

ESTIMATED DIETS, DIET OVERLAP, AND WINTER HABITAT
ASSOCIATIONS OF FOUR GRASSLAND SPARROWS
IN FLORIDA DRY PRAIRIE

by

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ABSTRACT

North American grassland birds show long-term population declines that generally exceed the declines of other bird groups. Efforts to conserve grassland birds require knowledge of diet and habitat requirements during both the breeding and nonbreeding periods of annual life cycles. This dissertation investigated sparrow habitat associations within two defined plant communities of the dry prairie ecosystem, the dry-mesic and wet-mesic prairie, for four prescribed fire treatments over two consecutive winters. Grasshopper and Henslow's sparrows showed higher relative abundance in wet-mesic prairie and Bachman's Sparrows were more abundant in dry-mesic prairie across all fire treatments. Abundances of Grasshopper and Bachman's sparrows were best predicted by plant community association and secondly by time since fire; whereas for Henslow's Sparrows, habitat and time since fire were equally important. Fall molt-period diets and diet overlap were modeled for resident Florida Grasshopper and Bachman's sparrows using stable carbon and nitrogen isotope ratios of bird feathers and potential food sources, e.g., arthropods and seeds. Grasshoppers (Orthoptera, including a variety of species foraging on both C₃ and C₄ herbs), spiders, dragonflies, flies, beetles and weevils comprised the majority of the diets of adult and juvenile Florida Grasshopper Sparrows and Bachman's Sparrows, but in differing proportions. Despite the similarity in reconstructed diets for the two sparrow species, analysis of diet overlap suggested that approximately half of the Florida Grasshopper Sparrows had diets consisting of higher trophic level prey than Bachman's Sparrows. Winter diets and diet overlap among Grasshopper, Henslow's, and Bachman's sparrows were reconstructed using stable carbon and nitrogen isotope ratios of feathers and potential arthropod and seed food sources. Sparrows were captured and recaptured in winter

2007-2008 using systematic flush-netting, removing a tail feather at first capture and then removing the regrown feather when birds were recaptured. Winter diets of all three sparrows included a variety of arthropods, grass seeds, and sedge seeds, but Bachman's Sparrow winter diets spanned greater trophic diversity than either of the migratory sparrows. Estimated diets of Henslow's and Grasshopper sparrows differed from that of Bachman's Sparrow but Henslow's Sparrow diets did not differ from Grasshopper Sparrow diets. This is the first study of fall and winter sparrow diets in Florida based on stable isotopes and the first study in peninsular Florida on habitat associations of ground-dwelling sparrows.

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CHAPTER 1: INTRODUCTION

At multiple scales, spatial and temporal distributions of animals are governed by factors such as food availability, the need for predator cover, adaptability to a range of disturbance types with varying frequencies of occurrence, and physiological tolerance for abiotic variables such as temperature, moisture, or water chemistry. Maintaining or recovering conditions required for animal population viability within increasingly human-fragmented ecosystems requires finer-scale knowledge of factors such as habitat associations and the array of relationships that comprise dynamic ecosystem food webs in which animals exist with other organisms.

A long-standing ecological theory (MacArthur and Levins 1967, Schoener 1974, Wiens 1977, Scheffer and van Nes 2006) is that niche differentiation results from natural selection acting on closely related or sympatric organisms sharing some of the same resources needed to survive or breed successfully such that coexistence is permitted under all but, perhaps, extreme environmental conditions in which prey may be limited. Sympatric, taxonomically related animals may forage on different prey (Pyke 1982, Herrera et al. 2002, Ahrestani et al. 2012) or they may forage on essentially the same prey but in differing proportions (Martinez 2010, Silva-Pereira et al. 2011, Steenweg et al. 2011). In species-rich ecosystems, suites of closely related species may coexist on a multigenerational, or even evolutionary, time scale provided the prey base and habitat expanse are sufficient to support them (Scheffer and van Nes 2006).

Florida dry prairie is a species-rich grassland ecosystem comprising 302 species of vascular plants (Orzell and Bridges 2006), 89 butterfly species (Lepidoptera) (Florida Park Service 2012); 10 species of damselflies and 30 species of dragonflies (Odonata); 54 species of ants (Formicidae); 108 spider species (Araneae); and more than 600 species of moths (Kissimmee Prairie Preserve State Park; L. Atherton and C. Wolf, pers. comm.). The prairie

supports two resident grassland sparrows: the federally Endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) and Bachman's Sparrow (*Peucaea aestivalis*).

