the selections. Songs were only selected when both their average and maximum powers (measured in Raven Pro) were at least 3 dB greater than the background noise. This cutoff was based on experiments that indicated a 3-dB difference between signal and noise is sufficient for Red-winged Blackbirds (*Agelaius phoeniceus*) to detect songs against background noise (Brenowitz 1982). Sounds below this threshold were often unidentifiable. All of the audio clips and selections were rechecked for errors to ensure accuracy.

Song Type Classification and Correlation

During the annotation process, we classified songs into groups based on functional differences (i.e. song types associated with different behaviors or purposes, as described in the literature) and based on specific song variations that may complicate species identification. We focused on major song types that are typically used for detection by human observers during field surveys. We did not annotate calls or other non-song vocalizations. We did not knowingly annotate “whisper” songs, although we may not have recognized a distinction between a song sung from a long distance and a nearby whisper song. We did not classify song types for Bachman’s or

Henslow's sparrows because these species only have one major song type for both inter- and intra-sex communication.

Prairie Warbler. Prairie Warbler song annotations were categorized into the following 5 groups (Figure 2.1): (1) typical type A songs (Figure 2.1A), (2) general type B songs (Figure 2.1B), (3) songs described as "sing-song" in Nolan Jr. (1978) and as a variant of type B in Houlihan (2000) (Figure 2.1C), (4) unusual type B song that is similar to a Field Sparrow song, also described in Nolan Jr. (1978) (Figure 2.1D), and (5) rare, abnormal songs (Figure 2.1E). Because Prairie Warbler songs vary continuously across all types (Houlihan 2000, S. C. Prevost personal observation), it can be difficult to distinctly classify songs that are intermediates between types. Therefore, we only classified a song as group 1, 3, or 4 if it clearly belonged to the group. The group 2 classification served as a catchall for intermediate songs. Songs were only classified as group 5 if they were truly aberrant vocalizations that were uncharacteristic of any of the described types. There were 28 songs (<1% of total) that we classified in a 6th category because species identification was uncertain. These songs were all either variants and/or degraded versions of group 4 songs, or they were unusually high frequency Field Sparrow songs. We excluded this sixth song category from all analyses because of the uncertainty of the species of origin.

Field Sparrow. Field Sparrow song annotations were classified into the following 3 groups: (1) simple songs, (2) complex songs, (3) songs similar to Prairie Warbler group 3 songs. Some of the group 3 songs (Figure 2.6) would have been difficult to classify if they were observed at Big Oaks NWR, where both Field Sparrows and Prairie Warblers coexist. However, this song type was only observed at the Fort Riley study area, which lacked Prairie Warblers.

Grasshopper Sparrow. Grasshopper Sparrow song annotations were classified as either primary song (group 1) or sustained song (group 2). Both song types are easy to identify and distinguish from one another. The observer song-count samples (*n* samples = 17) in this dataset (see sampling methods) were excluded from song classification analysis because song type was not recorded by field observers.

Correlation Analyses. We performed Spearman rank-order correlation analyses between the 2 most common song types for Prairie Warbler, Field Sparrow, and Grasshopper Sparrow and 2 temporal variables (i.e. day of season and time of day). We used the general "stats" package in program R (R Core Team 2015) for the correlation analyses and we used package "ggplot2" (Wickham 2009) to plot linear models (with 95% confidence intervals) of each song type (y-axis) by the explanatory variable day of season or time of day (x-axis) (see Table 2.2 for explanatory variable descriptions). We expected each song type to have a moderately different relationship with the temporal variables because song types have different behavioral functions and they are influenced by the breeding cycle and/or time of day (Prairie Warbler, Houlihan 2000; Field Sparrow, Nelson and Croner 1991; Grasshopper Sparrow, Smith 1959). In all cases where pairwise correlations were greater than 20%, the 2 most common song types for a species were correlated to the temporal variable in the same direction (i.e. both positively or both negatively). Thus, the counts of all song types were summed in a single response variable referred to as total songs. We also plotted linear models between each major song type and temporal variable, which provided a visual comparison between each song type's relationships to the temporal variables.

Availability for Detection and Song Activity

Availability for detection for each species was calculated as the proportion of 5-min samples that contained at least one song of the specified species. Availability rates for each species were graphically examined for their relationships to male abundance. We also calculated species availability for detection for each dataset individually.

Song activity for a species is represented as the total number of songs annotated in a 5-min audio sample. For each species, we plotted the average song activity in each abundance category. We also individually examined each dataset for linear relationships between total songs and male abundance. We used program R (R Core Team 2015) with package "ggplot2" (Wickham 2009) to fit linear models (with 95% confidence intervals) between total songs (y-axis) and abundance (x-axis).

Negative Binomial Regression

For each species, we modeled the total number of songs per 5 min with estimated abundance, 2 temporal variables, 3 weather variables, and up to 3 categorical variables (see Table 2.2 for variable descriptions). Weather data were retrieved from the National Climatic Data Center in surface hourly abbreviated format (http://www7.ncdc.noaa.gov/CDO/cdopoemain.cmd). Weather stations used for Big Oaks NWR were Big Oaks (WIMS127301) and Cincinnati/Northern Kentucky [WBAN93814; Cincinnati/Northern Kentucky weather data were used only for the atmospheric pressure variable (henceforth referred to as "pressure") and to fill gaps in the Big Oaks weather data]. For Fort Bragg, we used Simmons Army Airfield (WBAN93737) and Fayetteville Pope Air Force Base (WBAN13714), and for Fort Riley, we used Marshall Airfield

(WBAN13947). The ranges of values for all continuous variables, by species, site, and year, are in Table A.1 in the thesis Appendix.

For the regression analyses, we used program R (R Core Team 2015) with packages "MASS" (Venables and Ripley 2002), "ggplot2" (Wickham 2009), and "car" (Fox and Weisberg 2011). We used function "glm.nb" to run negative binomial regressions on total number of songs per 5 min. Regressions were first run by species with pooled data (all applicable study areas and years for each species). Preliminary model results for pooled data indicated that study area and year were important explanatory variables in all applicable cases. Therefore, we modeled species data for each study area and year separately. The abundance variable was included in every candidate model because we are interested in the relationship between total songs and the number of males. The corrected Akaike Information Criterion (AIC_c) was used for model selection among all possible regressions. We considered models where $\Delta AIC_c \leq 2$ as having strong support (Burnham and Anderson 2002). We also visually examined the relationships between the response variable and each non-categorical explanatory variable with scatterplots ("ggplot" function in R). If exponential and/or multimodal relationships were apparent in the plots, these terms were added to a new set of candidate models based on the top models from the first candidate set. We selected a new best model from the second candidate set if its AIC_c score was $\geq$2 points less than the previous best model. The final model selected was evaluated for regression coefficient significance ($\alpha = 0.05$), multicollinearity (with variance inflation factors), deviance / degrees of freedom, distribution of residuals, and studentized residuals against predicted.

RESULTS

The total number of hours of recordings analyzed (sum of the 5-min samples) was ~92, or ~18 hr per species (minimum = 9, maximum = 30). The total number of songs annotated ranged from 2,407 songs (Bachman's Sparrow, 19 hr of recording) to 10,337 songs (Henslow's Sparrow, 11 hr of recording) (Table 2.1).

Song Type Classification and Correlation

Prairie Warbler. Prairie Warbler group 1 songs were the most common (57%), followed by group 2 (32%), at both study areas. Song groups 3 and 4 were only observed in recordings from Big Oaks NWR where group 3 made up 13% and group 4, 5% of the area total. There were only 3 songs (0.2% of area total) from group 5 observed among samples from Big Oaks NWR and 23 songs at Fort Bragg (2% of area total).

There was one strong negative correlation ($r_s \geq 50\%$) between Prairie Warbler group 1 songs and day of season but correlation coefficients were similar for both song groups (Table 2.3). Both song groups 1 and 2 were negatively correlated with day of the season, and uncorrelated ($r_s < 15\%$) with time of day (Table 2.3, Figure 2.7). All 5 Prairie Warbler song groups were summed for further analyses.

Field Sparrow. Group 1 songs made up 95% of total annotated Field Sparrow songs. Most of the remaining 5% of songs belong to group 2. Group 3 songs (2% of Fort Riley total) were only observed in Fort Riley recordings where there were no Prairie Warblers. The songs were restricted to 3 territories within the same vicinity. Samples from the other territories on Fort Riley (geographically separate from the former 3) did not have any group 3 songs on their recordings.

There were no strong correlations ($r_s \geq 50\%$) between the 2 most common song groups nor between either song group and a temporal variable. Group 1 Field Sparrow songs were negatively correlated with time of day ($r_s = -0.39$; Table 2.3, Figure 2.8B). There was no support ($r_s < 15\%$) for any pairwise correlations with group 2 songs (Table 2.3, Figure 2.8C and D). We pooled all 3 song groups for further analyses.

Grasshopper Sparrow. Group 1 songs made up 92% of total annotated Grasshopper Sparrow songs; the remaining 8% were group 2 songs. There were no strong correlations ($r_s \geq 50\%$) between song groups nor between either song group and a temporal variable. Like Field Sparrow, group 1 Grasshopper Sparrow songs were negatively correlated with time of day ($r_s = -0.46$), but not with day of season (Table 2.3, Figure 2.9A and B). Group 2 songs were negatively correlated with day of season ($r_s = -0.21$), but not with time of day (Table 2.3, Figure 2.9C and D). We pooled both song groups for further analyses.

Availability for Detection and Song Activity

The availability for detection (proportion of the 5-min audio samples that contained at least one song of a given species) was positively related to male abundance across all focal species except Grasshopper Sparrow (Figure 2.10). Availability for detection reached 1.0 for Field Sparrow at an abundance of 5 males, Grasshopper Sparrow at an abundance of 3 males, and Henslow's Sparrow at an abundance of 4 males (Figure 2.10). Prairie Warbler availability changed dramatically between observed abundances (Figure 2.10). At an abundance of one male, Prairie Warbler availability was only 0.1. At an abundance of 5 males, Prairie Warbler availability exceeded 0.9. For Field Sparrow and Grasshopper Sparrow, availability was high (>0.8) and did not vary much among abundances (Figure 2.10). In contrast, Bachman's Sparrow availability was modest (<0.8), even at an abundance of 6 males.

The average number of songs in each 5-min sample appeared to increase with abundance (Figure 2.11), with the exception of Bachman's Sparrow (2013 only) and Grasshopper Sparrow (Figure 2.12). In 2013, Bachman's Sparrow song activity remained approximately the same at various male abundances (Figure 2.12E). The average numbers of songs for Field and Henslow's sparrows peaked and then decreased before abundance was at its maximum (Figure 2.11).

Negative Binomial Regression

All of the final models fit the data reasonably well (Table 2.4, Figure 2.13). There were no indications of multicollinearity or patterns in studentized residuals. The final models had acceptable levels of deviance with deviance differing from degrees of freedom at a maximum rate of 1.3. The model deviances were least for Prairie Warbler and Bachman's Sparrow at Fort Bragg.

In the majority of the models, the abundance explanatory variable was significantly related to the total songs response variable, with 2 exceptions. Abundance was not significant in the 2013 Bachman's Sparrow model or the Grasshopper Sparrow model ($P > 0.05$, Table 2.5). In all other models, abundance was positively related to the total number of songs ($P \leq 0.02$; Table 2.5, Figure 2.12).

Day of season was included in 4 of the 10 final models (Table 2.5). In 3 of these 4 models, each additional day in the breeding season led to an incremental decrease in the total number of songs (rate ratios in Table 2.5). In contrast, day of season in the 2012 Fort Bragg Bachman's Sparrow model had a positive relationship with total songs.

Time of day was included in 4 of the 10 final models and had a negative relationship with total songs (Table 2.5). For a one-unit increase in time (1 unit = 5 min), total songs decreased by 2-3% for Field, Grasshopper, and Henslow's sparrows. Temperature (negative effect) was included in one of the best-supported Bachman's Sparrow's models for 2013 (Table 2.5). Alternatively, a model that included the positive effect of pressure on total songs performed equally well for Bachman's Sparrows in 2013. Pressure was also included in the best model for Field Sparrow at Fort Riley, but it had a negative relationship with total songs (Table 2.5).

For 3 of the final models, having an exponentiated term in the model decreased ΔAIC_c by 2 or more. The exponentiated terms (i.e. day of season and wind speed) had negative relationships with total songs (Table 2.5, Figure 2.14) but the rates of decrease in the response variable accelerated as values of the explanatory variables increased (Figure 2.14). The top candidate models and AIC_c for each dataset are listed in Table A.2 in the Appendix.

DISCUSSION

Factors Related to Song Activity

Song activity (total songs) was positively related to male abundance for all but one of the study species (i.e. Grasshopper Sparrow). These results supported our hypothesis that the number of songs increase with conspecific abundance. Numerous other studies also supported the existence of positive relationships between avian song activity and abundance (Penteriani et al. 2002, Cunningham et al. 2004, Warren et al. 2013, Borker et al. 2014, Lambert and McDonald 2014). We also hypothesized that there would be a curvilinear relationship between song activity and abundance where song activity would increase proportionately with abundance at lesser densities but these increases would gradually level-out at greater densities (because of signal saturation in the environment). We expected a curved relationship because of intraspecific song asynchrony where individuals alternate singing to avoid overlapping songs with conspecific neighbors (Morrison-Parker 1977, Wasserman 1977). Overlapping songs among conspecific neighbors should generally be avoided because the acoustic interference would reduce the strength of each song signal while simultaneously limiting signal interpretation by the singers. As density increases, individuals may need to reduce their song rates to avoid signal overlap. However, introducing a curvilinear relationship into the negative binomial regression models (by exponentiating the abundance term) did not improve model performance. This result thus failed to support the stated hypothesis. Inadequate sampling at very low and/or very high densities, however, may have confounded our ability to detect the hypothesized curvilinear relationships.

Results from the negative binomial regression models also supported our second hypothesis that song activity would be related to one or more temporal or weather-related covariates. All final models included a temporal and/or weather-related covariate, in addition to abundance (Table 2.5). Day of season and time of day were the most important explanatory variables (excluding abundance) related to total songs. Other studies have also found that day of season and time of day were influential factors for song rate in the Mourning Dove (*Zenaida macroura*) (LaPerriere and Haugen 1972), Wood Thrush (*Hylocichla mustelina*), Ovenbird (*Seiurus aurocapillus*), and Northern Cardinal (*Cardinalis cardinalis*) (McShea and Rappole 1997). Detection rates, which are directly related to availability for detection, were also influenced by temporal factors in a range of species (Best 1981, Robbins 1981b, Skirvin 1981).

Day of season had a consistent negative relationship with song activity in all 3 Prairie Warbler models. The exponential day of season relationships, observed in 2 of these models, is supported by previous Prairie Warbler observations. Nolan Jr. (1978) and Houlihan (2000) observed a general decline in singing over the breeding season and/or fluctuations in song activity that corresponded to particular stages of the breeding cycle. In contrast to the Prairie Warbler models and our expectations (based on the literature), day of season had a positive relationship with Bachman's Sparrow song activity in 2012. This positive relationship, however, was inconsistent between years, and may have been an artifact of our sampling design in 2012 (further discussed in the Study Limitations section).

Day of season was not a component of the best models for Field, Grasshopper, or Henslow's sparrows. However, relationships between song activity and breeding stage and/or date have been documented for these species elsewhere [Field Sparrow, (Morrison-Parker 1977, Carey et al. 2008); Grasshopper Sparrow, (Smith 1959); Henslow's Sparrow, (Hyde 1939, Borror and Reese 1954)]. Assuming that our samples were representative of song activity across the season, the absence of day of season in the models suggested either that song activity in our study populations was not influenced by the progression of the breeding season/cycle or that males in our populations were asynchronous in stages of the breeding cycle. Asynchrony can occur as individual nests fail at various stages of the nesting cycle. If nest survival rates were low, then asynchrony was likely to occur.

Time of day only appeared to influence song activity for the 3 species that were not influenced by day of season (Field, Grasshopper, and Henslow's sparrows). The relationship between time of day and song activity has been documented in other studies of Field (Nelson and Croner 1991), Grasshopper (Smith 1959), and Henslow's (Robins 1971) sparrows. The magnitude and direction of the effect (negative in all cases) of time of day in the models did not differ among species or between Field Sparrow study area/year (all rate ratios for time of day = 0.97-0.98; Table 2.5).

Weather covariates were related to song activity in 4 of the 10 final models [temperature (negative effect for Bachman's Sparrow, 2013), pressure (positive effect for Bachman's and negative effect for Field sparrows in 2013), and wind speed^2 (negative effect for Grasshopper Sparrow); Table 2.5]. The effect of pressure on avian song activity is not widely documented but both barometric pressure and wind speed (among other factors) have been useful predictors of Northern Bobwhite (*Colinus virginianus*) calling rates (Wellendorf et al. 2004). In the BBS, detections of several species were negatively related to wind speed, but temperature was positively or negatively related to detection, depending on the species (Robbins 1981a).

The negative relationship between wind speed and Grasshopper Sparrow song activity at Fort Riley is supported by Smith (1959), who observed decreases in song activity during adverse weather conditions. Wind speeds at Fort Riley regularly interfered with acoustic detection of bird songs (S. C. Prevost, personal observation). At high wind speeds (≥ 8 m s^{-1}), the benefits of singing would be small because of high sound attenuation. Presumably, birds should reduce or discontinue singing activity as costs start to outweigh benefits. The effects of wind speed on song activity may have been apparent in other models if we had included recordings during high wind conditions. However, we generally excluded audio files obtained under very windy conditions because the signal to noise ratio was problematic for audio analyses. For this reason, our model results are only applicable for the reduced wind speeds under which we conducted the study.

Models for species that were studied at more than one study area and/or during more than one year (i.e. Prairie Warbler, Bachman's Sparrow, and Field Sparrow models), suggested that the relationships between song activity and our covariates can vary across space and time. Study area and/or year were significant in the top models for all applicable species. Although the significant explanatory variables and the direction of the effects (positive or negative) remained consistent in the different Prairie Warbler and Field Sparrow models, the magnitude of the effects changed (Table 2.5). The differences in effect magnitude could reflect actual response differences in the populations (by region, year, and/or factors that were not accounted for in the study) and/or sampling error.

Song Activity Models for Abundance Prediction

Negative binomial regression was a successful method for modeling songbird cue-count data with male abundance and with temporal and weather-related covariates. A suitable candidate model, with 1-3 covariates was always found among the top models. Our selection criteria specified choosing the model with the fewest and simplest (i.e. exponent with least value) terms that was within 2 ΔAIC_c of the top model. In all cases, these criteria specified models with significant ($\alpha = 0.05$) covariates (except where abundance was insignificant for the 2013 Bachman's and Grasshopper sparrow models). The residual deviances of the selected models never exceeded 1.3 times the degrees of freedom, indicating good model fit.

Although our regression models fit the data well, the differences among models for a species across study area and year may challenge the practicability of using these models to predict male abundance from song cue counts. Additional monitoring may be needed to collect the data necessary to create new cue-count abundance models for each species, study area, and year of interest. However, differences among the models for a given species may have also been a function of factors that we did not account for among the explanatory variables (e.g., habitat characteristics). Model differences could also have resulted from random variation that significantly affected the data because of our limited sample sizes. A larger and more robust sampling strategy may be more capable of determining if and why there are variations across study areas and years. Another useful endeavor would be to study the same individual males for multiple breeding seasons to determine if song activity changed at the individual level, while accounting for conspecific abundance.

To construct abundance prediction models, the terms in the negative binomial regression models were remodeled with abundance as the response variable and the model was forced through zero (thus, abundance would equal zero when there were zero songs). The forced intercept allowed the models to predict abundances less than the abundances in the original data. The resulting negative binomial models were in the following form:

Equation 2.1

$$\text{Abundance} = \exp^{(\beta_S X_S + \beta_1 X_1 + \cdots + \beta_k X_k)}$$

In Equation 2.1, β_S = regression coefficient for the total number of songs observed in a 5-min time period, X_S = the total number of songs observed in a 5-min time period, $\beta_1 \cdots \beta_k$ = additional covariate coefficients, and $X_1 \cdots X_k$ = additional covariate values. The resulting equations after remodeling are in Table A.3 in the thesis Appendix.

Implications for Acoustic Monitoring

Availability for detection. Species availability for detection (proportion of the 5-min audio samples that contained at least one song of the specified species) generally increased with male abundance. For some species, availability was ~1 at moderate (3-5 males) and high (6-8 males) abundances. Maximum species availability at low abundance (1-2 males) was 0.6. A positive relationship between auditory availability and abundance has also been documented for other songbirds [Eastern Kingbird, *Tyrannus tyrannus* (Sexton et al. 2007); Dupont's Lark, *Chersophilus duponti* (Laiolo and Tella 2008); Golden-cheeked Warblers, *Setophaga chrysoparia* (Warren et al. 2013)]. The relationship between availability for detection and abundance can be a problem for population monitoring when using methods that rely on an assumption of independent detection, that are based on short-duration observation periods, and/or that use cue counts without accounting for changes in abundance.

Conversely, species availability (or detection probability) can be used as an index of general abundance (Royle and Nichols 2003). Low detection rates would indicate small populations and high detection rates would indicate large populations. For species that sing frequently and thus have high availability for detection even when abundance is moderate (Field, Henslow's, and Grasshopper sparrows), the duration of the sample could be reduced to allow for a wider range of detection rates and potentially, a finer-scale abundance index. This abundance index may have applications for surveys with repeated visits or for stationary acoustic recordings that are sampled or analyzed in short-duration segments. However, more studies are needed to confirm that the relationship between availability and abundance is consistent.

Song type. The existence of multiple song types will affect acoustic monitoring of some species more than others. Intra-specific variation in song characteristics will likely pose the largest challenge to an automated detection process. Use of automated detection software will likely be the analysis approach for future acoustic signal processing because it substantially decreases the effort required to process acoustic data and it excludes observer bias during this stage of data analysis (Brandes 2008, Blumstein et al. 2011, Stowell and Plumbley 2014). The 3 species that had different functional song types in our study (Prairie Warbler, Field Sparrow, and

Grasshopper Sparrow) mostly sang (≥57% of total songs) their primary song type (classified as group 1). For Field and Grasshopper sparrow, alternative song types were sung at such low rates (≤8% of total songs) that these songs may be disregarded in acoustic analysis without impacting results. Considering that group 2 songs of Field and Grasshopper sparrows were extremely variable in structure, note choice, and duration (S. C. Prevost, personal observation), choosing to analyze only the primary song-type for these species would be desirable to simplify an automated song-detection process. However, pooling observations of all song types would provide a more accurate representation of total song activity. Pooling all song types may become a viable option as detection software continues to improve.

Prairie Warbler song repertoires, like many other Paruline repertoires, may be difficult to fully account for with an automated detection process. The Prairie Warbler, and many of its relatives, sing songs from both of 2 song categories at substantial rates (Spector 1992). Alternative Prairie Warbler song types made up a large portion of song activity (43%) in our study. Thus, alternative song types should be included in analysis of acoustic data for this species. Another challenge posed by Prairie Warblers and similar species is the diversity of song types within each of the 2 functional song categories (Spector 1992). As the automated detection process attempts to accommodate these song variations, the range of possible values attributed to each song characteristic will need to increase, and greater numbers of false positives will likely result.