In the nonbreeding season, the dry prairie supports several species of overwintering and migratory sparrows including Henslow's (*Ammodramus henslowii*), Grasshopper (*Ammodramus savannarum pratensis*), Savannah (*Passerculus sandwichensis*), Swamp (*Melospiza georgiana*), Chipping (*Spizella passerina*), and small numbers of Le Conte's (*Ammodramus leconteii*), Lincoln's (*Melospiza lincolni*), and Vesper (*Pooecetes gramineus*) sparrows (P. Miller and MGK, unpubl. data).

Habitat loss was a critical factor in listing of the Florida Grasshopper Sparrow (Delany et al. 1985, Federal Register 1986); less than 10% remains of an estimated 5,000 km² of pre-settlement extent of dry prairie (Noss 2013). Annual point count surveys on public lands, where most of the remaining individuals are thought to reside, produced the lowest historic population count on record in 2012 (n = 74 males; Florida Fish and Wildlife Conservation Commission, unpubl. data). Recent, dramatic declines in reproductively isolated Florida Grasshopper Sparrow populations on publicly managed lands (Tucker et al. 2010; Florida Grasshopper Sparrow working group, unpubl. data), there is urgency to research factors that may affect survival and breeding success, such as investigating winter habitat associations and diet overlap among Florida Grasshopper Sparrows, Bachman's Sparrows and the two most abundant sympatric, migratory sparrows, Henslow's Sparrow and Grasshopper Sparrow.

Defining winter habitat associations can be accomplished by use of various sampling methods developed for cryptic grassland birds that do not perch and sing during the nonbreeding winter months. Line and strip transects, area searches, point counts, and transect flush surveys using ropes or sweep sticks provide estimates of winter species richness, abundance, density, and

habitat associations of grassland birds but cannot provide data on spatial use or physiology of individual birds (Repasky and Schluter 1994, Plentovich et al. 1998, Carrie et al. 2002, Roberts and Schnell 2006, Butler et al. 2009). Tape-playback was shown to be effective in winter surveys of Bachman's Sparrows (Cox and Jones 2004) but is ineffective for surveying cryptic sparrows that are unresponsive to tape-playback during non-breeding periods, e.g., Henslow's and Grasshopper sparrows. Radio-telemetry effectively tracks spatial movements of individual birds during nonbreeding periods but such studies are limited temporally by short-lived transmitter batteries; also, tracking individuals is labor-intensive and impractical for use with numerous individuals of multiple species (Dean and Vickery 2003, Bechtoldt and Stouffer 2005).

Active flush-surveys provide for greater detection of cryptic species in non-breeding periods than do passive survey methods such as point counts (Fletcher et al. 2000). In-flight identification of overwintering species can be accomplished using distinctive flight behaviors, vocalizations, and observed differences in plumage coloration and body shape (Tucker and Robinson 2003, Butler 2007). Even with skilled observers, results of repeated surveys may show high variability (e.g., with standard error equal to the mean, Repasky and Schluter 1994).

Flushing, with or without use of a weighted rope or sweep sticks, has been used to locate focal taxa, which are then singly target-captured in mist nets for radio-transmitter deployment (Dean 2001, Dean and Vickery 2003, Johnson 2006, Thatcher et al. 2006). This approach is useful for targeting individuals of habitat-restricted, imperiled taxa (Dean 2001) or for targeting an easily-identified species in plots with few other species present (Tucker and Robinson 2003) but is labor-intensive for use in a multi-species study or in those with multiple, similar species present simultaneously.

Flush-netting, a field method in which wintering grassland birds are driven toward a line of mist nets, has been used in research testing for interactions between sparrow occupancy and habitat, fire, or cattle grazing, and for research on within-season movement patterns, winter site fidelity, and winter territoriality (Plentovich et al. 1998, Gordon 2000, Dean 2001, Carrie et al. 2002). Published mark-recapture winter research in Florida is limited to work focused on Bachman's Sparrow and the federally Endangered Florida Grasshopper Sparrow wherein radio-telemetry was used to track movements and winter home ranges of individual Florida Grasshopper Sparrows (Dean 2001). Radio-telemetry also was used in conjunction with flush-and-target-netting to study use of animal burrows by wintering Bachman's Sparrow (Dean and Vickery 2003).

Whereas winter habitat associations can be sampled by flushing birds only, birds must be captured to obtain tissue samples for quantitative methods of diet reconstruction. Animal diets can be estimated using conventional methods such as observational studies, crop flushing, or examination of fecal samples, regurgitated pellets, or stomach contents but these methods tend to overestimate diet proportions of indigestible prey and to underestimate proportions of easily-digested prey (Hobson and Clark 1992, Inger and Bearhop 2008).