Song variants, where species identification is questionable, increases concern for species misidentification in both automated detection and general acoustic detection where additional identification clues (e.g., visual, habitat, etc.) are absent. Certain variants of Prairie Warbler and

Field Sparrow songs may pose challenges to species identification. The Prairie Warbler variant of type B song (group 4; Figure 2.1D) that is nearly identical to a primary Field Sparrow song composed 5% (91 songs) of total Prairie Warbler songs detected at Big Oaks NWR. At least one Field Sparrow at Fort Riley sang a song type [Figure 2.6; Field Sparrow group 3; comprised 1% (*n* = 56) of total Field Sparrow songs detected at Fort Riley] that was very similar to some versions of Prairie Warbler group 3 songs. Documenting and gaining a better understanding of song types that resemble songs of other species will help inform and guide classification of acoustic data.

Prairie Warbler and Field Sparrow song variants may be related to region and/or interspecific co-occurrence. Group 3 and 4 Prairie Warbler songs (Figure 2.1C and D), were only observed in recordings at Big Oaks NWR (where Prairie Warblers and Field Sparrows co-occurred), and not at Fort Bragg. Co-occurrence could explain why we only observed Prairie Warblers singing Field Sparrow-like group 4 songs at Big Oaks NWR. Allen (quoted in Bent 1937) also described this song variant for Prairie Warblers singing alongside Field Sparrows. Interestingly, Field Sparrow group 3 songs (which resemble some Prairie Warbler group 3 songs) were observed only at Fort Riley, in the absence of Prairie Warblers. We have not found documented evidence that this song variant has been described before. The song could be part of a local dialect but it also could have been an anomaly in a single male's repertoire. More observations of Field Sparrow songs in the Fort Riley area are needed to further document the use of this song type.

Study Limitations

Song classification. Variation in the acoustic landscape between Big Oaks NWR and Fort Riley led us to forego analysis of Henslow's Sparrow data at Fort Riley. The short duration of Henslow's Sparrow songs make them susceptible to obscurement by other sounds in similar frequency bands. In this case, the great abundance of Dickcissel (*Spiza americana*) vocalizations on Fort Riley recordings made it extremely difficult to annotate Henslow's Sparrow songs, such that the resulting data were compromised and incomparable to the Big Oaks NWR study area.

Song activity. Average song activity was unexpectedly high at intermediate abundances for Field and Henslow's sparrows (Figure 2.11) but we suspect these data points may have been influenced by inconsistencies with our sampling scheme, rather than reflective of actual songbird behavior. Although we used a balanced sampling design by day of season and time of day, the number of samples at each level of abundance was determined by the abundances encountered in the field. In this case, Field Sparrow territories with abundances of 5 had twice as many samples in the first date interval (May 15-28) than in any of the 4 subsequent date intervals, which likely inflated the song counts for that abundance level. The large peak in Henslow's Sparrow song activity can be primarily attributed to 2 adjoining territories. The high song activity could have been due to unusually high activity associated with these territories or to an inaccurate abundance index. At this point, we are unable to distinguish between these 2 possible explanations.

Sampling limitations and regression model applicability. Abundance had the greatest magnitude of influence on total songs in the model for Prairie Warbler at Fort Bragg in 2012. The model specified that total songs (in a 5-min interval) increased by a factor of 8.13 for each additional male (Table 2.5). This estimate may be inflated because of the limited number of territories sampled (Figure 2.12B). Fort Bragg in 2012 had only 2 Prairie Warbler territories that had enough quality data to sample from. Thus, all samples were taken from 2 locations, with abundances of 1 and 4. Further inflating this estimate, only 1 song was detected among the 55 audio samples from the territory with an abundance of 1 male. Because of these limitations, we suggest that a model based on pooled Fort Bragg Prairie Warbler data (both years) would be more appropriate for prediction purposes.

Data limitations may have also affected all of the Bachman's Sparrow models in terms of abundance and day of season. As described in the Methods section, only single-channel audio recordings were used for the Bachman's Sparrow analysis. This approach may have reduced the detection radius of the recording units. Depending on the distribution of birds around the recorder, a shorter detection radius may have been insufficient to reflect the observed abundance index. Temporal sampling limitations could have influenced the relationship (or lack thereof in 2013) between Bachman's Sparrow song activity and day of season. The dates of the first Bachman's Sparrow recordings were May 22 in 2012 and May 27 in 2013, both of which are well into the breeding cycle for this species (Dorsey 1976, Meanley 1990). Our samples likely missed the peak of Bachman's Sparrow song activity at the beginning of the breeding season. If the first samples taken in 2012 occurred during an intermediate stage of breeding where song activity was low, the regression model would reflect an increase in song activity with the progression of the breeding season, which is consistent with our 2012 model (Table 2.5). The lack of a relationship between total songs and day of season in the 2013 Bachman's Sparrow models may be explained by beginning the sampling period while song activity levels were intermediate. Although preliminary modeling showed a significant difference between the 2012 and 2013, a model based on pooled data for both years may remediate some of the sampling concerns.

The Grasshopper Sparrow model may have been influenced by the sampled abundances and/or numbers of territory samples in each abundance category. The model may have failed to detect a relationship between song activity and abundance because we only obtained song activity data for abundances of 3, 4, and 5 males. Variation in song activity related to abundance may only exist across broader scales of abundance (e.g., low vs. medium vs. high), whereby sampling within only one scale would not detect a relationship. Alternatively, song activity in this species might not be affected by individual density. In either case, our Grasshopper Sparrow model as developed would not be useful for predicting abundance from song activity.

Conclusion

The goal of this chapter was to study the relationship between song activity and abundance across a variety of songbird species and across a variety of landscapes. We constructed models that not only quantitatively define detection opportunity (one opportunity = one song) in terms of local male abundance and influential covariates, but that also may be used to predict male abundance from song cue-count data gathered from stationary or mobile acoustic recorders. The strategy to population estimation offered by our models challenges the perception that density-dependent availability for detection is a problem to be accounted for in population estimation. Instead, we defined the relationship between number of individuals and number of acoustic signals for 5 species so the relationship can be used to predict abundance, given the covariates defined in the models and the number of songs detected per unit time. We were successful in developing models that can be used for abundance prediction for 4 of the 5 study species. We found that day of season, time of day, temperature, wind speed, and atmospheric pressure were related to song activity but not all of these factors are influential for each species. Variation in song activity across species, study areas, and years challenges the broad applicability of our models because new data will need to be collected and modeled for each species, location, and time period of interest. Species that regularly use more than one song type will require additional attention during the acoustic detection process, especially if automated software is employed.

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CHAPTER 2 APPENDIX

Table 2.1. Sample sizes, average male abundances, and availability for detection by species, study area, and year. The average male abundance was calculated by totaling the estimated abundances associated with the 5-min samples and dividing by the number of samples. Availability for detection is the proportion of 5-min samples that contained at least one song of the specified species. Sample sizes shown here were used for all analyses unless noted otherwise.

Species	**Study area**	**Year**	**Territories (*n*)**	**5-min samples (*n*)**	**Songs annotated (*n*)**	**Average male abundance**	**Availability for detection**
Prairie Warbler (*Setophaga discolor*)	Big Oaks NWR	2012	9	131	1,756	3.6	0.76
	Fort Bragg	2012	2	110	762	2.5	0.32
		2013	5	121	664	1.9	0.43
Bachman's Sparrow (*Peucaea aestivalis*)	Fort Bragg	2012	5	125	1,355	3.1	0.49
		2013	5	103	1,052	2.0	0.54
Field Sparrow (*Spizella pusilla*)	Big Oaks NWR	2012	10	140	3,300	5.3	0.95
	Fort Riley	2013	6	131	5,016	4.1	0.93
Grasshopper Sparrow (*Ammodramous savannarum*)	Fort Riley	2013	7	112	2,501	3.8	0.89
Henslow's Sparrow (*Ammodramus henslowii*)	Big Oaks NWR	2012	8	133	10,337	5.1	0.86

Table 2.2. Response and explanatory variables used in negative binomial regression modeling of song activity (total songs per 5-min) for 5 passerine species at 3 Department of Defense study areas, 2012-2013.

Variable	**Descriptions and units**
Total songs	Response variable. Total number of songs of a given species in a 5-min audio sample. Obtained by listening to and viewing spectrogram of audio in Raven Pro (Bioacoustics Research Program 2014).
Abundance	Abundance index. Maximum number of singing males detected from SM2 location during song counts and/or territory mapping.
Day of season	Modified Julian date. (May 1 = 1).
Time of day	Modified Julian time divided by 5. (30-min before sunrise = 0, 25-min before sunrise = 1, sunrise = 6, etc.).
Temperature	Degrees in Celsius. (C^{o})
Wind speed	Average wind speed measured over a fixed time period. (meters per second).
Pressure	Atmospheric pressure given as altimeter setting (station pressure corrected to sea level). This variable was transformed by subtracting the mean (761 mm) from each value. (millimeters of mercury).
Study area	Categorical. Used when species dataset included more than one study area (i.e. Big Oaks NWR, Fort Bragg, and/or Fort Riley).
Year	Categorical. Used when species dataset included more than one year (i.e. 2012 and 2013).
Sample type	Categorical. Indicates whether or not a human observer was present at the time of the audio recording.

Table 2.3. Spearman rank-order correlation coefficients for pairwise comparisons between numbers of songs classified as group 1 and classified as group 2, song group and day of season, and song group and time of day. Prairie Warbler song group data were from audio recordings made at Big Oaks NWR (2012) and Fort Bragg (2012-2013). Field Sparrow song group data were from audio recordings made at Big Oaks NWR (2012) and Fort Riley (2013). Grasshopper Sparrow song group data were from audio recordings made at Fort Riley (2013).

		Group 2	**Day of season**	**Time of day**
Prairie Warbler	Group 1	0.31	-0.52	0.01
	Group 2		-0.33	-0.13
Field Sparrow	Group 1	0.00	-0.09	-0.39
	Group 2		-0.05	-0.13
Grasshopper Sparrow	Group 1	0.25	-0.04	-0.46
	Group 2		-0.21	-0.07

Table 2.4. Negative binomial regression models with abundance. The response variable was the total number of songs counted in 5-min audio samples from 3 Department of Defense study areas, 2012-2013. *K* = number of parameters, df = degrees of freedom, Dev = residual deviance.

Species	**Study area**	**Year**	**Best model(s)**	***K***	**df**	**Dev**
Prairie Warbler	Big Oaks NWR	2012	Abundance + Day of season^6	3	128	151.2
	Fort Bragg	2012	Abundance + Day of season	3	107	69.4
		2013	Abundance + Day of season^4	3	118	97.4
Bachman's Sparrow	Fort Bragg	2012	Abundance + Day of season	3	122	114.4
		2013[a]	Abundance + Temperature	3	100	101.3
			Abundance + Pressure	3	100	101.3
Field Sparrow	Big Oaks NWR	2012	Abundance + Time of day	3	137	163.5
	Fort Riley	2013	Abundance + Time of day + Pressure	4	127	164.8
Grasshopper Sparrow	Fort Riley	2013	Abundance + Time of day + Wind Speed^2	4	108	133.9
Henslow's Sparrow	Big Oaks NWR	2012	Abundance + Time of day	3	130	161.2

[a] Two models performed equally well for Bachman’s Sparrow, 2013. Both are shown.

Table 2.5. Details for the explanatory variables in the chosen models for negative binomial regression on total songs in 5-min audio samples from 3 Department of Defense study areas, 2012-2013. Effect denotes whether the relationship between the explanatory variable and the response variable is positive (+) or negative (-). The rate ratio is the exponentiated coefficient of the model term; it reflects the rate at which the response variable changes with a one-unit increase in the explanatory variable (see Table 2.2 for variable units). A rate ratio that is less than one indicates that the explanatory variable has a negative relationship with the response variable, whereas a ratio greater than one indicates a positive relationship.

Species	**Study area**	**Year**	**Term**	**Effect**	**Rate ratio**	**Lower CI**	**Upper CI**	***z***	***P***
Prairie Warbler	Big Oaks NWR	2012	(Intercept)	+	6.95	3.36	14.86	5.09	< 0.001
			Abundance	+	1.30	1.08	1.56	2.79	0.01
			Day of season^{6}	-	1.00	1.00	1.00	-8.25	< 0.001
	Fort Bragg	2012	(Intercept)	-	0.14	0.00	1.43	-1.36	0.17
			Abundance	+	8.13	4.76	21.39	6.03	< 0.001
			Day of season	-	0.92	0.90	0.94	-7.07	< 0.001
		2013	(Intercept)	+	3.04	1.11	9.00	2.04	0.04
			Abundance	+	2.12	1.28	3.58	3.04	0.00
			Day of season^{4}	-	1.00	1.00	1.00	-6.61	< 0.001
Bachman's Sparrow	Fort Bragg	2012	(Intercept)	-	0.16	0.04	0.60	-3.17	0.00
			Abundance	+	1.73	1.40	2.17	5.72	< 0.001
			Day of season	+	1.04	1.02	1.06	3.69	< 0.001
		2013	(Intercept)	+	110.09	12.59	1532.84	4.08	< 0.001
			Abundance	-	1.00	0.60	1.64	-0.01	0.99
			Temperature	-	0.89	0.79	0.98	-2.06	0.04
		2013[a]	(Intercept)	+	7.97	2.95	25.28	3.51	< 0.001
			Abundance	-	0.96	0.59	1.56	-0.16	0.88
			Pressure	+	1.12	1.01	1.23	2.11	0.04
Field Sparrow	Big Oaks NWR	2012	(Intercept)	+	20.47	12.06	35.19	11.77	< 0.001
			Abundance	+	1.17	1.07	1.28	3.78	< 0.001
			Time of day	-	0.97	0.96	0.98	-6.34	< 0.001

Table 2.5 (continued)

Species	**Study area**	**Year**	**Term**	**Effect**	**Rate ratio**	**Lower CI**	**Upper CI**	***z***	***P***
	Fort Riley	2013	(Intercept)	+	3.30	1.79	6.13	3.60	< 0.001
			Abundance	+	1.94	1.69	2.23	8.86	< 0.001
			Time of day	-	0.98	0.97	0.99	-4.71	< 0.001
			Pressure	-	0.96	0.93	0.99	-2.22	0.03
Grasshopper Sparrow	Fort Riley	2013	(Intercept)	+	135.66	31.07	625.78	6.76	< 0.001
			Abundance	-	0.76	0.52	1.09	-1.55	0.12
			Time of day	-	0.98	0.97	0.99	-3.79	< 0.001
			Wind speed^2	-	0.98	0.97	0.99	-3.49	< 0.001
Henslow's Sparrow	Big Oaks NWR	2012	(Intercept)	+	69.53	33.18	151.68	11.34	< 0.001
			Abundance	+	1.15	1.01	1.30	2.32	0.02
			Time of day	-	0.97	0.96	0.99	-3.48	< 0.001

[a] Two models performed equally well for Bachman’s Sparrow, 2013. Details for both are shown.

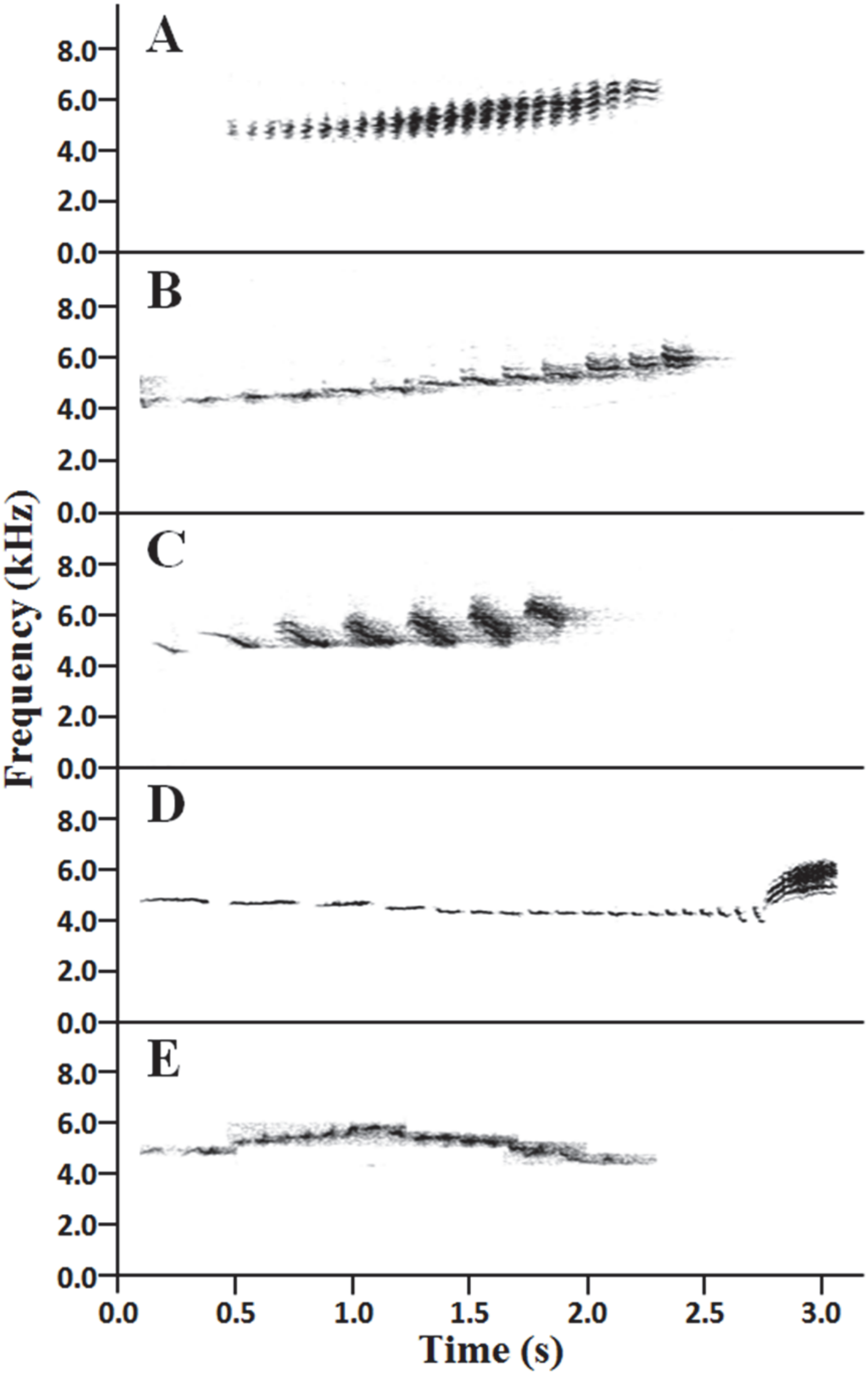

Figure 2.1. Prairie Warbler song groups including a typical type A song (**A**), a typical type B song (**B**), a song described as "sing-song" by Nolan Jr. (1978) (**C**), an unusual type B song that is similar to a Field Sparrow song (**D**), and (5) a rare, abnormal song (**E**). A through D songs were recorded at Big Oaks NWR in 2012; E was recorded at Fort Bragg in 2012.

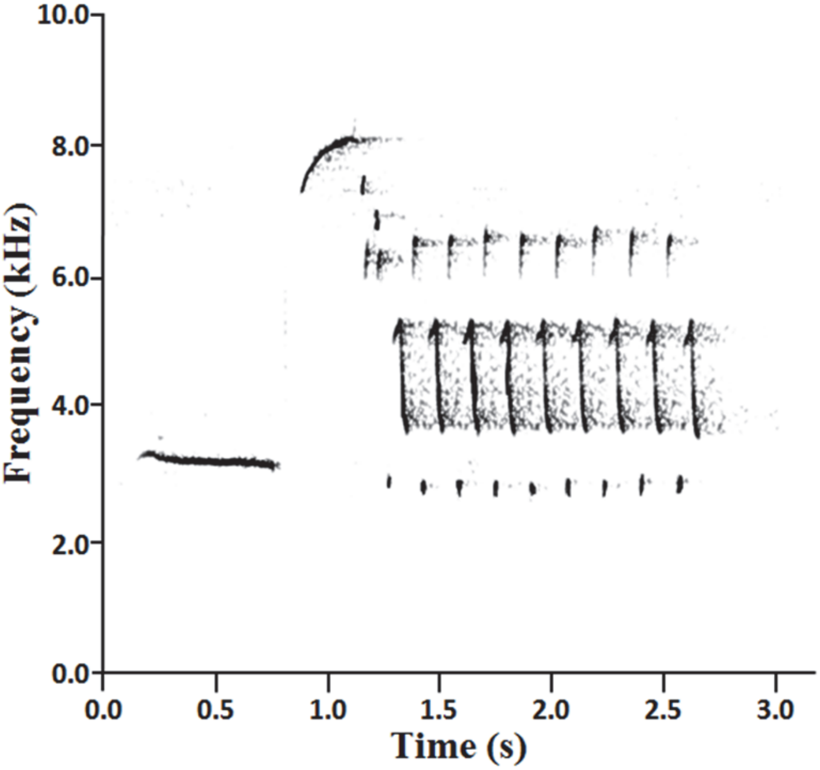

Figure 2.2. Bachman’s Sparrow song recorded at Fort Bragg in 2012.

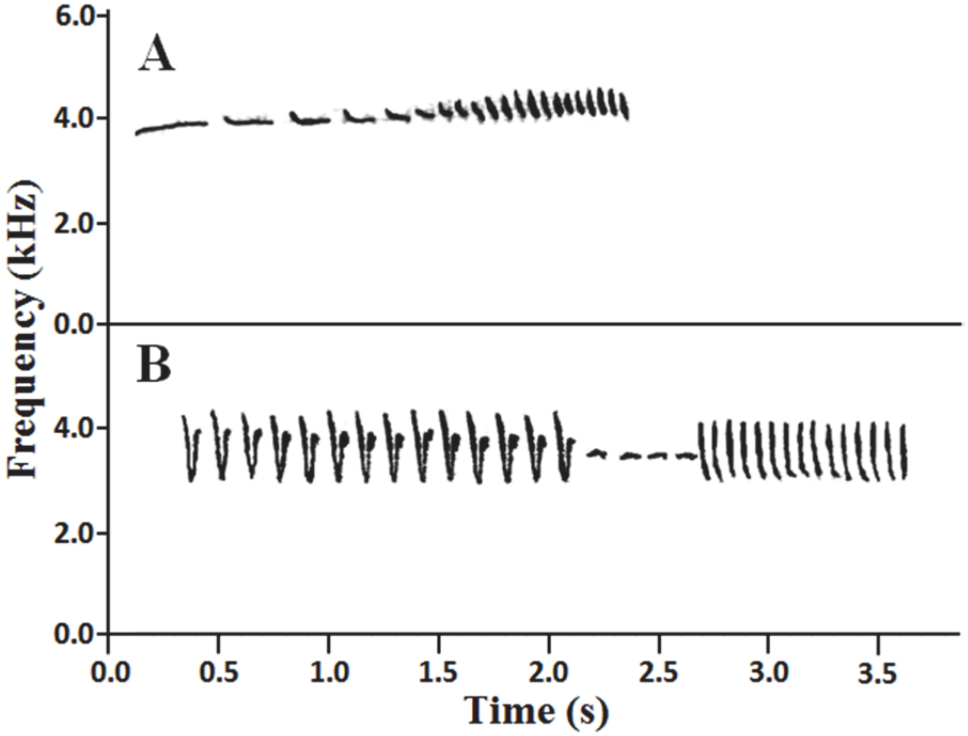

Figure 2.3. Field Sparrow song groups including simple song (**A**), recorded at Big Oaks NWR in 2012, and complex song (**B**), recorded at Fort Riley in 2013.

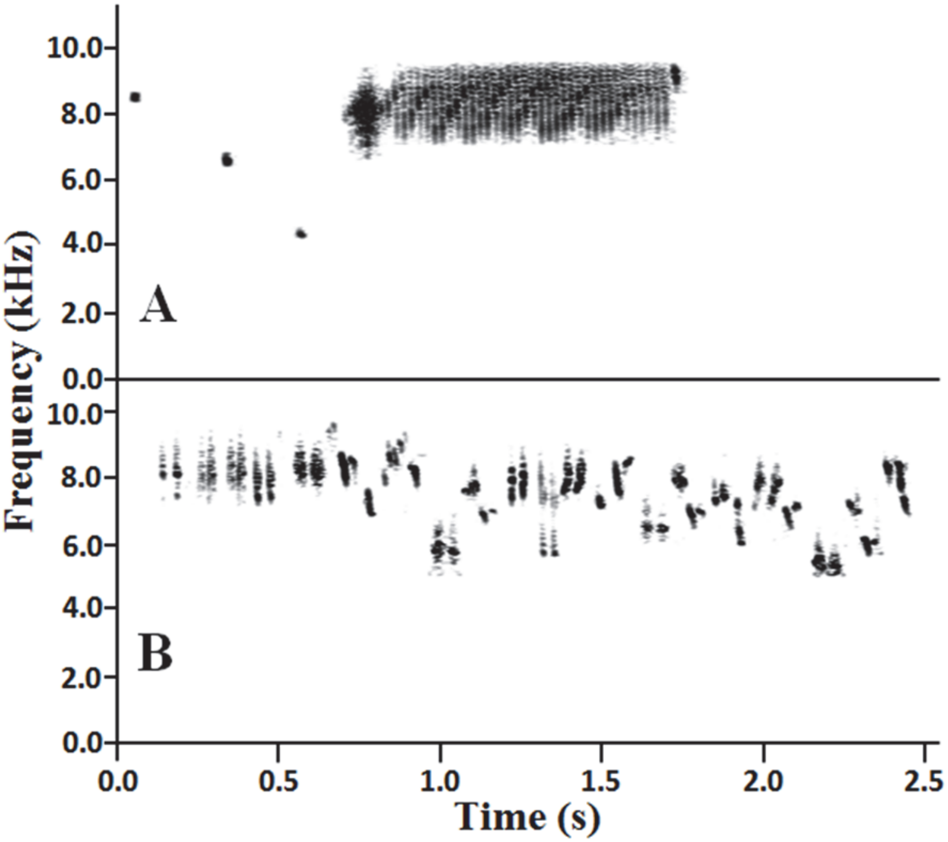

Figure 2.4. Grasshopper Sparrow song groups including primary song (**A**) and sustained song (**B**), recorded at Fort Riley in 2013.

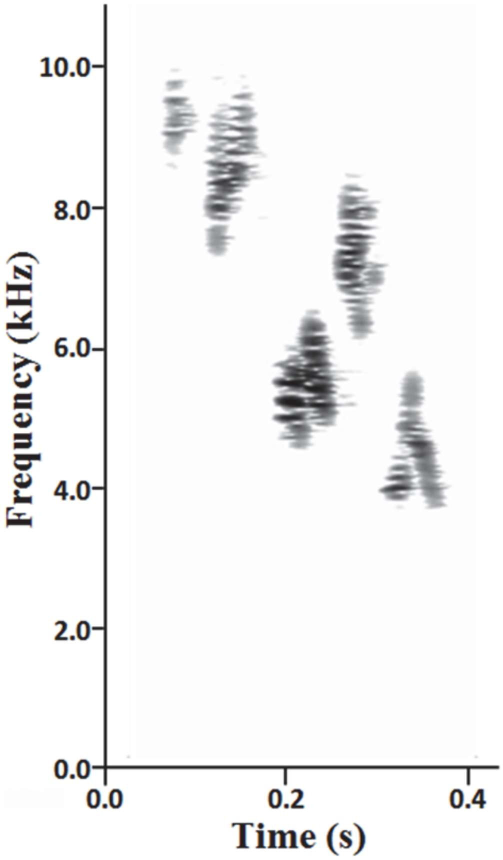

Figure 2.5. Henslow's Sparrow song recorded at Big Oaks NWR in 2012.

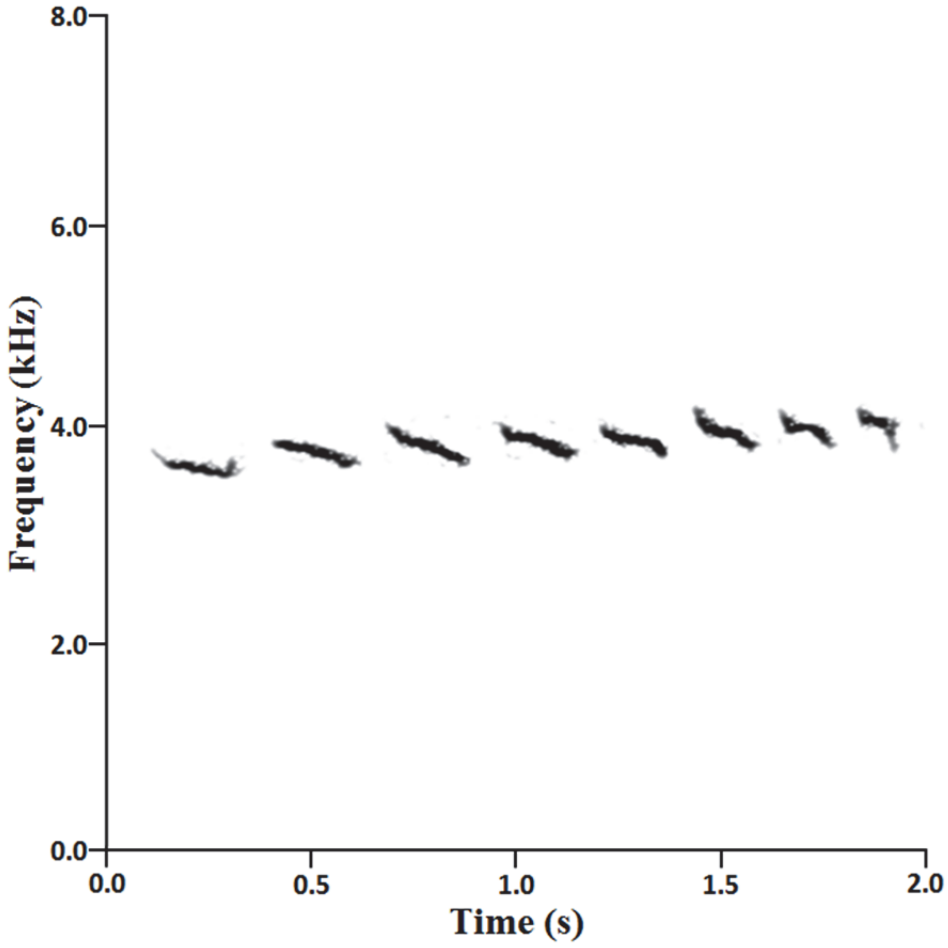

Figure 2.6. Group 3 Field Sparrow song that resembles some variations of Prairie Warbler group 3 songs (Figure 2.1C), recorded at Fort Riley in 2013.

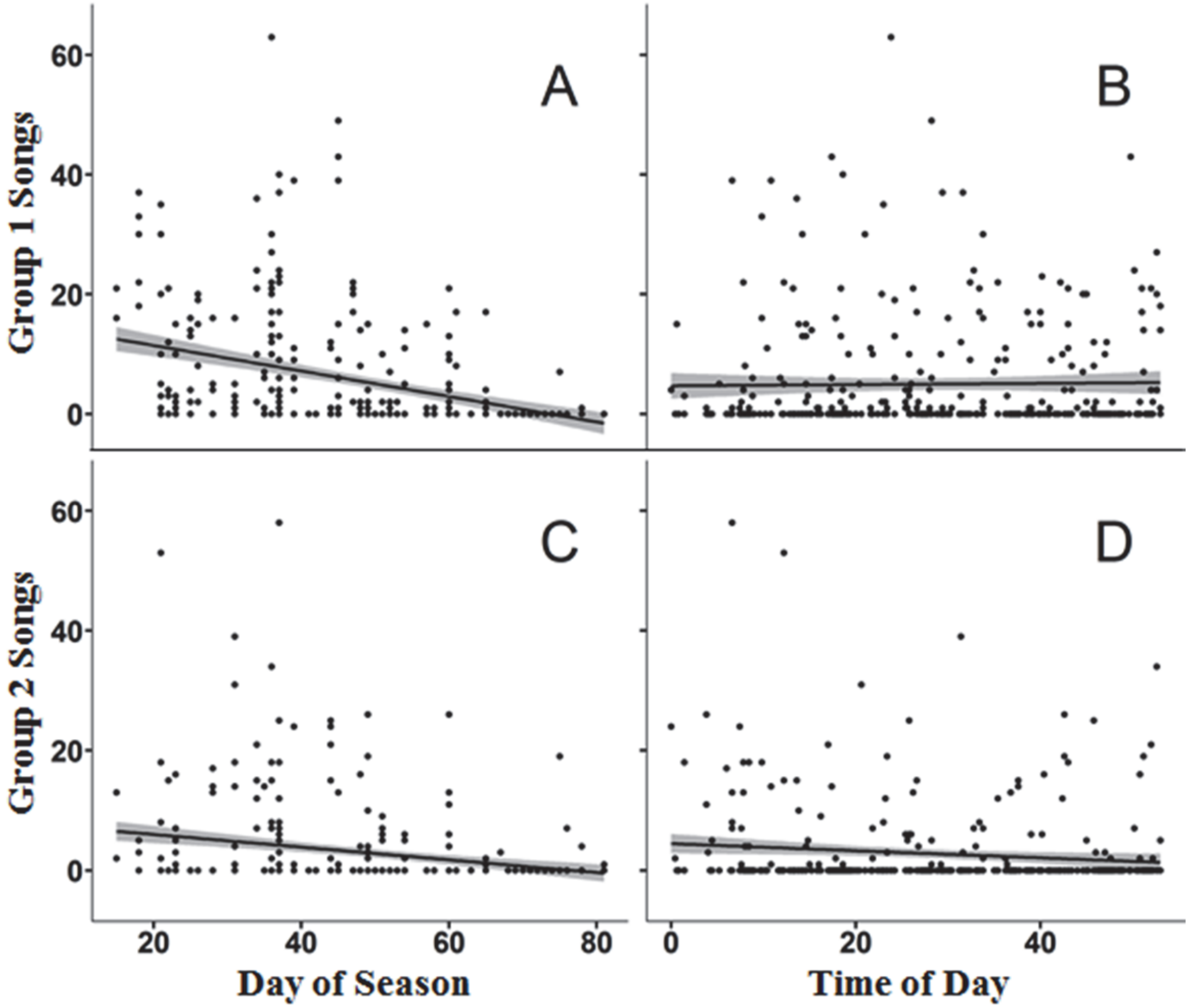

Figure 2.7. Prairie Warbler fitted linear models (with 95% confidence intervals) of songs (per 5-min sample) by day of season (May 1 = 1) or time of day (1 unit = 5 min; 30-min before sunrise = 0). The scatter plots show day of season by group 1 songs (**A**), time of day by group 1 songs (**B**), day of season by group 2 songs (**C**) and time of day by group 2 songs (**D**). The 5-min audio samples were taken from recordings made between May and July at Big Oaks NWR (2012) and Fort Bragg (2012-2013).

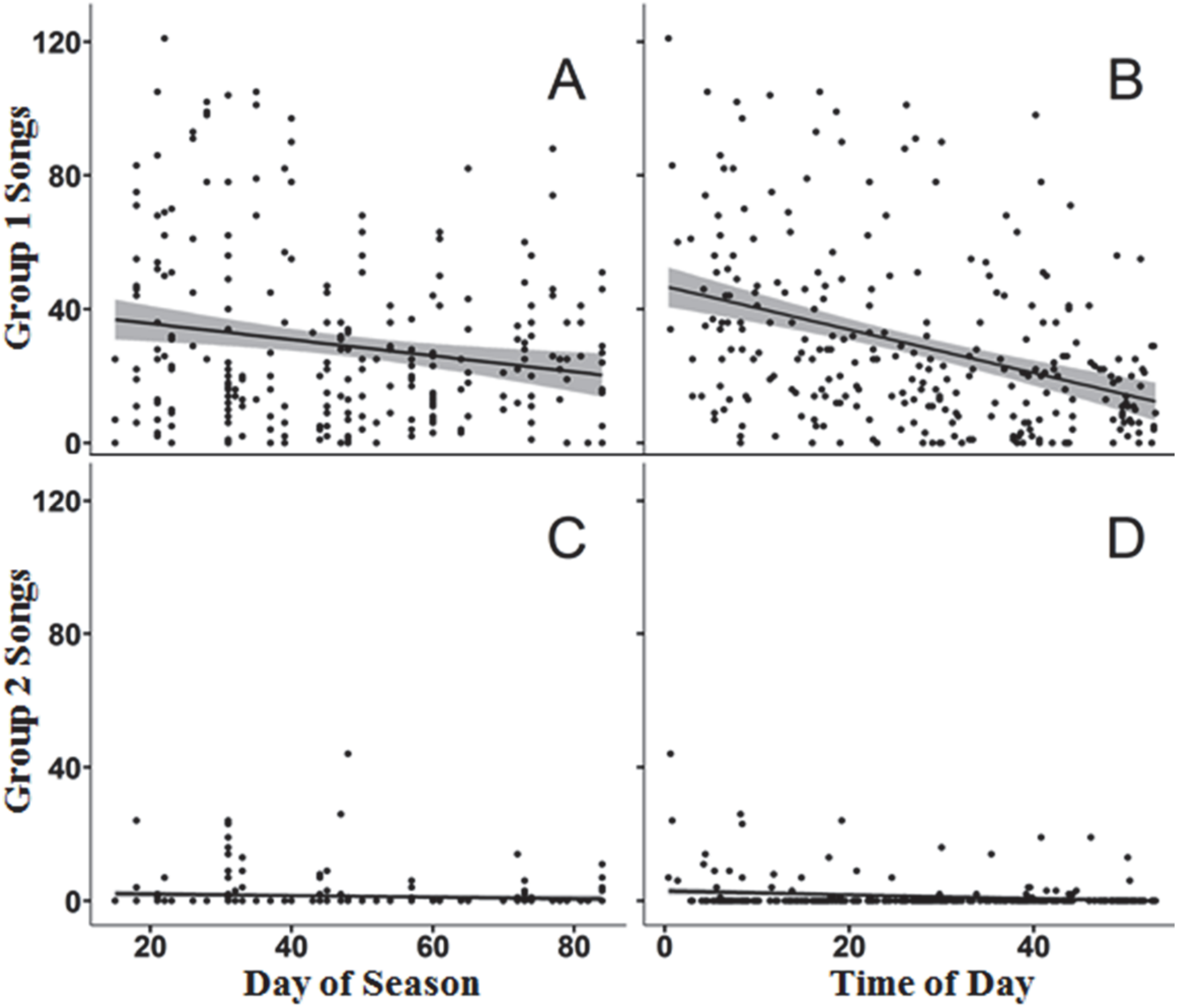

Figure 2.8. Field Sparrow fitted linear models (with 95% confidence intervals) of songs (per 5-min sample) by day of season (May 1 = 1) or time of day (1 unit = 5 min; 30-min before sunrise = 0). The scatter plots show day of season by group 1 songs (**A**), time of day by group 1 songs (**B**), day of season by group 2 songs (**C**) and time of day by group 2 songs (**D**). The 5-min audio samples were taken from recordings made between May and July at Big Oaks NWR (2012) and Fort Riley (2013).

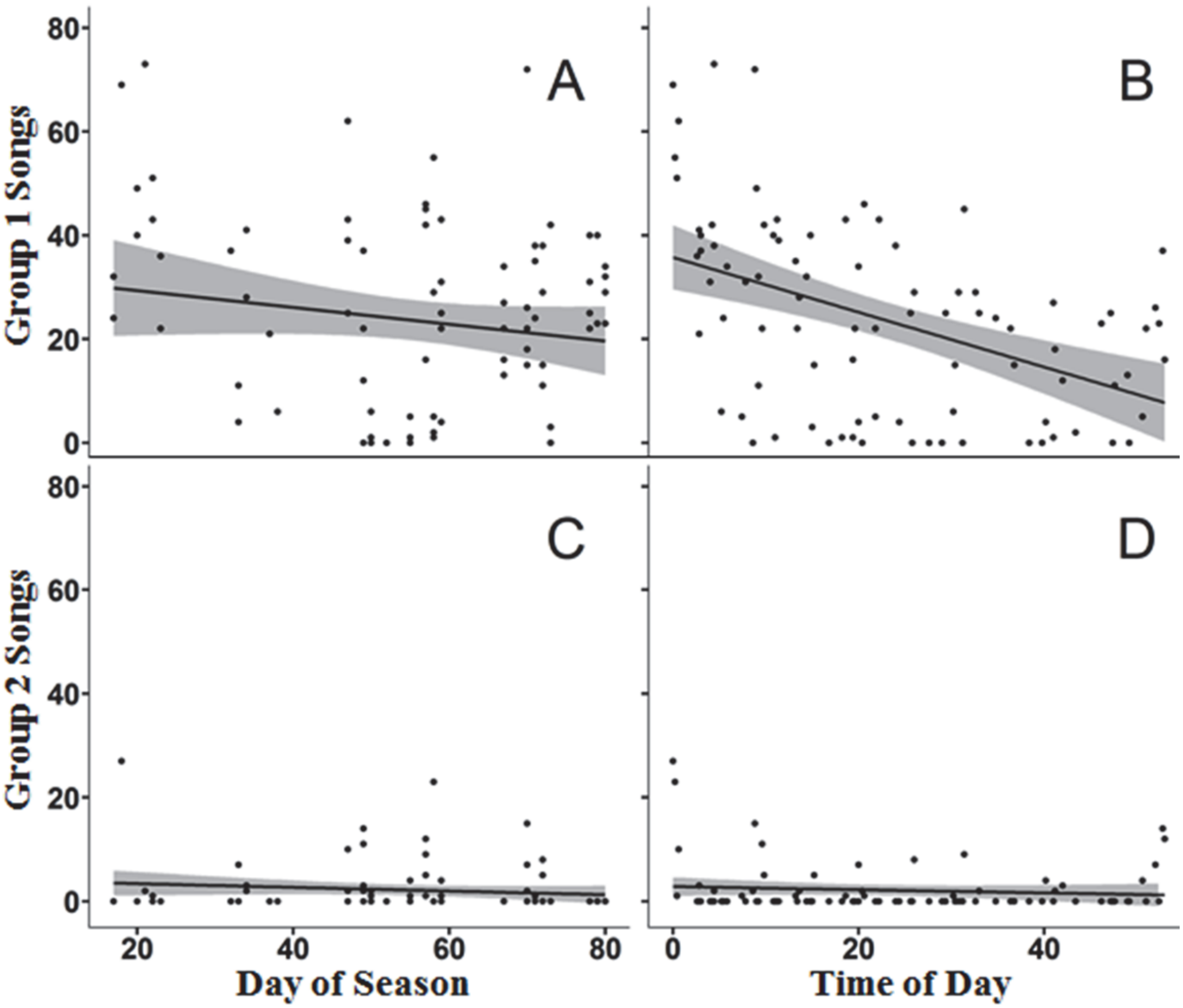

Figure 2.9. Grasshopper Sparrow fitted linear models (with 95% confidence intervals) of songs (per 5-min sample) by day of season (May 1 = 1) or time of day (1 unit = 5 min; 30-min before sunrise = 0). The scatter plots show day of season by group 1 songs (**A**), time of day by group 1 songs (**B**), day of season by group 2 songs (**C**) and time of day by group 2 songs (**D**). The 5-min audio samples were taken from recordings made between May and July at Fort Riley (2013).

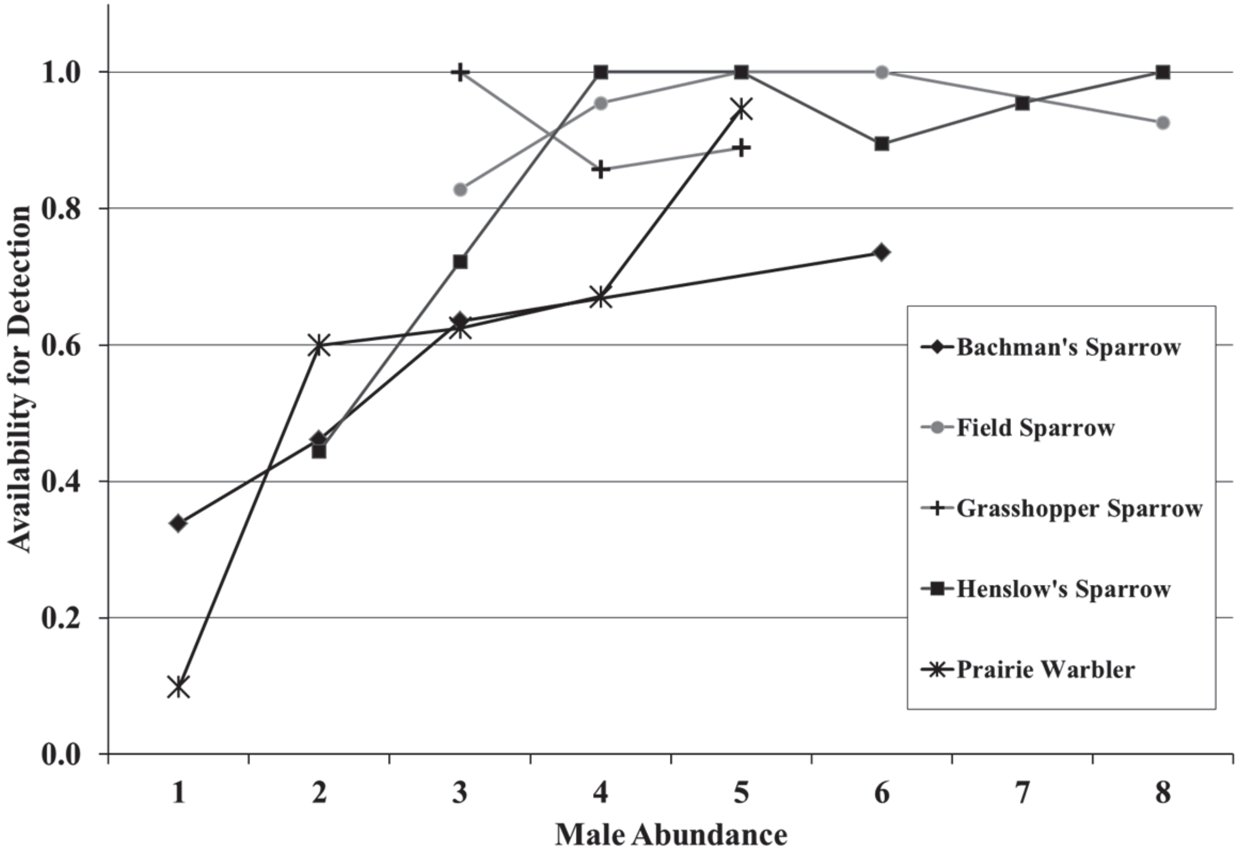

Figure 2.10. Species availability for detection (proportion of the 5-min audio samples that contained at least one song of a given species) by male abundance based on 5-min samples of audio recorded at 3 Department of Defense study areas, 2012-2013. Availability for detection was calculated as the proportion of 5-min samples that contained at least one song of the specified species.