Stable isotope ratios ($^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$) in animal consumer tissues are related to the stable isotope ratios of their prey. Carbon isotope signatures differ characteristically for C_3 and C_4 plants (DeNiro and Epstein 1978) and for arthropods that forage on C_3 and C_4 plants; therefore, consumer tissue isotopic signatures can reflect the proportion of seeds from grasses or forbs in the diet (Cerling et al. 2006) and from arthropods that forage on C_3 and C_4 seeds. For nitrogen, the heavy isotope (^{15}N) is preferentially incorporated into the tissues of the consumer from the diet, resulting in a systematic enrichment in nitrogen-isotope ratios with each trophic

level (DeNiro and Epstein 1981, Roth and Hobson 2000). Stable isotope analysis has become widely used for investigating animal diets and is particularly suitable for use with imperiled bird species because isotopic signatures of feather or claw samples can be used to reconstruct diets rather than more invasive sample extraction of blood or muscle tissue (Hobson and Clark 1992, Kelly 2000). Once formed, keratin comprising a bird's feathers is metabolically inactive so that stable isotope ratios reflect diet at the time the feather was grown (Hobson 1999).

Diet proportion estimates of different food types can be inferred from feather samples or other animal tissues using nonproprietary mixing model software packages such as IsoSource or more recently developed Bayesian mixing models (e.g., MixSIR, SIAR) (Phillips 2001, Phillips and Eldridge 2006, Inger and Bearhop 2008, Moore and Semmens 2008, Jackson et al. 2011, Layman et al. 2011). Mixing models have been used widely in recent years to gain insights into terrestrial and marine food webs and the efficacy of use continues to be debated with regard to applications in underdetermined food webs with a large number of potential foods sources (Phillips and Gregg 2001, 2003, Phillips et al. 2005, Parnell et al. 2010, Layman et al. 2011, Fry 2013a, b, Semmens et al. 2013).

The goal of this dissertation was to investigate winter habitat associations and diet niches of Florida Grasshopper Sparrow, Bachman's Sparrow, Henslow's Sparrow, and Grasshopper Sparrow in Florida dry prairie and relationships between winter habitat associations and diet niches. In Chapter 2, entitled "Winter habitat associations of four grassland sparrows in Florida dry prairie" dry-mesic and wet-mesic habitat associations for the four sparrows were investigated using flush-net sampling and vegetation classification within plots defined at the marked location of each flushed sparrow. Associations between burn class and prairie habitat category (i.e., wet-mesic and dry-mesic) were tested with 4 x 2 chi-square analysis by species within each burn

class. Akaike Information Criteria scores for small sample sizes (AICc) were used to rank candidate models that best predicted relative abundance of each sparrow species.

In Chapter 3, entitled “Stable isotopes delineate estimated fall molt period diets and diet overlap between resident Florida Grasshopper Sparrow and Bachman’s Sparrow in Florida dry prairie” average diets of the two sympatric, resident sparrows were reconstructed for the August – October annual molt period using stable carbon and nitrogen isotope ratios in feather and food reference samples. Age and sex differences in diets within the sampled Florida Grasshopper Sparrow group also were tested.

In Chapter 4, entitled “Stable carbon and nitrogen isotope ratios reveal winter diet estimates and diet overlap for three grassland sparrows in Florida dry prairie”, winter diets of resident Bachman’s Sparrows and sympatric, migratory Henslow’s and Grasshopper sparrows were reconstructed from feather samples obtained by capturing and recapturing individual birds using flush-netting in plots sampled three times during the winter. The fall to winter diet overlap for resident Bachman’s Sparrows was estimated and diet overlap of Bachman’s, Henslow’s, and Grasshopper sparrow winter diets was investigated.

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CHAPTER 2: WINTER HABITAT ASSOCIATIONS OF FOUR GRASSLAND SPARROWS IN FLORIDA DRY PRAIRIE

Korosy, M. G., J. S. Reece, and R. F. Noss. 2013. Winter habitat associations of four grassland sparrows in Florida dry prairie. *Wilson Journal of Ornithology* 125(3):502-512.

2.1 Abstract

North American grassland birds show long-term population declines that generally exceed the declines of other bird groups. Efforts to conserve grassland birds require knowledge of ecological and habitat requirements during both the breeding and nonbreeding periods of annual life cycles. Nonbreeding habitat associations may affect survival and the acquisition of resources needed for migration and breeding. We focused on the winter habitat associations of a suite of co-occurring grassland sparrows in the dry prairie of south-central Florida, an understudied region within the wintering range of Grasshopper Sparrow (*Ammodramus savannarum pratensis*) and Henslow's Sparrow (*A. henslowii*). During the nonbreeding winter months, these two migratory sparrows comingle with resident Bachman's Sparrow (*Peucaea aestivalis*) and the federally Endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*). We investigated sparrow habitat associations within two defined plant communities of the dry prairie ecosystem, the dry-mesic and wet-mesic prairie, for four prescribed fire treatments over two consecutive winters. Grasshopper and Henslow's sparrows showed higher relative abundance in wet-mesic prairie and Bachman's Sparrows were more abundant in dry-mesic prairie across all fire treatments. Florida Grasshopper Sparrows were detected only in the first and second years post-burn; samples were too small to yield

information on potential preferences between the two prairie communities evaluated. We used an information-theoretic approach to select models that best predicted abundances for each species (except Florida Grasshopper Sparrow) based on time since fire and plant community.

Grasshopper and Bachman's sparrow abundances were best predicted by plant community association and secondly by time since fire, whereas for Henslow's Sparrows habitat and time since fire were equally important. This is the first concurrent study of these four sparrow taxa in peninsular Florida and indicates that time since fire influences the habitat preferences exhibited by wintering sparrows, but that this role differs across co-occurring species and dry prairie plant communities.

2.2 Introduction

Global biodiversity indicators show continued declines despite international commitments to slow the rate of loss (Butchart et al. 2010). Habitat loss and degradation are primary factors cited in the steady declines of grassland birds in North America, including Bachman's Sparrow (*Peucaea aestivalis*), Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*), the eastern North American subspecies of Grasshopper Sparrow (*A. s. pratensis*, hereafter, "Grasshopper Sparrow"), and Henslow's Sparrow (*A. henslowii*) (Delany et al. 1985, Sauer et al. 2011). Each of these sparrows is classified as a species of conservation concern in more than one North American region (USFWS 2008) and in several southeastern states that provide winter habitat for migratory Grasshopper and Henslow's sparrows (Sauer et al. 2011). Mitigating grassland bird declines requires better knowledge of their winter ecology, because winter habitat selection cues may differ from the cues used during the breeding season, and managing landscapes solely for favorable breeding habitat may ignore important wintering habitat needs (Vickery and Herkert 2001, Newton 2004, Macias-Duarte et al. 2009).

The dry prairie of south-central Florida is a predominantly mesic ecosystem that provides both breeding and nonbreeding habitat for grassland sparrows. The dry prairie is a treeless, pyrogenic mosaic of plant communities comprised of more than 20 plant species per square meter ($\bar{x} = 21.6$ species/m²; range 9 to 41 species/m²) and up to 49 species per square meter in the wet calcareous type, one of the highest plant species richness values globally at this spatial scale (Orzell and Bridges 2006a, b). Less than 10% remains of an estimated 5,000 km² of pre-settlement Florida dry prairie (Noss 2013).

Dry prairie is characterized by a predominance of saw palmetto (*Serenoa repens*), runner oak (*Quercus minima*), and wiregrass (*Aristida beyrichiana*). Relative abundance of these and other plants characteristic of dry prairie varies along a soil moisture gradient from graminoid-dominated wet-mesic and wet prairies to the more shrubby mesic, dry-mesic, and sub-xeric prairies. Plant communities within this heterogeneous mosaic can be distinguished by indicator species associated with segments of a wet to sub-xeric soil moisture gradient (Noss et al. 2008). Infrequent fire results in encroachment of woody shrubs and trees that shade out pyrogenic bunchgrasses, increased herbaceous density at ground level, and reduction or elimination of bare ground areas, which in turn impair movement, foraging efficiency, and predator detection by ground-dwelling sparrows (Vickery 1996, Bechtoldt and Stouffer 2005, Tucker et al. 2006, Cox and Jones 2009).

The frequency of lightning-ignited fires in the Florida dry prairie, averaging approximately two years, is among the highest in the world (Noss 2013). Previous research on grassland sparrows emphasized relationships between sparrow abundance and the effects of fire frequency on vegetation structure and seed production. Fire frequency plays a key role in breeding habitat selection by Bachman's and Florida Grasshopper sparrows (Shriver et al. 1999,

Shriver and Vickery 2001, Delany et al. 2002, Tucker et al. 2004, 2006), Henslow's Sparrow (Cully and Michaels 2000, Reinking et al. 2000, Powell 2006, 2008), and Grasshopper Sparrow (Powell 2006, 2008). Fire also plays an important role in wintering habitat selection for Henslow's Sparrows in Louisiana, Mississippi, Alabama, Georgia, and the western Florida panhandle (Tucker and Robinson 2003, Tucker et al. 2004, Bechtoldt and Stouffer 2005, Tucker et al. 2006, Cox and Jones 2009, Palasz et al. 2010b). Previous research suggested that winter survival of these grassland birds may be linked to fire frequency in overwintering habitat (Tucker and Robinson 2003, Thatcher et al. 2006), but other studies disputed this (Johnson et al. 2011). The effect of fire history on winter habitat selection of both the non-migratory Florida Grasshopper Sparrow (Dean 2001, unpublished) and the migratory Grasshopper Sparrow (Butler et al. 2009) in Florida dry prairie has been studied, but no published information is available on winter habitat preferences of Henslow's or Bachman's Sparrows in peninsular Florida. In fact, Christmas Bird Count records and published reports of Henslow's Sparrow in peninsular Florida are scarce (Robertson and Woolfenden 1992, Stevenson and Anderson 1994, Pranty and Scheuerell 1997).