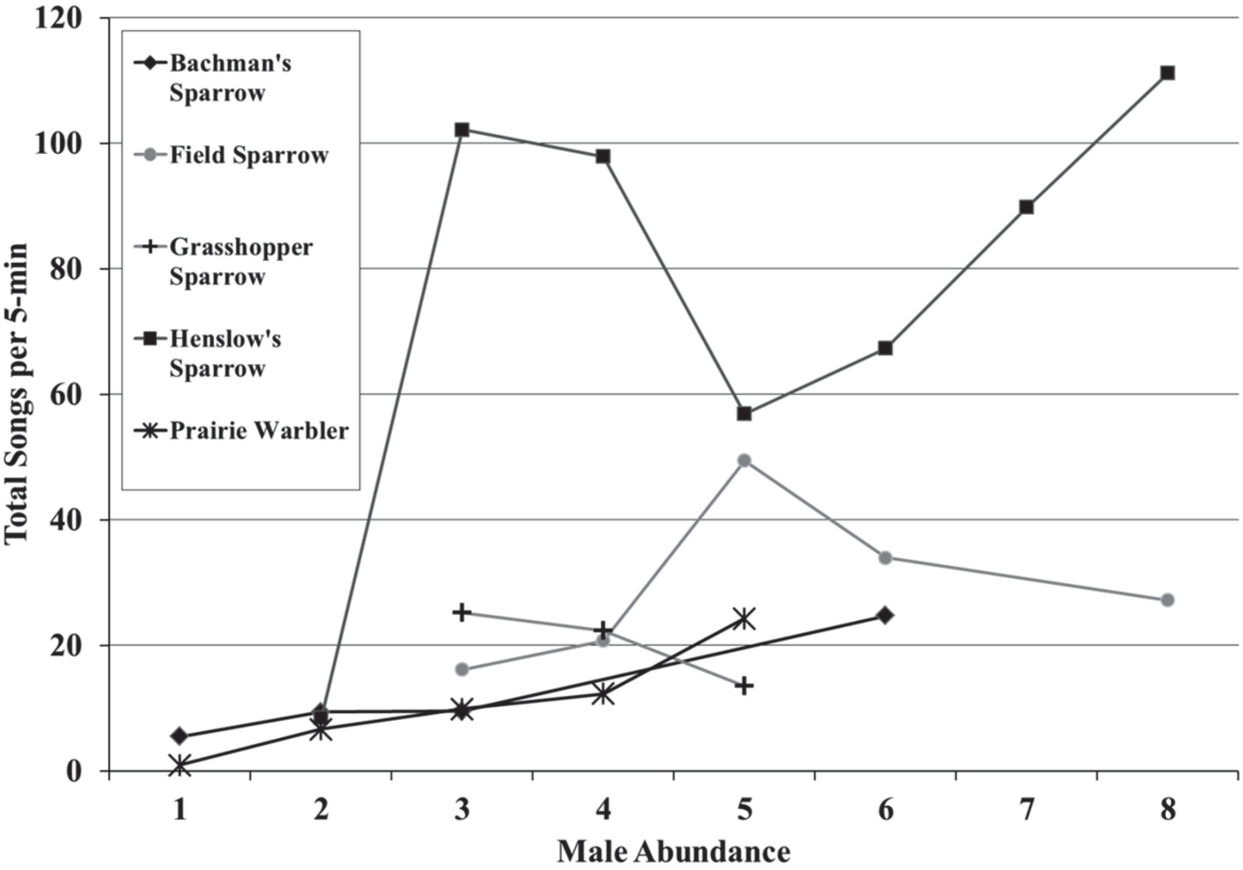

Figure 2.11. Average number of songs by male abundance based on 5-min samples of audio recorded at 3 Department of Defense study areas, 2012-2013.

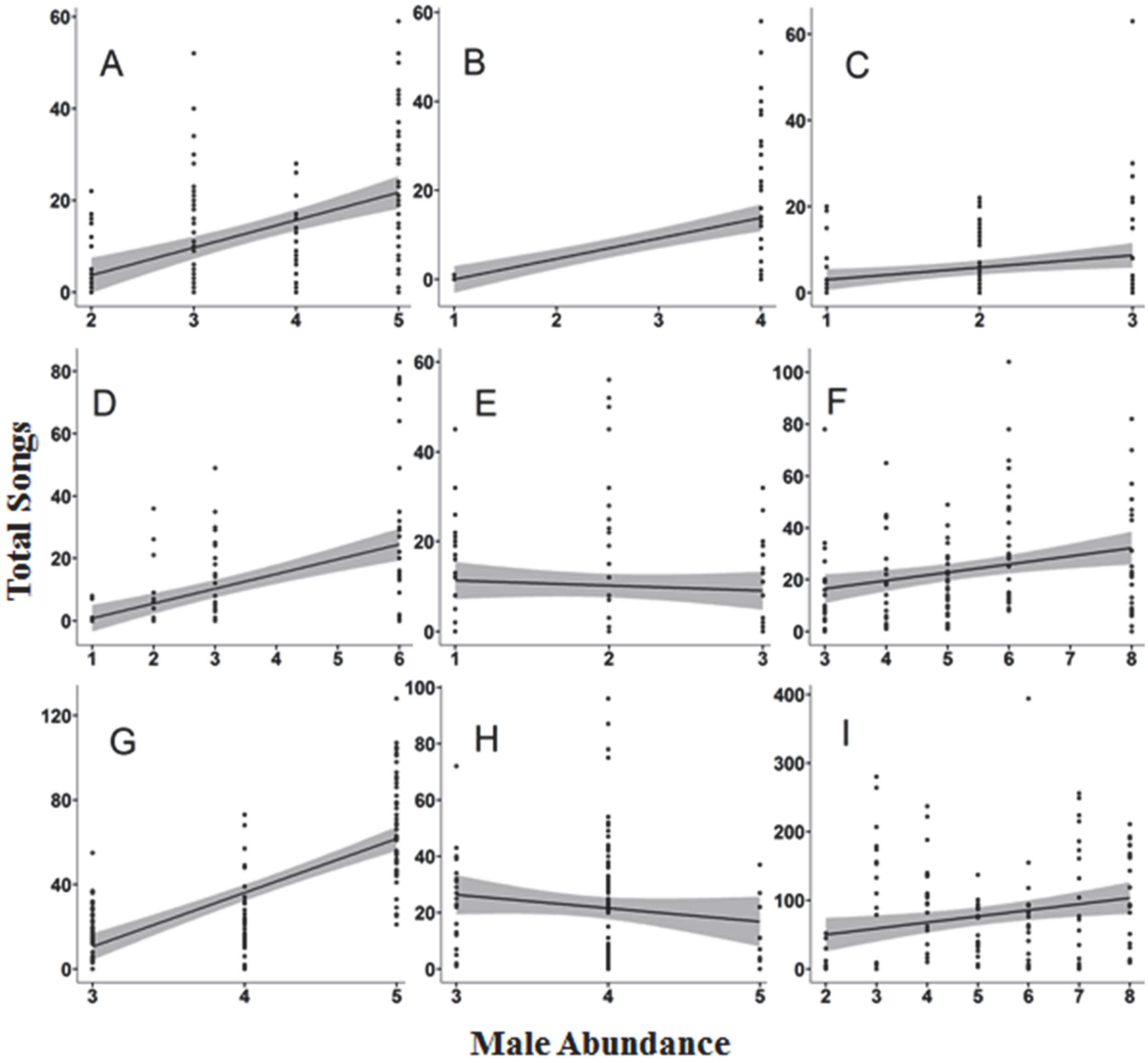

Figure 2.12. Fitted linear models (with 95% confidence intervals) of total number of songs in 5-min by male abundance. Models show the following: Prairie Warbler at Big Oaks NWR in 2012 (**A**), Fort Bragg in 2012 (**B**), and Fort Bragg in 2013 (**C**); Bachman's Sparrow at Fort Bragg in 2012 (**D**) and 2013 (**E**); Field Sparrow at Big Oaks NWR in 2012 (**F**) and Fort Riley in 2013 (**G**); Grasshopper Sparrow at Fort Riley in 2013 (**H**); and Henslow's Sparrow at Big Oaks NWR in 2012 (**I**).

Figure 2.13. Fitted negative binomial models (Table 2.4) and 95% confidence intervals of total numbers of songs observed by the total numbers predicted. Models show the following: Prairie Warbler at Big Oaks NWR in 2012 (**A**), Fort Bragg in 2012 (**B**), and Fort Bragg in 2013 (**C**); Bachman's Sparrow at Fort Bragg in 2012 (**D**) and 2013 [model with temperature (**E**) and model with atmospheric pressure (**F**)]; Field Sparrow at Big Oaks NWR in 2012 (**G**) and Fort Riley in 2013 (**H**); Grasshopper Sparrow at Fort Riley in 2013 (**I**); and Henslow's Sparrow at Big Oaks NWR in 2012 (**J**).

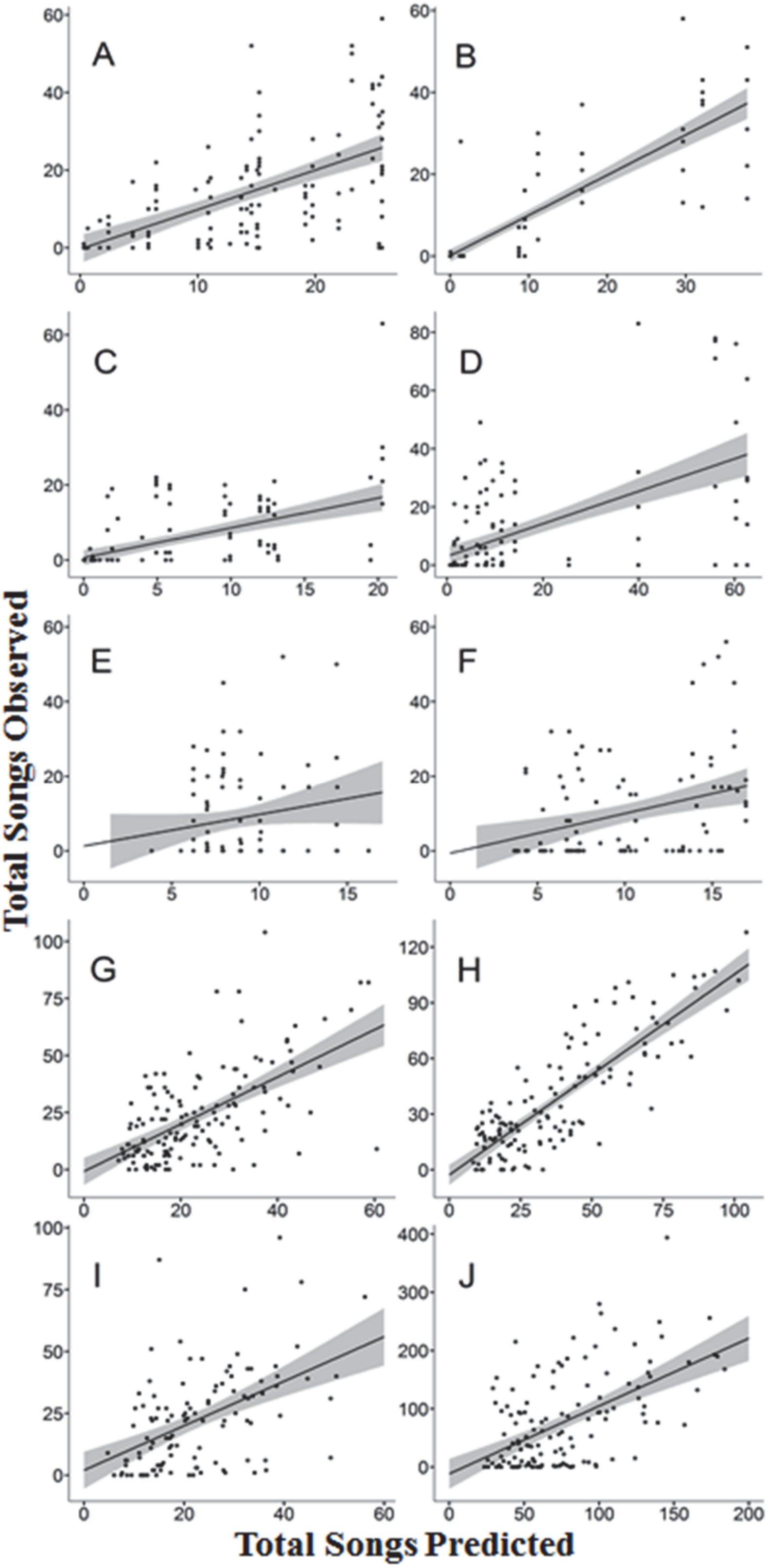

Figure 2.13 (continued)

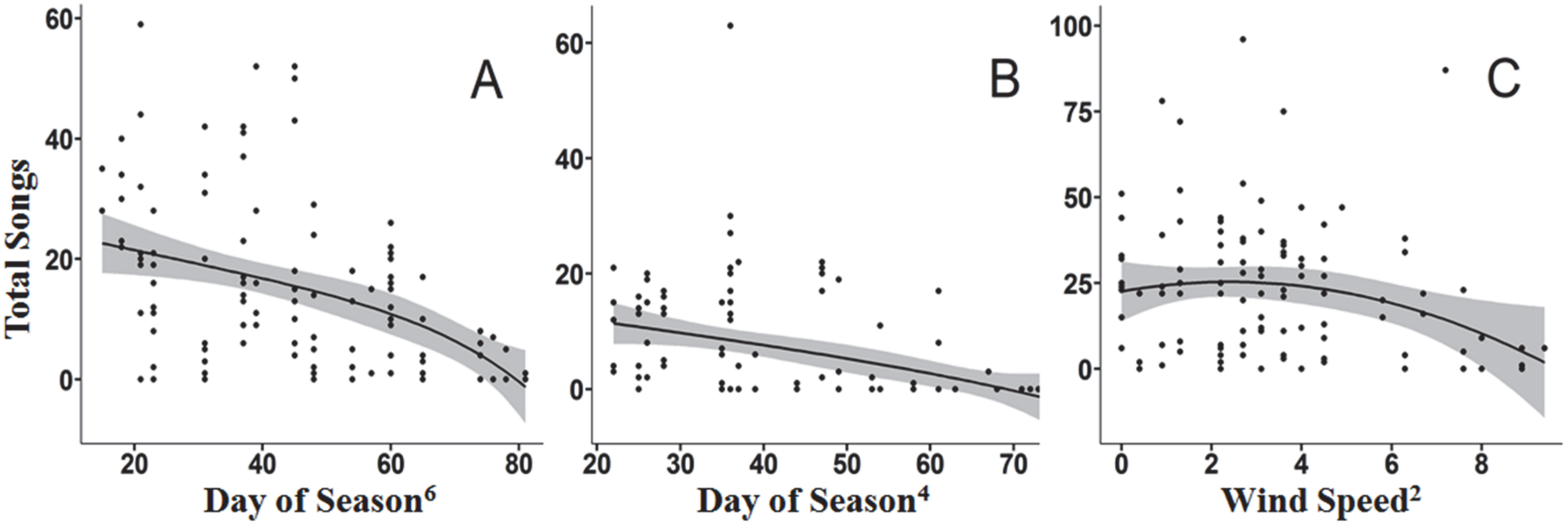

Figure 2.14. Fitted linear models (with 95% confidence intervals) depicting the relationships between the response variable and a significant exponentiated explanatory variable. Models show the following: total songs for Prairie Warbler at Big Oaks NWR in 2012 by day of season^6 (**A**); total songs for Prairie Warbler at Fort Bragg in 2013 by day of season^4 (**B**), and total songs for Grasshopper Sparrow at Fort Riley in 2013 by wind speed^2, m s^{-1} (**C**).

CHAPTER 3

Estimating Songbird Densities with a Passive Acoustic Cue-counting Approach

ABSTRACT

The need for improvements in avian wildlife monitoring efficiency, accuracy, and scope has led to increased development and use of new technologies such as autonomous recording devices and unmanned aerial vehicles. This chapter introduces the Balloon Aerial Recording System (BARS, or “balloon”), a novel technology that addresses these issues as well as the problem of ground-based land accessibility. The balloon takes advantage of the benefits of aerial monitoring and autonomous acoustic recording. The objectives of this chapter are (1) to describe and evaluate a novel acoustic approach for estimating densities of breeding songbirds and (2) to compare acoustic-based density estimates with estimates derived from typical avian population monitoring methods. Point- and line-based field tests were implemented across 3 study areas during 2011-2013 to directly compare balloon data and data collected with human-observer techniques in both real-bird communities and remotely controlled simulated-bird communities with known populations. The accuracy of both real- and simulated-bird estimates depended upon species and survey method. Excluding estimates from point counts, the balloon-based density estimates did not differ from spot map estimates for Prairie Warbler (*Setophaga discolor*), Bachman’s Sparrow (*Peucaea aestivalis*), or Henslow’s Sparrow (*Ammodramus henslowii*) but balloon estimates for Field Sparrow (*Spizella pusilla*) were much greater than the spot-map estimate. The human distance-sampling approach performed similarly to the balloon approach for real birds except the distance-sampling estimates for Field Sparrow did not differ from the spot-map estimates. Abundance estimates of simulated birds were closer to true abundances for the balloon than for human observers but simulated-bird density estimates from distance sampling were more similar to simulated-bird densities. Sources of variation in balloon

methodology that likely affected the accuracy and precision of population estimates included balloon flight dynamics (e.g., movement, speed, and altitude), human error in song selection during acoustic analyses, and calculation of effective detection areas available for recording. Some of these sources of variation can be controlled by additional development of the analytical methods. The accuracy of the balloon approach for Prairie Warbler, Bachman's Sparrow, and Henslow's Sparrow, under certain conditions, demonstrated the viability of the acoustic cue-count approach, especially if the suggested methodological improvements are adopted. Balloon technology can provide a feasible solution for wildlife monitoring in large and/or inaccessible areas and its versatility allows for broad wildlife applications beyond both military installations and avian population monitoring.

INTRODUCTION

Wildlife Monitoring Technologies

Passive acoustic techniques have many benefits for wildlife research and monitoring applications. Passive acoustics increase the amount of data that can be collected, eliminate the need for skilled field observers, and produce permanent, unbiased records. Marques et al. (2013) noted additional benefits of acoustic surveys in contrast to visual-based surveys including (1) increased detection range for animals that are more detectable by sound than by sight, (2) ability to survey during low-visibility conditions (e.g., fog, nighttime, etc.), (3) amenable to automated data collection and processing, and (4) data collection in environments that are inhospitable to humans.

Autonomous aerial monitoring systems also benefit wildlife research and monitoring in many of the same ways that passive acoustic monitoring does. Aerial systems also have additional benefits of potential increases in effort efficiency and sampling area extent, and ease of data collection in remote and/or hard-to-access areas. Beyond these benefits, aerial systems may also enable monitoring in previously inaccessible areas due to safety concerns, including Department of Defense (DoD) impact areas and regions of civil unrest.

A combined approach of passive acoustics and aerial monitoring systems has had very little attention in wildlife monitoring. Mobile acoustic recording systems have primarily been limited to towed and autonomous marine hydrophone systems and animal-borne recording tags (Marques et al. 2013). Autonomous aerial methods for monitoring wildlife typically employ unmanned aerial vehicles (UAVs) that are limited to either visual-based detection of animals (Jones et al. 2006, Koh and Wich 2012) or detection of radio-tagged animals (Dos Santos et al. 2014, Cliff et al. 2015). Therefore, UAV monitoring has been restricted to easy-to-spot, medium- to large-sized vertebrates (Jones et al. 2006, Vermeulen et al. 2013) and/or flocks of large birds (Chabot and Bird 2012), or radio-tagged animals. Furthermore, UAVs are not always feasible because of expense (Watts et al. 2010, Vermeulen et al. 2013) and UAV regulatory restrictions (Watts et al. 2010, Linchant et al. 2015).

Combining acoustic and aerial technologies could reap the benefits of both monitoring strategies. However, aerial acoustic monitoring is untested and it presents challenges in both application (i.e. noise interference from aerial device) and acoustic data analysis (i.e. density estimation without locating individual animals). With current available technology, powered UAVs are problematic for acoustic monitoring because motor noise and turbulence severely limit acoustic data quality. An alternative to UAVs is a passive, wind-propelled payload that uses an un-powered lifting system, such as a helium-filled weather balloon. One such system was developed and tested by Fristrup and Clark (2009). Although not validated, Fristrup and Clark (2009) estimated the number of individual birds recorded per flight based on average species song intervals (s song^{-1}). However, without information on species detection probabilities (given by distance sampling or otherwise), population densities could not be estimated from the numbers of detected individuals. As a result, Fristrup and Clark (2009) used the number of songs recorded as an index to relative abundance.

Acoustic-Based Population Density Estimation

Distance-sampling approaches are a common method for density estimation in both observer-based survey methods (Buckland et al. 2001) and passive acoustic methods (Thomas and Marques 2012, Marques et al. 2013). Distance sampling requires some form of localization of detected animals so distances from the observer/detector can be estimated. Although multi-sensor arrays are typically used for signal localization (Blumstein et al. 2011, Thomas and Marques 2012), distances to acoustic signals have been estimated with single-sensor hydrophones via multipath signal transmission under water (McDonald and Fox 1999, Aubauer et al. 2000). However, these conditions are generally not applicable to terrestrial single-microphone systems. Even if distances to signals could be estimated from aerial recordings, the assumed environment under which distance sampling is based does not apply to aerial monitoring of animals on the ground. Unlike the assumed distance-sampling environment, animals of interest in aerial monitoring are not in the vicinity of the recorder and detection distances would likely be within a relatively narrow range based on the recorder’s conical footprint. Thus, acoustic-based population estimation approaches that do not include distance sampling are needed.

Cue counts are the most plausible approach to density estimation when individual animals cannot be distinguished (Marques et al. 2013). Cue-count population estimates are based on a known cue rate that is applied to a count of cues detected per unit of time and area (Buckland 2006). Cue counting was originally introduced as a method for estimating densities of great whales (Hiby 1985) but has also been applied to bird surveys (Buckland 2006). Cue counts have some advantages and disadvantages when compared to standard point- or line-transect sampling (Buckland et al. 2015). Detection at zero distance (from a survey point or line transect) during a cue count is assumed to be 100% only if an individual presents a cue, whereas detection is assumed to be 100% during typical point/line-transect sampling whether the animal presents itself or not. Another advantage of the cue-count approach is that individual animals do not need to be identified or accounted for to avoid double sampling. A statistical disadvantage of cue counts is that repeated cues from the same individual are not independent (Buckland et al. 2015). However, traditional sampling methods that largely rely on acoustic cues also violate the assumption of detection independence because avian auditory availability often increases with abundance (Chapter 2; Sexton et al. 2007, Laiolo and Tella 2008, Warren et al. 2013). The practicality of cue counts is challenged by the need to estimate mean cue rate, which may vary with factors such as weather, habitat, bird density, time of day, and season (Chapter 2; Buckland et al. 2015).

Cue counts are traditionally used as a variation of distance sampling where counts of cues and distances to cues are recorded by observers (Buckland 2006). Although uncommon, other studies have used cue-count approaches without distance estimation. Thompson et al. (2010a) and Thompson et al. (2010b) created and validated an abundance index (based on linear regression of abundance and cue rate) for estimating abundances of African forest elephants (*Loxodonta africana cyclotis*) from acoustic recordings. Elephant population estimates were similar to, but much more precise than, dung-based survey estimates (Thompson et al. 2010a). Abundance indices have also been used to estimate abundances/densities from acoustic cue counts of Pacific humpback dolphins (*Sousa chinensis*) (Van Parijs et al. 2002), Fowler's toads (*Bufo fowleri*) and bullfrogs (*Rana catesbeiana*) (Shirose et al. 1997), and *Rhyzopertha dominica* larva (Hagstrum et al. 1988).

Study Objectives

The primary objective of this chapter is to describe and evaluate a novel acoustic approach for estimating densities of breeding songbirds from mobile, single-microphone recordings. The recordings were collected by the Balloon Aerial Recording System (BARS, or "balloon"), an instrumentation payload designed and built by personnel in the Environmental Sensors Lab, Department of Biosystems Engineering and Soil Science, University of Tennessee, Knoxville (Hockman in prep.). The design of the balloon was conceptually based on the aerial recording system developed by the Cornell Lab of Ornithology and implemented by Fristrup and Clark (2009). The focal songbird species, studied across 3 study areas, were Prairie Warbler (*Setophaga discolor*), Bachman's Sparrow (*Peucaea aestivalis*), Field Sparrow (*Spizella pusilla*), Grasshopper Sparrow (*Ammodramous savannarum*), and Henslow's Sparrow (*Ammodramus henslowii*). Northern Bobwhite (*Colinus virginianus*) was also included in part of the study (i.e. simulated-bird tests).

The second objective was to compare acoustic-based density estimates with estimates derived from typical avian population monitoring methods (i.e. human observer-based point-count and line-transect distance sampling). In addition to these objectives, this study addressed 2 of the major research needs for passive acoustic population estimation described by Marques et al. (2013). First, the analysis approach used in this study incorporated information on the acoustic behavior of the focal species (Chapter 2). Second, this study evaluated the use of the balloon when true bird densities were known.

METHODS

Study Areas

We selected 3 study areas from eastern Department of Defense (DoD) installations for this research based on their ability to represent (1) a range in cover types that occur on eastern United States DoD installations (i.e. grasslands, forests, savannas), (2) a range in climate (e.g., wind conditions, temperature, relative humidity), and (3) avian species of interest to land managers for acoustic monitoring (Fischer et al. 2011). DoD installation willingness to host our research, as well as the practicality of fulfilling our objectives without interfering with DoD training activities, were also critical factors in the selection process.

Big Oaks National Wildlife Refuge (NWR), Indiana. The northern-most installation, previously known as Jefferson Proving Ground (JPG), is a deciduous forest intermixed with open grasslands and oak savannahs. JPG is representative of other midwestern installations, such as forts Campbell, KY, Knox, KY, Leonard Wood, MO, and McCoy, WI. The climate is warm with intermediate humidity and moderate winds. Prairie Warbler, Field Sparrow, and Henslow's Sparrow were the focal species at this study area. We collected data at this study area during May-August 2011 and May-July 2012.

Fort Riley, Kansas. Fort Riley is located in an open grassland/scrub/agricultural landscape. It is representative of the open landscapes found in many Great Plains (e.g., Fort Sill, OK) and southwestern (e.g., Fort Bliss, TX) installations. Climatic conditions are hot, semi-arid, and windy. The focal species for this study area were Field Sparrow, Grasshopper Sparrow, and Henslow's Sparrow. We collected data at this study area during May-August 2011 and May-July 2013.

Fort Bragg, North Carolina. Fort Bragg is located within a Longleaf (*Pinus palustris*) and Loblolly (*Pinus taeda*) pine-dominated landscape. The Fort Bragg landscape is representative of many other southeastern coastal plain installations, such as Eglin Air Force Base, FL, Camp Lejeune, NC, Fort Benning, GA, and Fort Stewart, GA. The climate is hot and humid with generally light winds. The focal species for study at Fort Bragg were Prairie Warbler and Bachman's Sparrow. We collected data at this study area during May-July, 2012 and 2013.

Real-bird Surveys

Each study area was visited twice over the course of 3 years. We established 3 survey sites (at least 4 km apart) in each of the 3 study areas each year for a total sample size of 18 sampling units (3 sites × 2 years × 3 study areas = 18). Survey site size ranged from 21 to 25 ha. Point counts and 2 types of line transects (henceforth referred to as line transects and free flights) were performed at each site, unless noted otherwise (survey sample sizes in Table 3.1). Real-bird surveys were carried out during peak singing hours generally between sunrise and 4 hr after sunrise from May 15 to July 23, 2011-2013.

Point-count surveys. Standard 10-min unlimited-distance point counts were performed on real-bird communities at each site on Big Oaks NWR and Fort Riley. For each survey, a trained human observer recorded focal species and distances from a fixed point following established methods derived from Reynolds et al. (1980) and Ralph et al. (1995). Simultaneously, the balloon was deployed on a tether system ~100-150 m above the survey point. The tether system was comprised of a fishing rod with 14-kg fishing line and a technician who operated the system from the ground. The balloon (attached to the end of the fishing line) was allowed to reach the desired altitude by free-spooling line from the reel. The tether system not only allowed for easy deployment and recovery of the balloon, technicians were also able to control the position of the recording system. Since the wind was likely to alter the position of the aerial system within the duration of a survey, the system was monitored with real-time GPS (global positioning system) from a laptop base station (via radio-frequency modem). If the balloon shifted from its location above the survey point, the technician at the base station instructed the tether operator to move in such a way that would correct for the change in wind. Real-bird point counts were not conducted at Fort Bragg because the area's forest canopy cover made the tether system impractical to use.

Line-transect surveys. Standard unlimited-distance line transects were performed along marked 500-m lines within each site on Big Oaks NWR and Fort Riley. For each survey, a trained human observer traveled at ~1 km hr^{-1} along the transect line and recorded individual detections of focal species on either side of the line. Observers followed standard line transect survey protocols from Burnham et al. (1980) and Buckland et al. (2001). Recorded data included time of detection, type of detection (aural or visual), and either the perpendicular distance of the bird from the line or the sighting angle and radial distance from observer to the bird at first detection. Simultaneously, the balloon was deployed along the transect line on the tether system,

~100-150 m above ground. The tether operator walked at ~5 km hr^{-1} to simulate a fast pace, more comparable to the speed the balloon would travel during un-tethered flights. The balloon was monitored from a laptop computer similar to point count surveys. The base station technician directed the tether operator to adjust the position of the balloon as needed so travel approximated a straight line over the designated transect.

Free-flight surveys. Free-flight surveys followed the same procedures as line transect surveys except there was no tether system and the transect line was determined by the wind-dependent flight path of the balloon. Due to the limited predictability of balloon travel during these surveys, free flights were only performed using real-bird communities (except on Fort Bragg where the forest canopy cover was not conducive to the tether system). For each survey, a human observer conducted a line transect survey according to the previously described line transect protocol. Instead of following a marked transect line, observers walked a 500-m line transect between the start and end GPS coordinates from the balloon flight path over the study site. Observer surveys began during or immediately following the balloon flight. Only flights that successfully traversed the established survey sites were included in the analyses. Balloon target altitude during free flights was ~100-250 m.

Spot-mapping surveys. Spot-mapping surveys were conducted to provide estimates of bird densities from which comparisons could be made to real-bird distance-sampling and balloon density estimates. This method was chosen because it has been considered a standard against which other survey methods are compared (Bibby 2000). Spot-mapping surveys for each study site were performed on a semi-weekly basis, ~8 times per field season. Each repetition covered the extent of the survey site. Based on methods derived from Franzreb (1976), a human observer started in a randomly selected corner of the survey area and systematically covered the site by walking at a slow, observant pace along lines that were marked with flagging every 100 m. Using descriptive symbols, the observer drew a detailed map of the target species detected within a 50-m buffer around the site, including age, sex, breeding status, behavior, and movement. Spot-mapping surveys were performed during peak activity hours (from 0.5 hr before sunrise to 4 hr after sunrise).

Simulated-bird Surveys

In addition to real-bird surveys, point counts and line transects were also performed on simulated-bird communities with known populations. Simulated-bird surveys were conducted according to the same protocols described for real-bird surveys except only simulated birds were considered for detections (and thus, all observations were aural) and distances were fixed to a maximum of 150 m. Free-flight surveys were only conducted with simulated birds at Fort Bragg where forest structure made tethered line-transects impractical. Simulated surveys took place in the same locations as real-bird surveys with the exception of point counts at Fort Bragg, which were performed in open areas near the survey sites.

The bird-simulator system was developed by personnel in the Environmental Sensors Lab, Department of Biosystems Engineering and Soil Science, University of Tennessee, Knoxville. The design of the system was modeled after the amplified mp3 playback system described in Simons et al. (2007). Bird simulator deployment aimed to reproduce real-bird point-count conditions, which are primarily based on auditory cues (Faanes and Bystrak 1981). For simulated point counts, a network of ~16 bird song simulators was deployed, with each simulator on a tripod within a 150-m radius of the fixed survey point. Simulator locations were predetermined by randomly selecting directional degrees (1°-360°) and distance (1-150 m) from the fixed point-center. For simulated line transects and free flights, ~20 simulators were deployed on tripods along either side of a 500-m transect, all within a 150-m perpendicular distance of the transect line. The distance down the transect line, as well the perpendicular distance from the line, were randomized for each simulator location. Randomizations were stratified so there were 4 simulators along each of the 5, 100-m segments of the transect. Simulators were elevated only to surrounding vegetation height so observers were only able to visually detect simulators close to the point or line, much like the case in real-bird surveys.

During surveys, a technician operated the simulators remotely from a laptop base station via radio-frequency modem. For each simulated-bird survey, a different randomly formulated playlist of songs was sent to each of the simulators. All songs (5 per species) were selected from typical field recordings of the focal species, obtained from the McCauley Library (Cornell Lab of Ornithology, Ithaca, NY). Species varied based on study area [Big Oaks NWR (Northern Bobwhite, Prairie Warbler, Field Sparrow, and Henslow's Sparrow); Fort Bragg (Northern Bobwhite, Prairie Warbler, Bachman's Sparrow, and Field Sparrow); Fort Riley (Northern Bobwhite, Field Sparrow, Grasshopper Sparrow, and Henslow's Sparrow)]. Each simulator played an assigned bird song at an interval (5-14 s) based on the average singing rate of the species. The song rates used for the simulators were calculated based on interval measurements from random samples of audio files in the McCauley Library. Amplitude/volume of each track was calibrated to average amplitudes measured in the field from a sample of individuals of each species using a 732A sound level meter (B&K Precision Corporation, Yorba Linda, CA).

Simulated-bird surveys were best performed with as little real-bird activity as possible. Therefore, these surveys were completed late in the field season and after peak singing hours. However, not all real-bird vocalizations could be avoided during these field tests, especially because the simulators themselves provoked responses from resident birds. To remedy this problem, a unique tone was appended to the end of each simulated song, which identified it from other simulated songs and from real-bird vocalizations. Observers were instructed to only record the detection of bird songs which had the appended unique tones.

Density Estimation for Observer-based Surveys

Densities based on point-count and line-transect distance sampling were estimated using Program DISTANCE software, Version 6.2 release 1 (Thomas et al. 2010). Only detections of singing males were used in the distance models. This prevented overestimations of densities caused by detecting both males and females at close distances but only males at far distances. Only including singing males in the analyses also made the distance-sampling density estimates more comparable to estimates from acoustic methods (also based on singing males) and from spot mapping (based on male territories). Depending on model performance, either the conventional distance sampling or the multiple covariates distance sampling analysis engine was used. Covariates used during distance model selection for all species and both bird types (i.e. real and simulated) were study area and year. For real birds only, temporal and weather-related covariates were also used during model selection. These covariates were chosen *a priori* for each species based on significant covariates in the song activity models from Chapter 2.

The analysis approach, guidelines, and model selection processes described in Marques et al. (2007) and Thomas et al. (2010) were followed. For each focal species and sampling method (point count or line transect), the detection function was modeled globally but densities were estimated for each type of survey (i.e. point count, line transect, or free flight) at each site in each study area (sample sizes in Table 3.1). All distances for each species were first examined without binning or truncation, after which strategic truncation distances and/or cut-points were chosen based on guidelines and recommendations from Buckland et al. (2001) and Thomas et al. (2010). Selection of the final model was based on model performance/fit (i.e. corrected Akaike's information criterion (AIC_c) and goodness-of-fit chi-square test) and logical feasibility of the detection function given the distance data.

Analysis of distance data from simulated-bird point counts was approached in a slightly different way from analysis of real-bird point counts. Bird simulator placement, for both points and lines, was randomized to simulate an approximately equal number of birds in each distance band out to 150 m. For point counts, this resulted in greater densities of simulators close to the observer because area increased with distance from point center. To account for this facet of the sampling design, simulated point counts were analyzed as line transects in Program DISTANCE. Line length for each survey was set to 235.62 m so the area of each point count ($A = \pi \times 150^2 = 70{,}686\ m^2$) equaled the area of each line transect ($A = 235.62 \times 300 = 70{,}686\ m^2$) in Program DISTANCE.

Simulated-bird line transect data were analyzed in the same way as real-bird data but line length for most free flights (Fort Bragg only) was adjusted in Program DISTANCE to account for the area of the simulator network (a 300- x 500-m rectangle) that overlapped the width of the surveyed transect. The area of overlap was measured using ArcMap 10.1 (ESRI 2012) by overlaying the simulator network area and a 150-m buffer on either side of the line transect (based on the start and end GPS coordinates used by the observer). Line length for each free-flight transect was then calculated by dividing the area of overlap by 300 m (150-m distance on either side of line transect). The areas of overlap were also used to calculate true simulator densities for the human-observer surveys.

Spot-map survey data were analyzed for each survey site following Bibby (2000). For sites with >8 visits, at least 3 detections, each ≥10 days apart qualified as a territory. For sites with ≤8 visits, at least 2 detections, ≥10 days apart, qualified as a territory. An active nest automatically qualified as a territory. Based on Bibby (2000), the total the number of delineated territories within the study site boundaries equaled the number of territories that fell completely within the site boundaries plus the proportions (visually estimated to the nearest 10th) of edge territories that overlapped site boundaries.

Acoustic Data Processing

Audio spectrograms for each balloon flight were created and annotated with Raven Pro software, Version 1.5 (Bioacoustics Research Program 2014). Technicians trained in aural and visual acoustic identification of focal species songs selected and annotated songs of each focal species for each flight on Raven Pro spectrograms. Total songs for each species and flight were summed based on the selections. I proofed the annotations of the flight audio files made by the technicians by examining a random sample of files, stratified across study area, year, bird type (i.e. real or simulated), and flight type (≥20 1-min samples per species per bird type). My song counts were then modeled with technician song counts as the explanatory variable using negative binomial regression (function "glm.nb") with package "MASS" (Venables and Ripley 2002) in program R (R Core Team 2015). Song counts for each species and bird type (i.e. real or simulated birds) were modeled separately. A quadratic function of technician song counts ($y = x + x^2$) was used if the function was significant ($\alpha = 0.05$) and if it lowered the model ΔAIC_c by 2 or more. The selected models for each species were used to adjust technician song counts for all audio files. In general, this approach increased the total number of detections per audio file by ~70% for real birds and ~30% for simulated birds.

Effective Flight Area Calculation

Effective flight area was an adjusted measure of the flight footprint (ground area exposed to the balloon microphone) based on the amount of time each squared meter was available to be recorded by the microphone. ArcMap 10.1 and ArcMap 10.1 ModelBuilder (ESRI 2012) were used for the following 4 calculation steps. First, balloon elevation for each flight GPS point was adjusted to height above ground based on 1-m Digital Elevation Models (DEMs). Second, a buffer was created around each balloon GPS point based on the experimentally-tested BARS footprint of acoustic detection [1:1 relationship between balloon height above ground and footprint radius (Hockman in prep.); Figure 3.1]. Third, the layered buffers were converted to individual raster matrices and added together at the pixel level. This step associated each 1-m pixel in the flight footprint with an exposure time expressed in the number of GPS points. Fourth, all pixel values were summed for a total flight exposure in m^2 GPS points.

To convert the ArcMap output (in m^2 GPS points) to m^2 seconds, each exposure (in m^2 GPS points) was multiplied by the average time value that each GPS point represented during the flight (typically ~1.5 s per GPS point). Effective flight area was then calculated by dividing the exposure m^2 seconds by the total duration (s) of the flight. For real-bird flights, effective flight area (m^2) was used to calculate bird density from estimated bird abundance.

Population Estimation from Acoustic Cue Counts

Real birds. Negative binomial regression models (based on Chapter 2 analyses) were used to predict bird abundances for Prairie Warbler, Bachman's Sparrow, Field Sparrow, and Henslow's Sparrow. To construct more robust models for Bachman's Sparrow and Prairie Warbler at Fort Bragg, the Fort Bragg song data for 2012 and 2013 were pooled and new models were selected (based on criteria described in Chapter 2 methods). The variables selected in the Chapter 2 models of song activity were used to construct a new set of negative binomial models (Table 3.2) with abundance as the response variable and a forced intercept through zero. The forced intercept allowed the models to predict abundances that were less than the abundances in the original data. Grasshopper Sparrow abundances could not be estimated because abundance was not a significant explanatory variable for song activity (Chapter 2).

For each balloon flight and applicable species, the corrected number of songs in the audio recording was first adjusted to reflect a 5-min period (songs × 5 min / audio duration in minutes). Songs per 5 min was then input into the corresponding model in Table 3.2 along with applicable temporal and/or weather-related data. The predicted abundance was divided by the effective flight area to estimate the density of singing males per hectare.

Simulated birds. Acoustic data collected by the balloon were used to estimate simulated-bird abundances with the following equation:

Equation 3.1

$$\frac{(Songs\ \times Mean\ song\ interval)}{Mean\ exposure\ time}$$

Songs were based on the adjusted counts from the acoustic analysis in Raven Pro. Mean song interval (duration between the initiation of a song and the initiation of the subsequent song) was species-specific and it varied from 5 s (Henslow's Sparrow) to 14 s (Field Sparrow). Mean exposure time for the available simulators of a given species was determined by the exposure time (in m^2 seconds; see section on Effective Flight Area Calculation). First, the flight footprint area was used to determine if a bird simulator was exposed to the balloon recorder. Second, the flight exposure model was used to approximate the duration that the simulator was exposed to the balloon recorder (i.e. exposure time). For each flight, the mean exposure time in Equation 3.1 was calculated as the average of the individual exposure times of the simulators for a single species. Simulators that were not available for recording based on the flight footprint were not included in the mean exposure time.

Similar to the procedure used for observer-based free-flight tests, true simulator abundances and densities were determined by overlaying the balloon flight footprint and the area containing the simulator network in ArcMap 10.1 (ESRI 2012). True simulator abundance for comparison to each balloon flight was the total number of simulators that fell within the flight footprint. Density was then calculated as the true abundance divided by the area of overlap between the simulator network and the flight footprint. Likewise, balloon-estimated densities were calculated as the estimated simulator abundance (Equation 3.1) divided by the area of overlap between the simulator network and the flight footprint.

Density Estimate Comparisons

A total of 28 mixed-effects model ANOVAs (analyses of variance), followed by Tukey's HSD (honest significant difference) tests, were performed on density and abundance data for real and simulated birds. Models were fitted with restricted maximum likelihood estimates. The fixed effects in real-bird models were the unique combinations of estimation method (i.e. spot map, human observer, or balloon) and survey type (i.e. point count, line transect, or free flight; applicable to human and balloon estimates only). Fixed effects included balloon population estimates from point counts, line transects, and free flights; human-observer based estimates and/or counts from point counts, line transects, and free flights; and either the spot-map density estimates or the true simulator "populations" during point counts, line transects, and free flights. The random effect in models comparing population density estimates was study site. The random effect in models comparing simulator abundances was the sample unit (i.e. each individual flight survey). All tests were performed with program R (R Core Team 2015), using packages "lme4" (Bates et al. 2015), "lmerTest" (Kuznetsova et al. 2015), "pbkrtest" (Halekoh and Højsgaard 2014), and "lsmeans" (Lenth 2015). Because significant ($P < 0.05$) ANOVA results did not necessary indicate differences in pairwise comparisons that were of interest for our analyses (differences, e.g., between "true PC" and "true LT" were irrelevant), only results from the subsequent Tukey's HSD tests were reported with the results. In the Results section, estimates were reported with standard errors and all density estimates were reported in singing males per 10 ha for ease of interpretation.

Real birds. Results of the 4 mixed-effects models (and subsequent Tukey's HSD tests on fitted ANOVAs) that were performed on real-bird data (1 model per species for Prairie Warbler, Bachman's Sparrow, Field Sparrow, and Henslow's Sparrow) were interpreted based on pairwise comparisons of least-squares means and Tukey's HSD groupings between each fixed effect and the spot-map estimate for the study site. The linear relationships between spot-map (x) and balloon (y) density estimates for each study site were also compared (with adjusted R^2) to the linear relationships between spot-map (x) and human-observer (y) estimates. The linear relationships were modeled with the “lm” function in program R (R Core Team 2015).

Simulated birds. Because effective areas sometimes varied between the balloon and human surveys (see section on Density Estimation for Observer-Based Surveys), the true simulator populations were often different for concurrent balloon and human surveys. Thus, mixed-effects were modeled separately for balloon data and human data. Four sets of six models (one per species for Northern Bobwhite, Prairie Warbler, Bachman’s Sparrow, Field Sparrow, Grasshopper Sparrow, and Henslow’s Sparrow) were used to compare fixed effects and simulated-bird population indices. The 4 sets of models made the following comparisons for each species: (1) simulator abundances estimated from balloon recordings (Equation 3.1) during each survey vs. true abundances within the balloon footprint, (2) numbers of individual simulators (of a species) recorded by human observers during each survey vs. true simulator abundances within 150 m of the observer, (3) means for balloon-based simulator density estimates for each study site vs. true means of simulator densities for each study site and (4) human-based simulator density estimates (from Program DISTANCE) for each study site vs. true means of simulator densities for each study site. The linear relationships between the true density estimates (x) and balloon (y) density estimates for each study area were also compared (with adjusted R^2) to the linear relationships between true density estimates (x) and human-based (y) distance-sampling estimates. The linear relationships were modeled with the “lm” function in program R (R Core Team 2015).

RESULTS

Real Birds

For Prairie Warbler, spot-map density estimates (2.92 ± 0.50) did not differ from balloon estimates for line transects (3.36 ± 0.65) or free flights (2.71 ± 0.55), nor from human-based estimates for point counts (3.59 ± 0.65) or line transects (2.55 ± 0.65) (Table 3.3). However, the balloon point-count estimate (5.88 ± 0.65) was greater than the spot-map estimate and the human-based estimate from free-flight surveys (1.12 ± 0.55) was less than the spot-map estimate. For Field Sparrow, spot-map (2.50 ± 1.19) and human-based (0.73-2.51 ± 1.23-1.39) density estimates did not differ for any survey type but all 3 balloon estimates (7.55-10.15 ± 1.23-1.39) were much greater than the spot-map and human estimates (Table 3.3). For Henslow's Sparrow, spot-map, balloon, and human estimates did not differ for line transects or free flights. Both balloon (22.14 ± 2.40) and human (15.08 ± 2.40) point-count estimates of Henslow's Sparrow densities were much greater than the spot-map estimates (7.84 ± 2.35). Bachman's Sparrow density estimates did not differ among methods (Table 3.3).