We examined four co-occurring taxa of wintering grassland sparrows in Florida dry prairie over a two-year period. We hypothesized that the relative abundance of each sparrow taxon would relate to prairie plant community and to the number of growing seasons post-fire. Knowledge of relationships between winter habitat occupancy of co-occurring sparrows and plant communities in peninsular Florida will allow better predictions of sparrow occurrence and potential viability on a landscape scale and a basis for habitat restoration, species recovery, and land acquisition (Noss et al. 2008).

2.3 Methods

2.3.1 Study Site

We conducted our research at Kissimmee Prairie Preserve State Park, which encompasses approximately 10,200 ha of dry prairie within the 22,500 ha Preserve (USFWS 1999). During our 2006-2008 field research, the Preserve was believed to support one of the largest extant populations of the endemic, non-migratory Florida Grasshopper Sparrow (Pranty and Tucker 2006), an abundant breeding population of Bachman's Sparrow, and several species of overwintering and migratory sparrows including Henslow's, Grasshopper, Savannah, Swamp, Chipping, and small numbers of Le Conte's, Lincoln's, and Vesper sparrows (P. Miller and M. Korosy, unpublished data).

2.3.2 Flush-Net Sampling

We used flush-netting, an active sampling method in which birds are systematically driven toward a stationary line of mist nets for mark and recapture (Gordon 2000). Variations of the method involve systematic flushing of plots with individual birds flushed into a mobile mist net set up at the location of each flushed bird (Johnson et al. 2009, Palasz et al. 2010a). We selected the flush-netting method to improve accuracy in identifying cryptic, closely related sparrows that might otherwise be misidentified in flight (Bechtoldt and Stouffer 2005). We assumed that all sparrows present were flushed at least once and counted or captured. We flushed sparrows using noisemakers (2 L plastic bottles containing pebbles) attached to a 30 m rope dragged over the vegetation by two observers toward a 120 m long mist net array centered within each established plot. A third observer walked behind the rope and marked sparrow flush locations with a numbered flag. The flag location was recorded with a hand-held Garmin Vista

Cx GPS unit. The area sampled in each flushed plot was determined by recording WAAS-enabled GPS locations (< 3 m error) at each end of the mist net line and at one end of the 30 m rope at initiation of each flush transect. We calculated the relative abundance of each flushed sparrow species by burn class as the number of sparrows per 100 ha to adjust for variation in sample plot size. Although capturing flushed birds was not required for the research presented in this paper, we suggest positive identification of cryptic sparrows improved the identification accuracy of sparrows flushed but not captured.

2.3.3 Wet-Mesic Versus Dry-Mesic Prairie Habitat

We adapted the dry prairie vegetation classification system developed by Noss et al. (2008) to two categories for this study. We defined dry-mesic prairie as populated predominantly by shrubs (e.g., *Serenoa repens*, *Quercus minima*, *Lyonia lucida*, *L. fruticosa*, *Hypericum reductum*, *Vaccinium myrsinites*, *Gaylussacia dumosa*, *Lechea torreyi*), with graminoids (e.g., *Sorghastrum secundum*, *Dichanthelium portoricense*, *Xyris caroliniana*) and non-woody forbs (e.g., *Carphephorus carnosus*, *Pityopsis graminifolia*, *Pterocaulon virgatum*). We defined wet-mesic prairie as populated predominantly by graminoids (e.g., *Ctenium aromaticum*, *Dichanthelium leucothrix*, *D. erectifolium*, *Xyris elliottii*, *X. ambigua*) and non-woody forbs (e.g., *Chaptalia tomentosa*, *Eriocaulon decangulare*, *Bigelowia nudata*, *Lachnocaulon anceps*). Wiregrass (*Aristida beyrichiana*) is an abundant and characteristic grass across this habitat gradient (Orzell and Bridges 2006a,b). The same observer visually classified the vegetation within a 10 m diameter circle centered on each sparrow flush location (n = 239: 2006-2007; n = 316: 2007-2008) into one of the two habitat categories, either dry-mesic or wet-mesic, based on the presence of the selected plant indicator species (Noss et al. 2008).