Based on linear models (Figure 3.2), balloon density estimates were moderately related to spot-map density estimates for Prairie Warbler (adjusted $R^2 = 0.39$), Field Sparrow (adjusted $R^2 = 0.46$), and Henslow's Sparrow (adjusted $R^2 = 0.58$). The balloon density estimates for Bachman's Sparrow were not significantly related to spot-map density estimates (adjusted $R^2 = -0.24$, $P = 0.89$). Human-based density estimates were strongly related to spot-map densities for Bachman's Sparrow (adjusted $R^2 = 0.70$); moderately related to spot-map densities for Prairie Warbler (adjusted $R^2 = 0.43$) and Field Sparrow (adjusted $R^2 = 0.40$); and weakly related to spot-map densities for Henslow's Sparrow (adjusted $R^2 = 0.21$) (Figure 3.2).

Simulated Birds

Abundance indices. Balloon abundance estimates did not differ from simulator abundances for Northern Bobwhite point counts or free flights; for any Prairie Warbler survey type; or for Bachman's Sparrow, Grasshopper Sparrow, or Henslow's Sparrow point counts (Table 3.4). Large standard errors and wide confidence intervals indicated a lack of precision in Northern Bobwhite estimates. Balloon estimates of simulator abundance tended to be high for Northern Bobwhite and Field Sparrow (Table 3.4). Line transect estimates for Northern Bobwhite (20.77 ± 2.03) were much greater than true abundances (3.92 ± 2.03). Balloon Field Sparrow estimates (4.94-8.89 ± 0.26-0.53) were greater than actual numbers of simulators (3.29-4.22 ± 0.26-0.53) for all survey-type comparisons (i.e. point count, line transect, and free flight). Bachman's Sparrow estimates based on free-flight data (5.46 ± 0.42) were greater than Bachman's Sparrow simulator abundances (3.21 ± 0.42). Balloon abundance estimates based on line transect surveys were less than true abundances for Grasshopper and Henslow's sparrows (Table 3.4).

Mean numbers of detections made by human observers did not differ from simulator abundances for Northern Bobwhite point counts or line transects, for Bachman's Sparrow free flights, or for Field Sparrow free flights (Table 3.5). Human observers recorded greater numbers of detections (compared to the numbers of simulators available within 150 m) when surveying Northern Bobwhite (3.72 ± 0.18; true = 2.44 ± 0.18) and Prairie Warbler (3.05 ± 0.15; true = 2.37 ± 0.15) during free-flight surveys (Table 3.5). Mean numbers of detections made by human observers were less than actual simulator abundances for Prairie Warbler point counts (2.86 ± 0.09; true = 4.05 ± 0.09) and line transects (3.37 ± 0.16; true = 4.93 ± 0.16), Bachman's Sparrow point counts (2.54 ± 0.13; true = 3.91 ± 0.13), Field Sparrow point counts (2.40 ± 0.07; true = 3.73 ± 0.07)and line transects (3.42 ± 0.12; true = 4.79 ± 0.12), Grasshopper Sparrow point counts (1.65 ± 0.11; true = 3.55 ± 0.11) and line transects (2.94 ± 0.16; true = 4.44 ± 0.16), and Henslow's Sparrow point counts (1.81 ± 0.10; true = 3.84 ± 0.10) and line transects (2.74 ± 0.13; true = 5.14 ± 0.13) (Table 3.5).

Density estimates. None of the balloon density estimates differed from true simulator densities but the standard errors for the density estimates were 3.9 times greater (average increase for each balloon estimate) than the standard errors for the abundance estimates (Table 3.4 and Table 3.6). The observer-based density estimates (from Program DISTANCE) did not differ from true simulator densities for Northern Bobwhite point counts, Prairie Warbler point counts or line transects, Bachman's Sparrow point counts) or free flights, Field Sparrow point counts or line transects, Grasshopper Sparrow point counts or line transects, or Henslow's Sparrow line transects (Table 3.7). Observer-based simulator density estimates were greater than true simulator densities for Northern Bobwhite line transects (4.84 ± 0.41; true = 3.24 ± 0.41) and free flights (6.33 ± 0.56; true = 2.94 ± 0.56), Prairie Warbler free flights (6.69 ± 0.42; true = 3.24 ± 0.42), Field Sparrow free flights (6.22 ± 0.57; true = 3.85 ± 0.57), and Henslow's Sparrow point counts (8.71 ± 0.84; true = 5.55 ± 0.84) (Table 3.7). The standard errors for observer-based density estimates were 3.0 times greater (average increase for each human estimate) than the standard errors for the abundance estimates (Table 3.5 and Table 3.7).

Based on linear models (Figure 3.3), balloon density estimates were strongly related to actual simulator densities for Grasshopper Sparrow (adjusted $R^2 = 0.89$) and moderately related to actual simulator densities for Prairie Warbler (adjusted $R^2 = 0.33$) and Henslow's Sparrow (adjusted $R^2 = 0.30$). Human-based density estimates were strongly related to actual simulator densities for Bachman's Sparrow (adjusted $R^2 = 0.99$) and Henslow's Sparrow (adjusted $R^2 = 0.80$) and moderately related to Field Sparrow (adjusted $R^2 = 0.47$). R-squared values were not significant for the linear models between truth and balloon Bachman's Sparrow estimates (adjusted $R^2 = -0.46$, $P = 0.83$) or between truth and human Grasshopper Sparrow estimates (adjusted $R^2 = -0.42$, $P = 0.77$).

DISCUSSION

Cue counts have traditionally been used in wildlife population estimation as a supplement to distance-sampling methods (Hiby 1985, Buckland 2006). However, cue counts are the best approach to population estimation under the conditions of certain acoustic methods (Marques et al. 2013), where distance sampling is inapplicable and/or impractical. The BARS approach is one such method that is conducive for cue counting but unconducive for distance sampling because the aerial microphone array that would be needed for distance sampling is unfeasible. The density-estimation process for the balloon is further complicated by the need to determine area of detection for an aerial, mobile acoustic recording system in which the altitude is not fixed and hence the footprint of the microphone changes continuously. This chapter examined a cue-count approach to songbird density estimation from aerial acoustic recordings. The approach incorporated the necessary components, described by Marques et al. (2013), for this type of methodological evaluation. The methodology incorporated information on the acoustic behavior of focal species (Chapter 2) and the evaluation of performance for both real birds in which true population densities were unknown, and for simulated birds in which population densities were known and fixed in the experiment.

Real Birds

We used a spot-mapping approach to provide the most accurate estimate of real, male songbird densities at each site. We compared the actual density estimates with ANOVAs but we also considered how strong the linear relationships were between estimates. Mean estimates that varied in magnitude, but were still strongly related, could be useful as unbiased indices to abundance, as opposed to actual density estimates (Schwarz and George 1999), given that sample sizes are large enough to avoid skewed estimates caused by random process error. Estimates that have relatively small standard errors are important for separating process error from observational error. Spot mapping is often considered the most reliable method for estimating the number of songbird breeding territories per unit area , but spot mapping can still be inaccurate (Bibby 2000). Spot-map density estimates from this study may have been biased low because of the minimum requirements for observations to be considered definitive male territories (i.e. 2 or 3 observations, depending on the number of visits, occurring ≥10 days apart) (Bibby 2000).

Excluding estimates from point counts, the balloon-based density estimates did not differ from spot map estimates for Prairie Warbler (balloon = 2.71-3.36 ± 0.55-0.65, spot map = 2.92 ± 0.50), Bachman’s Sparrow (balloon and spot map = 2.05 ± 0.36), or Henslow’s Sparrow (balloon = 13.14-14.32 ± 2.47-2.63, spot map = 7.84 ± 2.35) (Figure 3.2, Table 3.3). Thus, the acoustic cue-count approach mostly produced comparable results to the spot-map standard for Prairie Warbler, Bachman’s Sparrow, and Henslow’s Sparrow. Balloon estimates for Field Sparrow (7.55 ± 1.27 to 10.55 ± 1.23), however, were ~3-4 times greater than the mean spot-map estimate (2.50 ± 1.19), depending on the method. Although balloon estimates were high for Field Sparrow and for the Prairie Warbler and Henslow's Sparrow point counts, the estimates for these species were still linearly related to spot-map estimates (Field Sparrow adjusted $R^2 = 0.46$, Prairie Warbler adjusted $R^2 = 0.39$, Henslow's Sparrow adjusted $R^2 = 0.58$; Figure 3.2). The linear models between balloon estimates and spot-map estimates indicated that the balloon-based estimates may be used as an index of population abundance, even if actual density estimates are biased high. The lack of a linear relationship between balloon and spot-map estimates for Bachman's Sparrow (adjusted R^2 was not significant: $P = 0.89$) may be attributed to low sample sizes. Our experimental design resulted in ~3 density estimates (i.e. point count, line transect, and free flight) per study site per year for the other species ($n = 21$-30), which resulted in estimates with comparable confidence intervals when compared with spot-map estimate confidence intervals. However, Bachman's Sparrow was only present on one study area (Fort Bragg) and real-bird point counts and line transects were not logistically possible because the forest canopy precluded use of the balloon on tether. For that reason, sample sizes for Bachman's Sparrow balloon estimates were very small ($n = 6$) accounting for the large variance in estimates.

Balloon estimates based on the point-count method were consistently biased high for all 3 applicable species (Prairie Warbler, Field Sparrow, and Henslow's Sparrow), whereas line transect and free flight estimates were more comparable to spot map estimates (Table 3.3). Most point-count surveys were conducted earlier in the season than line transect flights and free flights. Song counts during these time periods were more likely elevated because many avian species sing more frequently earlier in the season (Chapter 2). Elevated song counts could have led to elevated density estimates especially if the song counts occurred prior to territory establishment when there were likely more males (breeders and floaters) fighting over territories than later in the season (S.C. Prevost, personal observation). Although the Prairie Warbler abundance models included day of season (Table 3.2), the models may not have been robust to the high activity during territory disputes early in the breeding season.

The human distance-sampling approach and the balloon approach to density estimation approximated spot-map density estimates at equal rates for Prairie Warbler, Bachman's Sparrow, and Henslow's Sparrow (Table 3.3). However, distance-sampling estimates for Field Sparrow (0.73 ± 1.27 to 2.51 ± 1.23) did not differ from the spot-map estimate (2.50 ± 1.19), whereas balloon estimates (7.55 ± 1.27 to 10.55 ± 1.23) were much greater (Table 3.3).

Simulated Birds

Analyses of audio recordings from simulated-bird flights provided a way to evaluate the acoustic cue-count process under more controlled conditions where the location and timing of an individual bird singing was fixed by the experiment. Comparisons (balloon vs. human observer) were made between simulator abundance indices (actual detections and numbers of simulators available), as well as between density estimates. The abundance index tests had many more degrees of freedom than comparisons among density estimates because abundances were analyzed at the level of individual flights/surveys. Density estimates were compared on a different scale (i.e. study area by year) to allow for distance sampling estimation with sufficient sample sizes for the human-based estimators.

Abundance indices. The BARS detected the most simulated songs for Northern Bobwhite and Field Sparrow, the species with the greatest-amplitude and lowest-frequency vocalizations among the focal species. This could be expected based on reduced sound attenuation for signals with greater amplitudes and lower frequencies (Ingård 1953, Marten and

Marler 1977). The balloon detected more simulated songs for Northern Bobwhite during 80% of flights and Field Sparrow during 75% of flights, than was expected based on the numbers of simulators available (and durations of exposure) within the calculated flight. These results suggested that the microphone footprint relationship for Northern Bobwhite and Field Sparrow was greater than the presumed 1:1 altitude to radius relationship. In contrast, balloon detection of Grasshopper and Henslow's sparrow songs during line transect flights were low, suggesting that the microphone footprint relationship is less than 1:1 for these species with lesser-amplitude and higher-frequency songs. Given that different species may have different detectability by the microphone based on frequency and/or amplitude, incorporating species-specific detectability into the density estimation equation would improve estimates.

Numbers of simulator detections made by human-observers during field surveys tended to be biased low compared to the true numbers of simulators available within 150 m (Table 3.5). This result was expected because observer probability of detection decreases with distance (Buckland et al. 2001) and 150 m may exceed the detection distance for some of the species being studied (e.g., Henslow's Sparrow). Although most differences were biased low, the human-observer counts of Northern Bobwhite (human = 3.72 ± 0.18, true = 2.44 ± 0.18) and Prairie Warbler (human = 3.05 ± 0.15, true = 2.37 ± 0.15) during free-flight surveys were biased high (Table 3.5). This result suggested that, during free-flight surveys, observers underestimated distances to these species because they counted simulators that were beyond 150 m from the transect line (and estimated distances of ≤150 m). One other possible explanation is that observers had trouble distinguishing between real and simulated birds, which could have resulted in counts that included some real-bird observations.

Density estimates. There were decreases in precision (increases in standard errors) of balloon density estimates (Table 3.6) when compared to precision of abundance estimates (from which the densities were based; Table 3.4). This loss of precision was because of the decrease in degrees of freedom for each estimate (density estimates were based on means for each study area, year, and survey type). Similarly, the standard errors of the human-based estimates were greater for density estimates than for abundance indices (Table 3.5 and Table 3.7).

Distance-sampling methods for simulated birds were accurate (i.e., no difference from simulator densities) in two-thirds of the density estimates for the 6 focal species (Table 3.7). Distance-sampling density estimates were more accurate than the abundance indices on which they were based. Of the 15 pairwise comparisons between human-based estimates and true simulator densities, 5 were different, whereas 11 of 15 comparisons were different for the abundance comparisons (Table 3.5).

The precision of human-based estimates of simulator densities (mean standard error = 0.45, mean degrees of freedom = 10; Table 3.7) was greater than the precision of balloon-based estimates (mean standard error = 1.69, mean degrees of freedom = 12; Table 3.6). The precision of human-based abundance indices (mean standard error = 0.13, mean degrees of freedom = 370; Table 3.5) was also greater than the precision of balloon-based abundance estimates (mean standard error = 0.65, mean degrees of freedom = 415; Table 3.4). The assumed microphone-footprint relationship (i.e. 1:1 altitude to footprint radius ratio) may have negatively affected the precision of the balloon-based estimates. Balloon abundance estimates were dependent upon the microphone footprint because the footprint was used to determine the numbers of simulators available to the microphone and the expected durations of simulator exposure to the microphone.

Balloon simulator-density estimates were then calculated by dividing the abundance by the effective flight area (also determined by the microphone footprint) that overlapped the simulator network. If the microphone footprint was biased, both abundance and density estimates would also reflect this bias to a certain extent. This bias may have introduced additional variance into the estimates because the magnitude of bias would change with flight altitude. The microphone footprint was calculated (in part) by squaring the detection radius (radius = altitude), thus the bias associated with the microphone-footprint relationship would be lesser at lower altitudes and greater at higher altitudes.

Sources of Variation for Cue-count Density Estimation

There were several sources of variation in balloon equipment, field implementation, and in each phase of the analytical process that led to the songbird density estimates (Figure 3.4). Any of these sources, in addition to random variation in bird behavior and population dynamics, could have influenced the accuracy and/or precision of the bird density estimates. Although the BARS design incorporated some technical improvements in command and control capability during the course of the study (2011-2013), the microphone and recorder remained the same during the entire study, such that changes in the BARS were likely unrelated to variation in density estimation. Field personnel and balloon deployment conditions were also sources of variation. The balloon’s deployment state, speed, and altitude were probably the most influential sources of variation during balloon implementation. The deployment state depended on the survey type (i.e. point count, line transect, or free flight), whether or not the balloon was tethered, and the wind conditions under which the tether system was used. Greater wind speeds and/or gustier wind conditions increased the amount that the payload (and microphone) swung back and forth while tethered, which would potentially increase the microphone footprint and increase the detectability of individuals on the footprint periphery. Background noise associated with balloon speed and/or wind resistance from the tether may have hindered the detection of songs of lesser amplitude that would have been detected on stationary recordings. Because the normal mode of operation for the BARS is free flying, the most valuable indicators of balloon performance would be obtained from density estimate evaluations based exclusively on free-flight deployment. Furthermore, free-flight deployment did not experience the swinging and audible wind-resistance problems associated with tether deployment.

The first phase of the analytical process was acoustic data processing, during which the songs (or cues) of focal species were identified on audio spectrograms and tallied for each balloon flight. This phase had technician error in song annotations (i.e. false positives, false negatives, and song misidentification). Quantities of annotation errors were likely influenced by variations in technician skill and experience, in levels of background noise on the recordings, and in intensities of bird song activity. To account for song annotation error, I reviewed a sample of audio files ($n \geq 20$ files per species for real and for simulated birds) and quantified the false positives and negatives within the first minute of each file. On average, I annotated 29% more songs that the technicians. To account for this source of variation, I modeled (with negative binomial regression) the total numbers of songs (in one min) annotated by me vs. by technicians for each species among real birds and among simulated birds. This correction procedure added an additional source of variation in the analytical process. Consistent, accurate audio file transcription is an important requirement for virtually any acoustic monitoring approach. Automated detection approaches may remove the human transcription error but would introduce their own source of variation based on the classification errors associated with the automated detection algorithms (Mellinger et al. 2007, Marques et al. 2013).

The second phase of the analytical process introduced variation associated with the balloon flight footprint calculation. Flight footprints were calculated based on the use of second by second GPS coordinates from the balloon flight and 1-m DEMs in ArcMap. Footprint calculation also depended on field tests that suggested the balloon had a ~45^0 angle of detection (1:1 relationship between balloon altitude and a circular footprint radius). However, the results from simulated-bird analyses suggested that the detection footprint may differ for different species. The biased-high estimates for Field Sparrow and Northern Bobwhite likely can be accounted for because their songs are greater in amplitude and lesser in frequency than the other species. The exposure footprints for Field Sparrow and Northern Bobwhite, thus, were likely to be overly conservative.

The third, and final, stage of the analytical process was the application of negative binomial regression models to estimate abundance. Inevitable sources of process error that affected this analytical phase included random variation in song behavior and population dynamics within the populations from which the abundance models were based. Balloon density estimates were dependent upon the number of songs on the audio recordings. Because the survey durations for the balloon experimental flights were relatively short (≤10 min) in comparison to a bird's total song activity on any given day, there was considerable variation in density estimates. Longer flights may lead to more accurate results when accounting for this effect.

Summary

The acoustic cue-count approach used in this study can be a viable method for making inferences about songbird populations. The BARS undoubtedly would be effective for covering large areas and for documenting the presence of rare species. The aerial balloon system approach has successfully been used for monitoring Golden-cheeked Warbler (*Dendroica chrysoparia*) and Black-capped Vireo (*Vireo atricapillus*) in Texas (Fristrup and Clark 2009). In addition, the aerial acoustic method appears suitable for collecting cue-count data as an index to abundance. The linear relationships between balloon density estimates and spot-map density estimates (Figure 3.2) or song-simulator density estimates (Figure 3.3) suggested that a cue-count index could be used as an index to relative abundance and to track population change. However, to actually estimate density, several improvements to the process could be considered. Such improvements include reducing the error and variance associated with song detectability (i.e. accounting for changes in the likelihood of detecting a song based on factors such as flight altitude, background noise, etc.), song enumeration (from acoustic recordings), and microphone footprint estimation.

Although we used the balloon on a tether to allow comparison of balloon-based point and line-transect counts with human-observer counts, this mode of operation adds variance to the estimates because of noise on audio files and variation in the microphone footprint from swinging of the payload as the wind blows. Free-flight procedures do not have these limitations; they are amenable to moderately windy conditions (<4-5 m s^{-1}) and the balloon flies freely and steadily without the resistance of a tether to induce swinging of the payload. For these reasons, free flights are recommended for future uses of BARS technology unless there is a unique application that requires a tethered approach. If a tether approach is used, flights should only be conducted under light wind conditions (ideally <1.5 m s^{-1}).

Further research is needed to better understand the relationships between acoustic aerial detection probability and the following: (1) flight speed and altitude, (2) background noise, and (3) song characteristics (e.g., frequency). These factors, once better understood, could be incorporated into models for balloon detection probability to produce more accurate, species-specific calculations of flight footprints.

The issue of human error associated with audio data processing is already being addressed in the field of wildlife acoustic monitoring. Numerous studies have focused on testing the implementation of unbiased acoustic-analysis programs (Potamitis et al. 2014, Stowell and Plumbley 2014, Rocha et al. 2015, Sebastián-González et al. 2015). The automation of the acoustic detection process with software programs is not only necessary to enable researchers to analyze the vast quantities of audio data being collected, it is also necessary to reduce variation and eliminate human bias in acoustic analysis procedures (Marques et al. 2013).

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CHAPTER 3 APPENDIX

Table 3.1. Sample sizes for acoustic and human-observer surveys at 3 Department of Defense study areas, 2011-2013. Dashes indicate that there were too few surveys (<3) to perform analyses. N/a (not applicable) indicates that surveys of the corresponding type and location were not attempted.

			Real bird surveys			**Simulated-bird surveys**		
Study area	**Year**	**Site**	**Point count**	**Line transect**	**Free flight**	**Point count**	**Line transect**	**Free flight**
Big Oaks NWR	2011	46	10	9	-	8	10	n/a
		52	9	9	-	9	8	n/a
		57	9	10	-	6	9	n/a
	2012	46	12	12	12	12	-	n/a
		52	7	12	12	12	4	n/a
		57	12	12	12	9	10	n/a
Fort Riley	2011	56	4	9	3	-	3	n/a
		90	6	11	-	9	7	n/a
		95	-	6	8	8	-	n/a
	2013	39	10	4	7	10	10	n/a
		49	6	-	10	10	8	n/a
		65	12	-	10	10	4	n/a
Fort Bragg	2012	Dragon	n/a	n/a	10	23	n/a	23
		Sanders	n/a	n/a	11	12	n/a	n/a
		Sicily	n/a	n/a	11	n/a	n/a	n/a
	2013	Dragon	n/a	n/a	10	30	n/a	20
		Jones	n/a	n/a	12	n/a	n/a	n/a
		Sanders	n/a	n/a	11	n/a	n/a	n/a

Table 3.2. Prediction models used to estimate abundances of 4 focal species from song cue counts of balloon audio recordings collected at 3 Department of Defense study areas, 2011-2013. Songs = total songs in 5 min; day of season = modified Julian date (May 1 = 1); Yr binary code = 0 (indicating 2012 data) or 1 (indicating 2013 data); pressure (mm of mercury) = altimeter setting transformed by subtracting the mean (761) from each value; time of day = modified Julian time divided by 5 (30-min before sunrise = 0, 25-min before sunrise = 1).

Species	**Study area**	**Abundance prediction model**
Prairie Warbler	Big Oaks NWR	Abundance = $\exp[(4.33 * 10^{-2})(Songs) + (-4.71 * 10^{-12})(Day\ of\ season^{6})]$
	Fort Bragg	Abundance = $\exp[(2.43 * 10^{-2})(Songs) + (1.19 * 10^{-2})(Day\ of\ season) + (-1.06 * 10^{-1})(Yr\ binary\ code)]$
Bachman's Sparrow	Fort Bragg	Abundance = $\exp[(2.61 * 10^{-2})(Songs) + (1.56 * 10^{-2})(Pressure^{2})]$
Field Sparrow	Big Oaks NWR	Abundance = $\exp[(2.34 * 10^{-2})(Songs) + (3.27 * 10^{-2})(Time\ of\ day)]$
	Fort Riley	Abundance = $\exp[(1.43 * 10^{-2})(Songs) + (2.12 * 10^{-2})(Time\ of\ day) + (2.50 * 10^{-2})(Pressure)]$
Henslow's Sparrow	Big Oaks NWR	Abundance = $\exp[(6.48 * 10^{-3})(Songs) + (3.47 * 10^{-2})(Time\ of\ day)]$

Table 3.3. Real-bird density estimate comparisons: Least-squares means and Tukey's HSD test results among real-bird density estimation methods for 4 species at 3 Department of Defense study areas, 2011-2013. Density estimation methods were grouped first by species and then as follows: spot mapping (spot map); human-observer point counts (human PC), line transects while balloon was tethered (human LT), and line transects while balloon was free-flown (human FF); balloon point counts (balloon PC), balloon tethered line transects (balloon LT), and balloon free flights (balloon FF). The least-squares means were based on estimated densities of male territories per 10 ha for each site/year where a species was expected to be present (sample sizes for balloon and human density estimates per site are in Table 3.1; there was only one spot-map density estimate per site/year). See Methods section for the density estimation procedures.