2.3.4 Effects of Time since Fire

We defined burn class in this study as the number of growing seasons post-burn. Samples were taken from 27 October 2006 to 28 February 2007 (2006-07 samples), and from 5 November 2007 to 11 March 2008 (2007-08 samples). Migrants persisted at the study location into April or later, but flush-net sampling terminated in early March due to federal permit conditions prohibiting flush-netting in the breeding season of the Endangered Florida Grasshopper Sparrow.

In the first year we sampled burn classes two and four, and in the second year burn classes one and three (Table 1); burn class sampling could not be replicated between years due to the biennial prescribed fire rotations implemented at the study site for recovery of the Florida Grasshopper Sparrow. Plots were established to ensure sampling of an approximately equal area of both dry-mesic and wet-mesic prairie within each burn class and were sized to permit systematic sampling of each plot in one work-day by a three-person field crew. Six plots, each approximately four to five ha, were selected in each burn class such that three plots in each group covered predominantly dry-mesic habitat and three plots covered predominantly wet-mesic habitat. Both habitat types were present to a varying extent in each plot due to the mosaic character of the dry prairie ecosystem. All plot groups were located in areas where Florida Grasshopper Sparrows were documented to be breeding in the season immediately before, after, or both before and after the winter sampling seasons.

In 2006-07, three groups of six plots were established in burn class two prairies. One set of six plots was established in burn class four prairies. In 2007-08, one set of six plots was established in burn class one habitat and one set of six plots was established in burn class three prairies. Due to biennial prescribed burn rotations in effect at the study site for the benefit of the Florida Grasshopper Sparrow, all samples from burn classes two and four were taken in 2006-07 and burn classes one and three were sampled in 2007-08 (Table 1).

A total of 36 plot samples was taken in each year, with four to six weeks between repeated samples of the same plot within a given year. Based on previous research (Carrie et al. 2002, Tucker and Robinson 2003, Butler et al. 2009, Johnson et al. 2009), we assumed that this time lapse was sufficient to consider sparrow locations in each plot as independent samples regardless of any within-season site fidelity by individual birds. Although research on wintering Henslow's Sparrows in longleaf pine habitat in southern Louisiana showed that radio-tagged birds remained within a 0.3 ha area for a period of up to three weeks (range 0.09-1.50 ha; n=16 individuals using 11 locations per individual) (Bechtoldt and Stouffer 2005), we found no published literature suggesting that grassland sparrows showing fidelity to a winter home range were associated exclusively with a single plant community, so we assumed that sparrow flush locations indicated a preferred habitat association.

2.3.5 Statistical Analyses

We used a 4 x 2 chi-square analysis to test for association between burn class and prairie habitat category (wet-mesic and dry-mesic) by species within each burn class. Florida Grasshopper Sparrow was excluded from the analyses for burn classes three and four because the expected abundances were zero, a violation of the assumptions for chi-square tests. We used an information-theoretic approach (Burnham and Anderson 2002) to rank generalized linear models regressing predictor variables of burn class, habitat category, and interactions between these two variables against sparrow abundance by species. Because we could not replicate sampling of the same burn classes in both years, we simplified the analysis by calculating a combined relative abundance for each sparrow in each habitat category for burn classes one and two combined and for burn classes three and four combined. We obtained Akaike information criteria (AIC) scores for each candidate model using R statistical computing software (R CoreDevelopmentTeam

2012) and corrected these scores for small sample size (AIC_c). We calculated Akaike weights (w_i), relative likelihood (L_i), and number of model parameters (K) for each candidate model and ranked the model weights to select the models that best predicted abundance of each species.

2.4 Results

Total area sampled in each burn class was 94.4 ± 1.9 (SD) ha for burn class one, 108.5 ± 1.3 (SD) ha for burn class two, 84.2 ± 1.9 (SD) ha for burn class three, and 55.6 ± 0.6 (SD) ha for burn class four. In 2006-07 sampling, 134 sparrows were captured; an additional 105 sparrows were identified as one of the focal sparrow taxa when flushed but were not captured. In 2007-08 sampling, 149 sparrows were captured; an additional 167 sparrows were identified as one of the focal taxa when flushed but were not captured. During the two winters of sampling, 130 Bachman's Sparrows were captured a total of 161 times, six Florida Grasshopper Sparrows were captured seven times, 78 Grasshopper Sparrows were captured 90 times, and 74 Henslow's Sparrows were captured 86 times. Recaptured birds were caught only in the plots in which they were captured initially and not in any other sampled plot. The number of unidentified birds averaged one bird per 4.1 ha; flush-net plot size ($n = 36$) averaged 4.7 ± 0.52 (SD).