Species	**Density estimation method**	**Least-squares mean**	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Tukey Group**
Prairie Warbler (*Setophaga discolor*)	Human FF	1.12	0.55	31	0.00	2.25	A
	Human LT	2.55	0.65	39	1.24	3.86	AB
	Balloon FF	2.71	0.55	31	1.59	3.83	AB
	Spot map	2.92	0.50	25	1.89	3.95	B
	Balloon LT	3.36	0.65	39	2.05	4.67	B
	Human PC	3.59	0.65	39	2.28	4.90	B
	Balloon PC	5.88	0.65	39	4.57	7.19	C
Bachman's Sparrow (*Peucaea aestivalis*)	Human FF	0.98	0.36	14	0.20	1.76	A
	Spot map	2.05	0.36	14	1.27	2.82	A
	Balloon FF	2.05	0.36	14	1.28	2.83	A
Field Sparrow (*Spizella pusilla*)	Human LT	0.73	1.27	43	0.00	3.29	A
	Human FF	0.84	1.39	50	0.00	3.63	A
	Spot map	2.50	1.19	38	0.09	4.90	A
	Human PC	2.51	1.23	40	0.03	4.99	A
	Balloon LT	7.55	1.27	43	4.99	10.12	B
	Balloon FF	9.36	1.39	50	6.57	12.15	B
	Balloon PC	10.15	1.23	40	7.67	12.63	B
Henslow's Sparrow (*Ammodramus henslowii*)	Human FF	4.23	2.63	34	0.00	9.58	A
	Human LT	7.29	2.47	29	2.24	12.34	AB
	Spot map	7.84	2.35	25	3.00	12.68	AB
	Balloon FF	13.14	2.63	34	7.79	18.49	BC
	Balloon LT	14.32	2.47	29	9.27	19.36	BC
	Human PC	15.08	2.40	26	10.14	20.01	C
	Balloon PC	22.14	2.40	26	17.20	27.08	D

Table 3.4. Balloon simulated-bird abundance estimate comparisons: Least-squares means and Tukey's HSD test results between balloon estimates of simulated-bird abundance and the true simulated-bird abundance within the flight footprint for 6 species at 3 Department of Defense study areas, 2011-2013. Abundance indicators were balloon point counts (balloon PC) and corresponding truth (true PC), balloon tethered line transects (balloon LT) and corresponding truth (true LT), and balloon free flights (balloon FF) and corresponding truth (true FF). The least-squares means were based on estimated numbers (balloon) and true numbers (true) of bird simulators within the flight footprint for each test. See Methods section for the balloon estimation procedure of simulated-bird abundance.

Species	**Abundance indicator**	**Least-squares means**	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Tukey Group**
Northern Bobwhite	True FF	3.10	2.71	584	0.00	8.43	AB
	True PC	3.41	1.29	584	0.87	5.94	AB
	True LT	3.92	2.03	584	0.00	7.91	AB
	Balloon PC	5.62	1.29	584	3.09	8.16	AB
	Balloon FF	12.97	2.71	584	7.64	18.30	BC
	Balloon LT	20.77	2.03	584	16.77	24.76	C
Prairie Warbler	True FF	3.42	0.34	402	2.74	4.09	AB
	True PC	3.55	0.21	402	3.15	3.95	AB
	True LT	4.27	0.35	402	3.58	4.96	ABC
	Balloon FF	4.35	0.34	402	3.67	5.03	ABC
	Balloon PC	4.47	0.21	402	4.07	4.88	BC
	Balloon LT	5.20	0.35	402	4.51	5.89	C
Bachman's Sparrow	True FF	3.21	0.42	210	2.39	4.04	A
	Balloon PC	3.24	0.34	210	2.58	3.91	A
	True PC	3.57	0.34	210	2.90	4.24	A
	Balloon FF	5.46	0.42	210	4.63	6.29	B
Field Sparrow	True PC	3.29	0.26	582	2.79	3.79	A
	True FF	3.31	0.53	582	2.27	4.35	AB
	True LT	4.22	0.40	582	3.43	5.01	AB
	Balloon PC	4.94	0.26	582	4.44	5.44	B
	Balloon FF	7.39	0.53	582	6.35	8.43	C
	Balloon LT	8.89	0.40	582	8.10	9.68	C
Grasshopper Sparrow	Balloon LT	2.50	0.27	180	1.97	3.03	A
	Balloon PC	2.95	0.19	180	2.58	3.32	AB
	True PC	3.05	0.19	180	2.68	3.42	AB
	True LT	3.67	0.27	180	3.14	4.20	B
Henslow's Sparrow	Balloon PC	2.96	0.17	372	2.61	3.30	A
	Balloon LT	3.19	0.23	372	2.74	3.63	A

Table 3.4 (continued)

Species	**Abundance indicator**	**Least-squares means**	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Tukey Group**
	True PC	3.28	0.17	372	2.94	3.62	A
	True LT	4.44	0.23	372	4.00	4.89	B

Table 3.5. Human-observer simulated-bird count comparisons: Least-squares means and Tukey's HSD test results between numbers of simulated birds detected by humans and the true simulated-bird abundances within 150 m of the observer for 6 species at 3 Department of Defense study areas, 2011-2013. Abundance indicators were point counts (human PC) and corresponding truth (true PC), line transects while balloon was tethered (human LT) and corresponding truth (true LT), and line transects while balloon was free-flown (human FF) and corresponding truth (true FF). The least-squares means were based on the numbers of simulators detected (human) and the true number (true) of bird simulators within 150 m of the observer.

Species	**Abundance indicator**	**Least-squares means**	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Tukey Group**
Northern Bobwhite	True FF	2.44	0.18	537	2.10	2.79	A
	Human PC	3.62	0.09	537	3.46	3.79	B
	Human FF	3.72	0.18	537	3.38	4.07	B
	True PC	3.86	0.09	537	3.70	4.03	B
	True LT	4.77	0.13	537	4.50	5.03	C
	Human LT	5.18	0.13	537	4.91	5.44	C
Prairie Warbler	True FF	2.37	0.15	345	2.07	2.67	A
	Human PC	2.86	0.09	345	2.68	3.04	AB
	Human FF	3.05	0.15	345	2.75	3.35	B
	Human LT	3.37	0.16	345	3.06	3.67	B
	True PC	4.05	0.09	345	3.87	4.23	C
	True LT	4.93	0.16	345	4.62	5.23	D
Bachman's Sparrow	True FF	2.49	0.16	182	2.17	2.80	A
	Human FF	2.53	0.16	182	2.22	2.85	A
	Human PC	2.54	0.13	182	2.28	2.79	A
	True PC	3.91	0.13	182	3.65	4.16	B
Field Sparrow	Human PC	2.40	0.07	521	2.26	2.55	A
	True FF	2.60	0.15	521	2.31	2.90	AB
	Human FF	2.98	0.15	521	2.68	3.28	BC
	Human LT	3.42	0.12	521	3.19	3.65	CD
	True PC	3.73	0.07	521	3.58	3.87	D
	True LT	4.79	0.12	521	4.56	5.02	E
Grasshopper Sparrow	Human PC	1.65	0.11	182	1.42	1.87	A
	Human LT	2.94	0.16	182	2.63	3.25	B
	True PC	3.55	0.11	182	3.33	3.77	C
	True LT	4.44	0.16	182	4.13	4.75	D
Henslow's Sparrow	Human PC	1.81	0.10	307	1.61	2.01	A
	Human LT	2.74	0.13	307	2.49	2.99	B

Table 3.5 (continued)

Species	**Abundance indicator**	**Least-squares means**	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Tukey Group**
	True PC	3.84	0.10	307	3.64	4.04	C
	True LT	5.14	0.13	307	4.88	5.39	D

Table 3.6. Balloon simulated-bird density estimate comparisons: Least-squares means and Tukey's HSD test results between true simulated-bird densities (based on the overlap of the simulator network and the balloon flight footprint) and densities estimated with the balloon method for 6 species at 3 Department of Defense study areas, 2011-2013. Density estimation methods were point counts (balloon PC) and corresponding truth (true PC), tethered line transects (balloon LT) and corresponding truth (true LT), and free flights (balloon FF) and corresponding truth (true FF). The least-squares means were based on mean estimated densities (balloon) and mean true densities (true) of bird simulators for each study site. See Methods section for the balloon estimation procedure of simulated-bird densities.

Species	**Density estimation method**	**Least-squares means**	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Tukey Group**
Northern Bobwhite	True LT	2.87	3.02	18	0.00	9.22	A
	True FF	3.63	4.38	18	0.00	12.82	A
	True PC	6.14	2.40	18	1.10	11.19	A
	Balloon PC	11.92	2.40	18	6.88	16.97	A
	Balloon LT	16.14	3.02	18	9.80	22.48	A
	Balloon FF	16.54	4.38	18	7.34	25.74	A
Prairie Warbler	True LT	3.02	1.79	10	0.00	7.01	A
	True FF	4.12	1.79	10	0.13	8.11	A
	Balloon LT	4.61	1.79	10	0.62	8.60	A
	Balloon FF	5.78	1.79	10	1.79	9.77	A
	True PC	6.28	1.18	10	3.64	8.92	A
	Balloon PC	8.82	1.18	10	6.19	11.46	A
Bachman's Sparrow	True FF	3.73	1.21	4	0.36	7.09	A
	Balloon PC	5.64	1.21	4	2.28	9.00	A
	True PC	5.74	1.21	4	2.38	9.10	A
	Balloon FF	6.92	1.21	4	3.56	10.28	A
Field Sparrow	True LT	2.98	1.26	18	0.34	5.63	A
	True FF	4.22	1.81	18	0.41	8.03	AB
	True PC	5.93	1.00	17	3.81	8.04	AB
	Balloon LT	6.73	1.26	18	4.09	9.37	AB
	Balloon FF	9.27	1.81	18	5.46	13.08	AB
	Balloon PC	9.88	1.00	17	7.77	12.00	B
Grasshopper Sparrow	Balloon LT	1.99	1.13	3.8	0.00	5.20	A
	True LT	2.77	1.13	3.8	0.00	5.98	A
	True PC	6.01	1.13	3.8	2.79	9.22	A
	Balloon PC	6.56	1.13	3.8	3.35	9.77	A
Henslow's Sparrow	Balloon LT	2.31	1.00	12	0.14	4.48	A
	True LT	3.20	1.00	12	1.03	5.37	A

Table 3.6 (continued)

Species	**Density estimation method**	**Least-squares means**	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Tukey Group**
	True PC	6.39	1.00	12	4.22	8.56	A
	Balloon PC	6.60	1.00	12	4.43	8.77	A

Table 3.7. Human-observer simulated-bird density estimate comparisons: Least-squares means and Tukey's HSD test results between true simulated-bird densities within 150 m of the observer and densities estimated by human observers for 6 species at 3 Department of Defense study areas, 2011-2013. Density estimation methods were point counts (human PC) and corresponding truth (true PC), line transects while balloon was tethered (human LT) and corresponding truth (true LT), and line transects while balloon was free-flown (human FF) and corresponding truth (true FF). The least-squares means were based on the estimated densities of bird simulators (human) and the true densities (true) of bird simulators within 150 m of the observer. See Methods section for the human-observer density estimation procedure.

Species	**Density estimation method**	**Least-squares means**	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Tukey Group**
Northern Bobwhite	True FF	2.94	0.56	18	1.76	4.12	AB
	True LT	3.24	0.41	16	2.37	4.10	A
	Human LT	4.84	0.41	16	3.98	5.70	BC
	True PC	5.50	0.34	13	4.76	6.23	C
	Human PC	6.06	0.34	13	5.33	6.80	C
	Human FF	6.33	0.56	18	5.14	7.51	C
Prairie Warbler	True FF	3.24	0.42	10	2.31	4.17	A
	True LT	3.30	0.42	10	2.37	4.22	A
	Human LT	3.74	0.42	10	2.81	4.67	A
	True PC	5.78	0.27	10	5.17	6.39	B
	Human FF	6.69	0.42	10	5.77	7.62	B
	Human PC	6.90	0.27	10	6.29	7.51	B
Bachman's Sparrow	True FF	3.36	0.22	1	1.34	5.38	A
	Human FF	3.65	0.22	1	1.63	5.67	A
	True PC	5.52	0.22	1	3.50	7.54	B
	Human PC	5.95	0.22	1	3.93	7.97	B
Field Sparrow	True LT	3.15	0.41	16	2.28	4.02	A
	Human LT	3.63	0.41	16	2.76	4.50	A
	True FF	3.85	0.57	18	2.65	5.05	AB
	True PC	5.33	0.34	13	4.60	6.07	BC
	Human PC	5.72	0.34	13	4.99	6.45	BC
	Human FF	6.22	0.57	18	5.01	7.42	C
Grasshopper Sparrow	True LT	2.90	0.43	4	1.69	4.11	A
	Human LT	4.59	0.43	4	3.38	5.81	A
	Human PC	4.77	0.43	4	3.56	5.98	A
	True PC	5.01	0.43	4	3.80	6.23	A
Henslow's Sparrow	True LT	3.30	0.84	7	1.30	5.29	A
	Human LT	4.71	0.84	7	2.72	6.70	A

Table 3.7 (continued)

Species	**Density estimation method**	**Least-squares means**	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Tukey Group**
	True PC	5.55	0.84	7	3.55	7.54	A
	Human PC	8.71	0.84	7	6.72	10.70	B

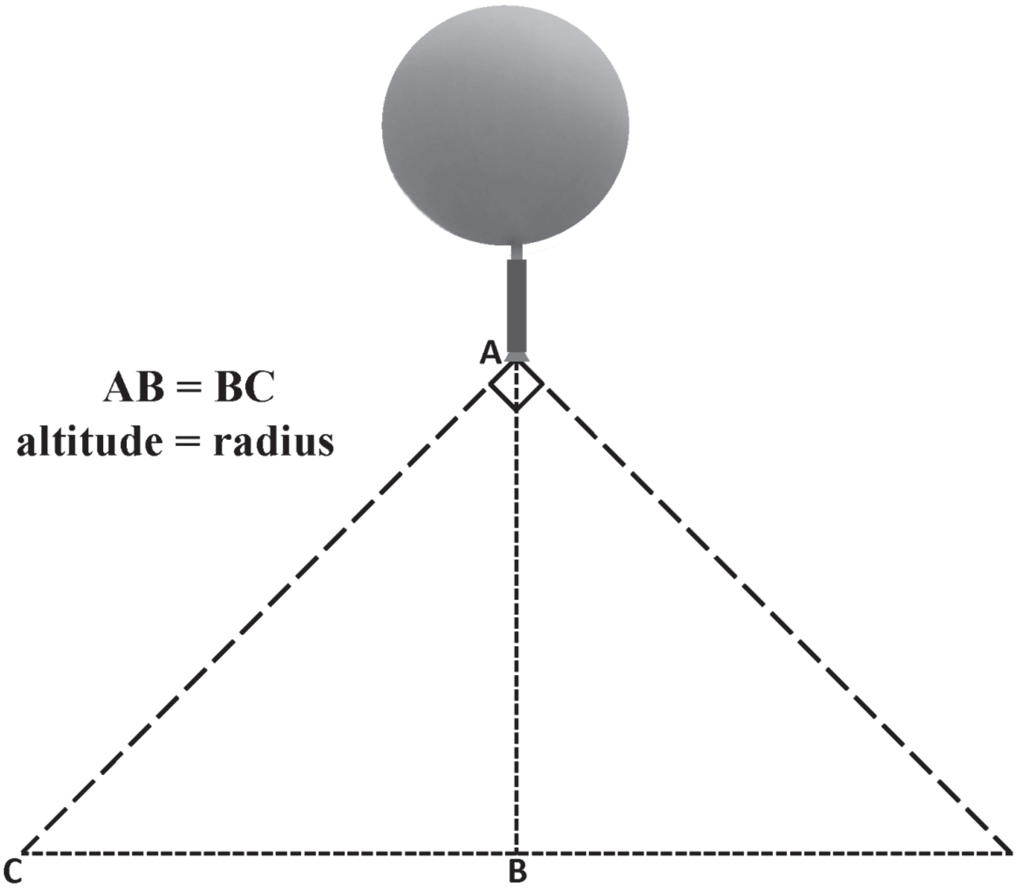

Figure 3.1. Relationship between the BARS (Balloon Aerial Recording System) microphone altitude and the circular footprint radius.

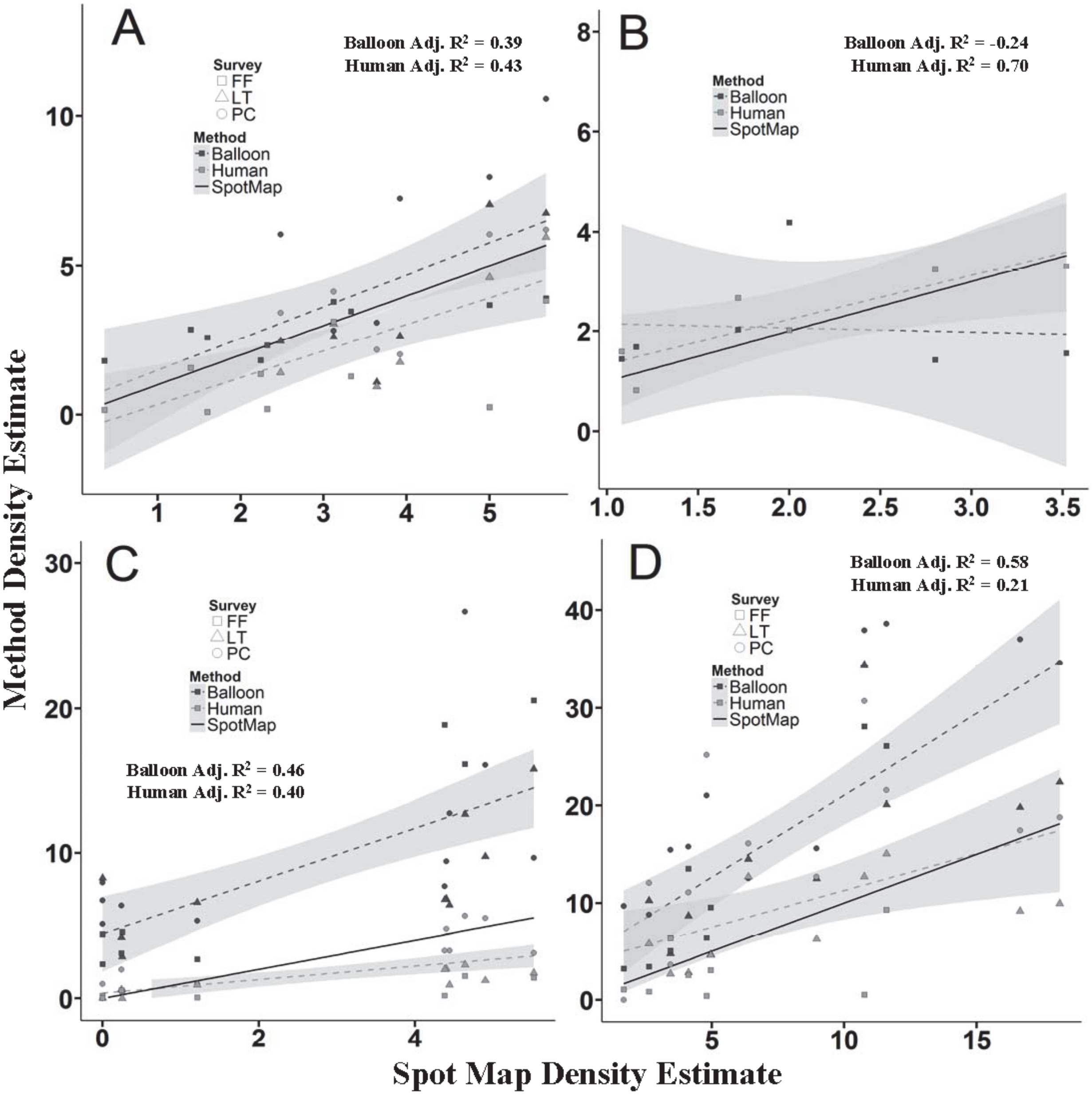

Figure 3.2. Real-bird density scatterplots of spot-map estimates (x-axis) by method (i.e. balloon, human, or spot map) estimates (y-axis) for Prairie Warbler (**A**), Bachman's Sparrow (**B**), Field Sparrow (**C**), and Henslow's Sparrow (**D**), at 3 Department of Defense study areas, 2011-2013. Each point for method=balloon or method=human represents a density estimate for a study site (sample sizes for each estimate are in Table 3.1). Linear models with 95% confidence intervals are plotted for balloon (dark-gray dashed line) and human (light-gray dashed line) density estimates, as each relates to its corresponding spot-map estimate. Solid black lines are the best estimation of actual bird densities at the study sites (plotted with spot-map estimates on both x and y axes for each study site). Adjusted R^2 values were obtained with the linear model ("lm") function in program R (R Core Team 2015).

Figure 3.3. Simulated-bird density scatterplots of true (x-axis) by estimated (balloon or human) densities (y-axis) for Northern Bobwhite (**A**), Prairie Warbler (**B**), Bachman's Sparrow (**C**), Field Sparrow (**D**), Grasshopper Sparrow (**E**), and Henslow's Sparrow (**F**), at 3 Department of Defense study areas, 2011-2013. Each point for method=balloon or method=human represents a density estimate for a study area and year (sample sizes for each estimate are in Table 3.1). Linear models with 95% confidence intervals are plotted for balloon (solid line) and human (dashed line) density estimates, as each relates to its corresponding true simulator density. Adjusted R^2 values were obtained with the linear model ("lm") function in program R (R Core Team 2015).

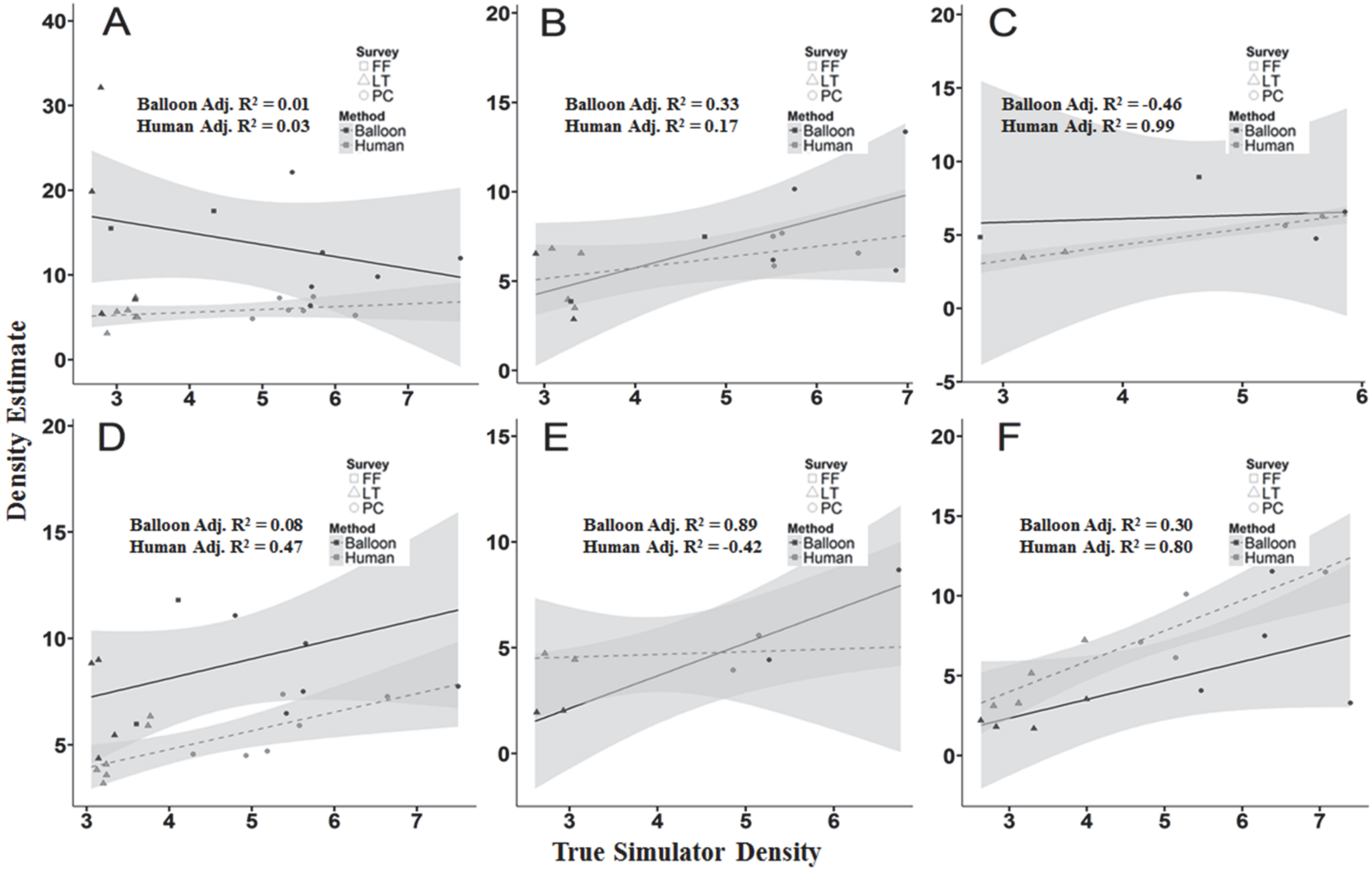

Figure 3.3 (continued)

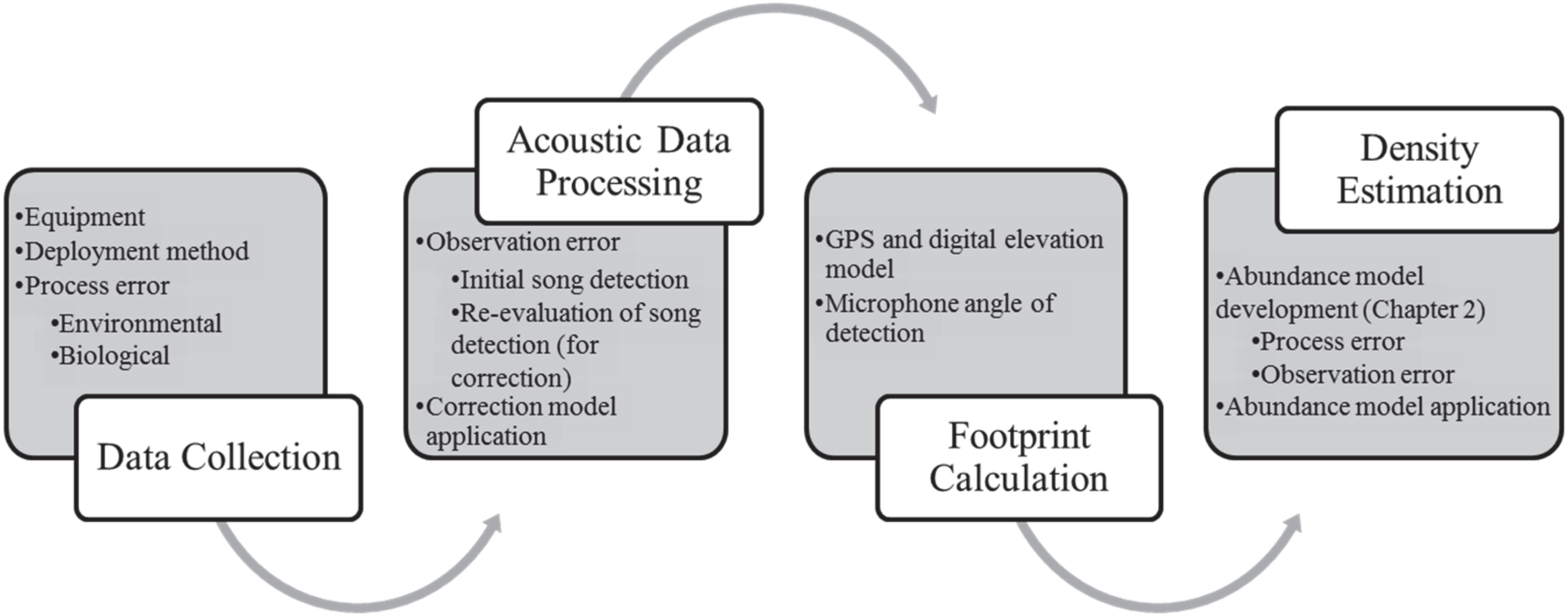

Figure 3.4. Analytical pathway and sources of variation for BARS (Balloon Aerial Recording System) density estimation.

CHAPTER 4

Conclusions

The primary objectives of this thesis were (1) to evaluate the extent to which song cue-counts can be used to predict songbird abundance and develop predictive models on this basis, and (2) to establish and implement an analytical pathway for bird population estimation from acoustic data recorded with the BARS. We succeeded in both of these objectives for 4 of 5 of our focal species. We found that day of season, time of day, temperature, wind speed, and atmospheric pressure were related to song activity but only 1-2 of these factors were influential for each species. Variation in song activity across species, study areas, and years challenges the broad applicability of the abundance prediction models.

This study documented the ability of the BARS to document species presence/absence, relative abundance, and density. Although documenting presence/absence and relative abundance of the focal species was generally successful, success in generating accurate density estimates varied by species. Based on territory densities, estimated with the best method available (spot mapping), the balloon analytical method successfully predicted densities of Prairie Warbler (line transects and free flights), Bachman's Sparrow, and Henslow's Sparrow (line transects and free flights), but over-estimated Field Sparrow densities. Field tests of the BARS with simulated-bird communities (and known song density) revealed that a species-specific microphone footprint is needed to improve density estimates. Future improvements in automated audio file analysis will also likely lead to more consistent acoustic monitoring results.

RECOMMENDATIONS FOR FUTURE RESEARCH

The BARS has wide terrestrial applicability across large and/or limited-access areas and across taxa that produce acoustic signals. The technology would be extremely effective for covering large areas and documenting species presence. The acoustic cue-count approach described in

Chapter 3 is also a viable method for making inferences about songbird populations. Given known relationships between acoustic cue densities and animal abundances (Chapter 2), the aerial acoustic method can provide population indices based on cue-count data. However, there are several improvements that we recommend for future research and applications of the BARS or similar technologies.

Flight Footprint of Detection

The effective area surveyed must be measured before population density estimates can be calculated. The BARS microphone footprint depends upon the flight altitude. From this study, we also determined that the size of the footprint depends on the signal of interest (Chapter 3). Thus, different bird songs have different detection footprints. Our results suggested that a 1:1 relationship between flight altitude and footprint radius is appropriate for Prairie Warbler but this radius was too small for Northern Bobwhite, Bachman’s Sparrow, and Field Sparrow and too large for Grasshopper and Henslow’s sparrows. More accurate footprint estimates are needed to generate accurate estimates of bird densities from aerial acoustic data across all species.

Song Enumeration

To ensure the best possible accuracy and precision in population estimation, the song enumeration process must be consistent when determining cue rates and when counting songs to estimate abundance. If songs are enumerated manually by humans, the same method, spectrogram parameters (if applicable), and personnel should be employed for all data used in the abundance estimation process to minimize variation. Likewise, if automated detection software is used for song enumeration (as recommended), the same software and settings must be employed for cue rate data and for analysis of sample data. Audio files also need to be screened so that files with background noise that interfere with detection consistency (e.g., insects, traffic, etc.) are not included in the analysis.

Detection Probability

Further research is needed to better estimate aerial acoustic detection probabilities. The 2 most important factors in determining BARS detection probability were addressed in chapters 2 and 3. Unlike many human-based methods, the abundance prediction models, based on cue counts, accounted for birds that were silent during a given count event (Chapter 2). In Chapter 3, a general detection probability, assuming a cue was available, was incorporated into the flight exposure-area calculation. Detection depended on the physical location of the balloon and the duration of the flight. However, detection likely depended on more than what was accounted for in the effective flight area calculation. Detection of a cue may depend upon cue amplitude and/or frequency (Chapter 3) or upon the background noise and interfering sounds (i.e. sounds that are similar to target sounds) on an audio recording (Marques et al. 2013). Thus, the effects of cue characteristics and acoustic noise/interference should be considered.

LITERATURE CITED

Marques, T. A., L. Thomas, S. W. Martin, D. K. Mellinger, J. A. Ward, D. J. Moretti, D. Harris, and P. L. Tyack. 2013. Estimating animal population density using passive acoustics. Biological Reviews 88:287-309.

APPENDIX

Table A.1. Data ranges for continuous variables in negative binomial models developed from song cue counts of 5 songbird species on 3 Department of Defense installations, 2012-2013 (Chapter 2). Total songs = total songs in 5 min; day of season = modified Julian date (May 1 = 1); time of day = modified Julian time divided by 5 (30-min before sunrise = 0, 25-min before sunrise = 1); pressure (mm of mercury) = altimeter setting transformed by subtracting the mean (761) from each value.

Species	**Study area**	**Year**	**Total songs**	**Abundance (males)**	**Day of season**	**Time of day**	**Temperature (C^0)**	**Wind speed (m/s)**	**Pressure (mm/Hg)**
Prairie Warbler	Big Oaks NWR	2012	0-59	2-5	15-81	0.0-53.0	8-29	0.0-4.9	-2.30-4.30
	Fort Bragg	2012	0-58	1-4	34-76	6.6-52.6	14-30	0.0-4.6	-6.59-5.86
		2013	0-63	1-3	22-74	6.0-53.0	8-27	0.0-4.0	-5.84-6.84
Bachman's Sparrow	Fort Bragg	2012	0-83	1-6	22-76	6.2-53.0	14-30	0.0-4.5	-4.84-5.86
		2013	0-56	1-3	27-72	6.2-52.6	12-28	0.0-6.7	-5.84-7.10
Field Sparrow	Big Oaks NWR	2012	0-104	3-8	15-81	0.6-53.2	8-29	0.0-6.7	-2.30-4.30
	Fort Riley	2013	0-128	3-5	18-84	0.4-52.8	12-29	0.0-9.4	-8.65-6.33
Grasshopper Sparrow	Fort Riley	2013	0-96	3-5	17-84	0.0-53.0	12-29	0.0-9.4	-7.38-8.37
Henslow's Sparrow	Big Oaks NWR	2012	0-394	2-8	15-81	1.2-53.0	8-29	0.0-4.9	-3.06-4.30

Table A.2. Sets of the top candidate negative binomial regression models (response variable = total songs in 5-min samples of audio recordings collected during May-July) for 5 songbird species on 3 Department of Defense installations, 2012-2013. Included in the table are number of parameters (*K*), degrees of freedom (df), difference in the corrected Akaike's Information Criterion when compared to top model (ΔAIC_c), Akaike weight (w_i), and corrected Akaike's Information Criterion (AIC_c) of the top model in each candidate set. The models selected as "best" models, based on selection criteria, are designated with an asterisk (*).

Species	**Study area**	**Year**	**Model**	***K***	**df**	**ΔAIC_c**	**w_i**	**AIC_c**
Prairie Warbler	All	All	Abundance + Study Site + Day of season^3	4	358	0.00	0.50	1832.38
			Abundance + Study Site + Day of season^4	4	358	0.94	0.31	
			Abundance + Study Site + Day of season^2	4	358	3.91	0.07	
			Abundance + Study Site + Day of season^5	4	358	4.43	0.05	
			Abundance + Day of season^4	3	359	5.95	0.03	
	Big Oaks NWR	2012	*Abundance + Day of season^6	3	128	0.00	0.42	859.71
			Abundance + Sample type + Day of season^6	4	127	0.76	0.28	
			Abundance + Day of season^5	3	128	2.11	0.14	
			Abundance + Sample type + Day of season^5	4	127	2.64	0.11	
			Abundance + Day of season^4	3	128	5.79	0.02	
	Fort Bragg	All	Abundance + Year + Day of season + Time of day	5	226	0.00	0.25	887.69
			Abundance + Year + Day of season	4	227	1.26	0.14	
			Abundance + Year + Day of season + Time of day + Pressure	6	225	1.87	0.10	
			Abundance + Temperature + Year + Day of season + Time of day	6	225	2.09	0.09	
			Abundance + Year + Day of season + Time of day + Wind speed	6	225	2.11	0.09	
		2012	Abundance + Day of season^2 + Day of season + Wind speed	5	105	0.00	0.23	353.75
			Abundance + Temperature + Day of season^2 + Day of season + Wind speed	6	104	1.85	0.09	

Table A.2 (continued)

Species	**Study area**	**Year**	**Model**	***K***	**df**	**ΔAIC$_c$**	***w$_i$***	**AIC$_c$**
			*Abundance + Day of season	3	107	1.96	0.09	
			Abundance + Day of season^2 + Day of season^6	4	106	2.42	0.07	
			Abundance + Day of season^2 + Day of season^5	4	106	2.76	0.06	
		2013	Abundance + Day of season^5	3	118	0.00	0.16	509.12
			Abundance + Day of season^6	3	118	0.35	0.13	
			*Abundance + Day of season^4	3	118	0.43	0.13	
			Abundance + Day of season^3	3	118	2.08	0.06	
			Abundance + Day of season^2 + Day of season^5	4	117	2.14	0.05	
Bachman's Sparrow	Fort Bragg	All	Abundance + Temperature + Year + Day of season + Pressure	6	222	0.00	0.24	1280.85
			Abundance + Temperature + Year + Day of season + Time of day	6	222	0.65	0.17	
			Abundance + Temperature + Year + Day of season + Wind speed + Pressure	7	221	1.89	0.09	
			Abundance + Temperature + Year + Day of season + Time of day + Pressure	7	221	2.12	0.08	
			Abundance + Temperature + Year + Day of season + Time of day + Wind speed	7	221	2.66	0.06	
		2012	Abundance + Day of season + Time of day	4	121	0.00	0.07	661.51
			Abundance + Day of season + Time of day + Wind speed	5	120	0.09	0.07	
			Abundance + Sample type + Day of season + Time of day	5	120	0.17	0.07	
			Abundance + Sample type + Day of season + Time of day + Wind speed	6	119	0.30	0.06	
			*Abundance + Day of season	3	122	0.52	0.05	

Table A.2 (continued)

Species	**Study area**	**Year**	**Model**	***K***	**df**	**ΔAIC$_c$**	***w_i***	**AIC$_c$**
			Abundance + Sample type + Day of season	4	121	0.66	0.05	
			Abundance + Day of season + Wind speed	4	121	1.41	0.04	
			Abundance + Sample type + Day of season + Wind speed	5	120	1.58	0.03	
			Abundance + Day of season^2	3	122	1.64	0.03	
			Abundance + Temperature + Day of season	4	121	1.77	0.03	
			Abundance + Temperature + Day of season + Time of day + Wind speed	6	119	1.80	0.03	
			Abundance + Day of season + Time of day + Pressure	5	120	1.84	0.03	
			Abundance + Temperature + Day of season + Time of day	5	120	1.91	0.03	
			Abundance + Temperature + Sample type + Day of season	5	120	1.94	0.03	
			Abundance + Day of season + Pressure	4	121	1.96	0.03	
			Abundance + Day of season + Time of day + Pressure + Wind speed	6	119	2.00	0.03	
		2013	Abundance + Pressure^3	3	100	0.00	0.07	609.32
			Abundance + Temperature^3	3	100	0.78	0.05	
			Abundance + Temperature^2	3	100	0.83	0.05	
			*Abundance + Temperature	3	100	0.90	0.05	
			*Abundance + Pressure	3	100	1.29	0.04	
			Abundance + Wind speed^3	3	100	1.81	0.03	
			Abundance + Temperature + Pressure^3	4	99	1.87	0.03	
			Abundance + Pressure^3 + Wind speed	4	99	1.90	0.03	
			Abundance + Wind speed^2	3	100	1.91	0.03	

Table A.2 (continued)

Species	**Study area**	**Year**	**Model**	***K***	**df**	**ΔAIC$_c$**	***w$_i$***	**AIC$_c$**
			Abundance + Temperature + Pressure	4	99	1.96	0.03	
			Abundance + Pressure^3 + Time of day	4	99	2.00	0.03	
Field Sparrow	All	All	Abundance + Temperature + Study Site + Time of day + Pressure	6	265	0.00	0.45	2304.33
			Abundance + Temperature + Study Site + Day of season + Time of day + Pressure	7	264	1.92	0.17	
			Abundance + Temperature + Study Site + Time of day + Wind speed + Pressure	7	264	2.10	0.16	
			Abundance + Temperature + Study Site + Day of season + Time of day + Wind speed + Pressure	8	263	4.03	0.06	
			Abundance + Study Site + Time of day + Pressure	5	266	4.48	0.05	
	Big Oaks NWR	2012	Abundance + Temperature + Day of season + Time of day	5	135	0.00	0.13	1129.84
			*Abundance + Time of day	3	137	0.92	0.08	
			Abundance + Temperature + Day of season + Time of day + Wind speed	6	134	0.96	0.08	
			Abundance + Temperature + Day of season + Time of day + Pressure	6	134	1.24	0.07	
			Abundance + Temperature + Sample type + Day of season + Time of day	6	134	1.72	0.06	
			Abundance + Temperature + Time of day	4	136	2.15	0.05	
	Fort Riley	2013	Abundance + Time of day + Wind speed + Pressure	5	126	0.00	0.14	1148.53
			*Abundance + Time of day + Pressure	4	127	0.53	0.10	
			Abundance + Day of season + Time of day + Pressure + Wind speed	6	125	1.73	0.06	
			Abundance + Time of day + Pressure^2	4	127	1.83	0.05	
			Abundance + Time of day + Pressure^3	4	127	1.87	0.05	

Table A.2 (continued)

Species	**Study area**	**Year**	**Model**	***K***	**df**	**ΔAIC_c**	**w_i**	**AIC_c**
			Abundance + Temperature + Time of day + Pressure	5	126	1.93	0.05	
			Abundance + Time of day^2 + Pressure	4	127	2.10	0.05	
Grasshopper Sparrow	Fort Riley	2013	*Abundance + Time of day + Wind speed^2	5	107	0.00	0.35	910.89
			Abundance + Time of day + Wind speed^4	5	107	0.90	0.22	
			Abundance + Time of day + Wind speed^3	5	107	2.83	0.08	
			Abundance + Sample type + Time of day + Wind speed	5	107	3.84	0.05	
			Abundance + Temperature + Sample type + Time of day + Wind speed + Pressure	7	105	4.17	0.04	
Henslow's Sparrow	Big Oaks NWR	2012	Abundance + Time of day + Pressure	4	129	0.00	0.15	1368.07
			Abundance + Day of season + Time of day + Pressure	5	128	1.54	0.07	
			*Abundance + Time of day	3	130	1.58	0.07	
			Abundance + Temperature + Time of day + Pressure	5	128	1.59	0.07	
			Abundance + Sample type + Time of day + Pressure	5	128	2.01	0.05	

Table A.3. Abundance prediction models based on the negative binomial regression results for 5 songbird species on 3 Department of Defense installations, 2012-2013. Songs = total songs in 5 min; day of season = modified Julian date (May 1 = 1); time of day = modified Julian time divided by 5 (30-min before sunrise = 0, 25-min before sunrise = 1); temperature (C^{o}); pressure (mm of mercury) = altimeter setting transformed by subtracting the mean (761) from each value.

Species	**Study area**	**Year**	**Abundance prediction model**
Prairie Warbler	Big Oaks NWR	2012	$\text{Abundance} = \text{exp}^{[(4.33 * 10^{-2})(Songs)\ +\ (-4.71 * 10^{-12})(Day\ of\ season^{6})]}$
	Fort Bragg	2012	$\text{Abundance} = \text{exp}^{[(2.59 * 10^{-2})(Songs)\ +\ (1.23 * 10^{-2})(Day\ of\ season)]}$
		2013	$\text{Abundance} = \text{exp}^{[(2.87 * 10^{-2})(Songs)\ +\ (2.28 * 10^{-8})(Day\ of\ season^{4})]}$
Bachman's Sparrow	Fort Bragg	2012	$\text{Abundance} = \text{exp}^{[(1.02 * 10^{-2})(Songs)\ +\ (1.73 * 10^{-2})(Day\ of\ season)]}$
		2013[a]	$\text{Abundance} = \text{exp}^{[(8.30 * 10^{-4})(Songs)\ +\ (3.25 * 10^{-2})(Temperature)]}$
			$\text{Abundance} = \text{exp}^{[(2.32 * 10^{-2})(Songs)\ +\ (-1.36 * 10^{-2})(Pressure)]}$
Field Sparrow	Big Oaks NWR	2012	$\text{Abundance} = \text{exp}^{[(2.34 * 10^{-2})(Songs)\ +\ (3.27 * 10^{-2})\ (Time\ of\ day)]}$
	Fort Riley	2013	$\text{Abundance} = \text{exp}^{[(1.43 * 10^{-2})(Songs)\ +\ (2.12 * 10^{-2})(Time\ of\ day)\ +}$ $(2.50 * 10^{-2})(Pressure)]$
Grasshopper Sparrow	Fort Riley	2013	$\text{Abundance} = \text{exp}^{[(1.69 * 10^{-2})(Songs)\ +\ (2.32 * 10^{-2})(Time\ of\ day) +}$ $(1.04 * 10^{-2})(Wind\ Speed^{2})]$
Henslow's Sparrow	Big Oaks NWR	2012	$\text{Abundance} = \text{exp}^{[(6.48 * 10^{-3})(Songs)\ +\ (3.47 * 10^{-2})(Time\ of\ day)]}$

[a] Two models performed equally well for Bachman's Sparrow, 2013. Both are shown.

VITA

Stephanie Prevost is from Somerset, Massachusetts. She attended Arizona State University where she received a Bachelor of Science degree in Conservation Biology. Upon graduation, Stephanie became a member of the Student Conservation Association where she participated in various research and monitoring projects in the southwestern United States. While working as a plant ecology intern for the U.S. Geological Survey, Stephanie developed an interest in birds. From there, she acquired extensive avian survey experience working with the U.S. Fish and Wildlife Service and Luke Air Force Base in southern Arizona. She also contributed to various projects including coyote and kit fox surveys, Sonoran Pronghorn reintroduction, and camera trap data analysis. During the spring of 2012, Stephanie accepted a Graduate Research Assistantship at the University of Tennessee, Knoxville, in the Avian Ecology Lab under Dr. David A. Buehler. She graduated in the spring of 2016 with a Master of Science degree in Wildlife and Fisheries Science and a minor in Statistics.