Florida Grasshopper Sparrows were captured only in one set of six plots in Five Mile Prairie in both years of this study (2006-07, burn class two ($n = 5$); 2007-08, burn class one ($n = 8$)). None was detected in burn class three or four prairies. The set of plots in which Florida Grasshopper Sparrows were captured was within a core breeding area for the subspecies within Kissimmee Prairie Preserve. In 2006-07, three individuals were flushed from wet-mesic prairie and two from dry-mesic prairie. In 2007-08, four individuals were flushed from wet-mesic prairie and four from dry-mesic prairie (Fig. 2.1). Although sample sizes are prohibitively small

for analyses, results suggest that Florida Grasshopper Sparrows have a wintering habitat preference for burn class one and two prairie over burn classes three and four. Potential inferences regarding habitat preferences are limited, however, because birds were captured only in proximity to a core breeding area, whereas none was captured in other prairies where breeding also was documented during our research period.

Bachman's, Grasshopper (*A. s. pratensis*), and Henslow's Sparrows were flushed at all sites sampled in both winters; however, the latter two species were more abundant in wet-mesic prairie in burn classes one, two, and three than Bachman's Sparrows (Fig. 2.1). Bachman's Sparrows also favored burn class one and two patches, but were significantly more abundant in burn class four prairies than Grasshopper or Henslow's sparrows sampled in 2006-07.

Grasshopper and Henslow's sparrows were more abundant in wet-mesic than in dry-mesic patches in all burn classes sampled. In contrast, Bachman's Sparrows were more abundant in dry-mesic than in wet-mesic patches in all burn classes (Fig. 2.1). Overall, each species showed a unique suite of responses to fire regimes that differed between wet and dry-mesic habitats.

Relative sparrow abundance was significantly associated with habitat category in all valid cases in which the expected abundance was not zero (all $P < 0.0001$; Table 2). This provides evidence that the four sparrow taxa sampled display different dry and wet-mesic habitat affinities that are also independent of burn class.

We used an information-theoretic approach to rank candidate models that predicted sparrow abundance as a function of burn class (burn classes one and two combined; burn classes three and four combined) and habitat category (dry-mesic and wet-mesic prairie; Table 3). Four models were identified as equally likely (within two AICc units of the best model) predictors of Henslow's Sparrow abundance (Table 3), with the best fit model including habitat and burn class

without interaction effects. Two models were equally likely for Grasshopper Sparrow, with the best model including only habitat and reflecting the preference of this species for wet-mesic prairie across all burn classes (Fig. 2.1). The best fit model for Bachman's Sparrow also included only habitat, reflecting this species' apparent affinity for dry-mesic prairie (Fig.1), although additional models that included burn class and interaction effects were within two AICc units of this model.

2.5 Discussion

This study determined that the number of years since fire strongly affected grassland sparrow abundance during the winter, but that relative abundance was equally, and in some cases more strongly, related to plant community type within the wet/dry mesic prairie mosaic. Each of the four sparrow taxa showed a unique response to the combination of burn year and plant community type, indicating that management and recovery strategies should maintain the heterogeneity in plant community patterns within prairie landscapes as well as heterogeneity in vegetation structure in order to provide habitat preferred both by resident and migratory birds. The federal recovery plan for the Florida Grasshopper Sparrow (USFWS 1999) focuses exclusively on habitat management for that single species and recommends a one to three year burn rotation. We show that co-occurring sparrows display affinities for burn rotations that, while not identical, are largely compatible with those recommended for the Florida Grasshopper Sparrow.

2.5.1 Management Implications by Taxon

2.5.1.1 Florida Grasshopper Sparrow

Despite documentation of singing male Florida Grasshopper Sparrows (*A. s. floridanus*) at all sampled sites during the breeding season between the two winters in which sites were sampled in this study, individuals of this resident, federally Endangered subspecies were captured in both study years only in one set of six plots in an area that has hosted a persistent breeding subpopulation at least since 1984 (Delany and Cox 1986). We could not differentiate between the two Grasshopper Sparrow subspecies in flight; therefore, Florida Grasshopper Sparrows may have been present in burn class three or four habitat but because none were captured, they were undetected by our sampling method. Based upon the low relative abundance of Florida Grasshopper Sparrows at the single location where they were captured in both years, we predict this subspecies would be in far lower abundance, if present, in burn class three or four habitat at other sites where they were undetected by our sampling method. Although we recorded small samples of the Florida Grasshopper Sparrow ($n = 8$, 2006-07; $n = 5$, 2007-08), we noted that individuals were flushed almost equally from both wet-mesic and dry-mesic prairie ($n = 7$, $n = 6$, respectively). Because this sparrow must be captured for positive subspecific identification, our sampling method proved insufficient for drawing inferences about winter habitat associations.

In 2006-07 Florida Grasshopper Sparrows were captured in burn class two prairies and in 2007-08, those same sample plots were in burn class one condition. These burn class associations are consistent with previous research demonstrating that this resident subspecies strongly prefers burn class one and two prairie year-round and that abundance declines steeply in areas that have gone un-burned for longer than two years (Shriver et al. 1999, Dean 2001, Shriver and Vickery 2001, Pranty and Tucker 2006).

Regionally declining abundance of the Florida Grasshopper Sparrow, juvenile dispersal, post-breeding adult dispersal, and significantly enlarged winter home ranges compared to breeding territories (Dean 2001) may explain the low detection rates observed in this study. Based on our results, we recommend that management for Florida Grasshopper Sparrows continue to emphasize fire at a frequency of one to three years to maintain a mosaic of vegetation structure along environmental gradients. Unfortunately, the recent and unexplained steep decline of the Florida Grasshopper Sparrow across its known range, with predicted extinction within a few years (Florida Grasshopper Sparrow Working Group, unpublished data) may make our recommendation purely academic.

2.5.1.2 Grasshopper Sparrow

The migratory Grasshopper Sparrow (*A. s. pratensis*) was found in comparable abundance in burn class one and three habitat in 2007-08 and significantly lower abundance in burn class two, sampled in 2006-07 (Fig. 2.1). Grasshopper Sparrows were least abundant in burn class four, sampled in 2006-07. Based on the comparable abundances we detected in burn classes one and three sampled in 2007-2008, we infer that in some years Grasshopper Sparrow may be at least as abundant in burn class two. The significantly lower abundance detected in 2006-07 in burn class two prairie may have resulted from variability in breeding success within the species' breeding range, from sampling timeframe within the winter season, or from inter-annual variation in temporal rainfall distribution at the study site with consequent prey base or vegetation density effects in the period between the two sample years. The Grasshopper Sparrow's preference for wet-mesic prairie habitat combined with drought conditions preceding 2006-07 sampling may have enabled birds to occupy depression marshes and shallow sloughs, which were communities that were not sampled in this study including because they normally are inundated.

Previous research on breeding Grasshopper Sparrows documented a range of relationships between breeding season abundance and time since fire. In some studies researchers found that the sparrow was least abundant or absent in burn class one habitat and more abundant in grasslands burned two to three years prior, whereas other studies found that Grasshopper Sparrows were most abundant in burn class one prairie with lower abundances in succeeding burn classes (Vickery 1996, USGS 2002, Powell 2006, 2008).

One previous study examined occupied breeding territory densities of Grasshopper Sparrow in relation to vegetation variables and found a strong negative relationship with woody plant cover (Ahlering 2005). Similarly, we find that overwintering Grasshopper Sparrows in Florida dry prairie have a strong affinity for graminoid and forb-dominated wet-mesic prairie devoid of woody shrubs.

In the only previous study on wintering Grasshopper Sparrows in Florida dry prairie, researchers documented that the migratory subspecies preferred burn class one prairie and recommended that dry prairie management include two-year burn rotations. Their research also examined sparrow occupancy as a function of vegetation variables such as saw palmetto (*Serenoa repens*), forb, and litter cover but did not link the vegetation variables to dry prairie plant communities (Butler et al. 2009). In contrast, our research demonstrated that Grasshopper Sparrow abundance is linked both to fire-return interval and to plant community type. The recovery-focused fire rotations recommended for the Florida Grasshopper Sparrow (*A. s. floridanus*) will support the migrant Grasshopper Sparrow (*A. s. pratensis*) although perhaps not at optimal levels in the case of one-year fire return intervals.

2.5.1.3 Henslow's Sparrow

The highest abundance of Henslow's Sparrows occurred within burn class three in 2007-08, in contrast with most of the previous winter research in which the species was most abundant

within burn class one longleaf pine savannas in Louisiana, Mississippi, Alabama, and northwest Florida (Carrie et al. 2002, Tucker and Robinson 2003, Bechtoldt and Stouffer 2005 but see Palasz et al. 2010). In longleaf pine savannas, however, pine needle duff accumulates quickly, increasing the structural density of the herbaceous layer and interfering with free movement of ground-foraging sparrows. Relatively frequent fire rotations are needed to minimize litter depth and encourage herbaceous growth in longleaf pine savannas (Carrie et al. 2002). The affinity of wintering Henslow's Sparrows to the low litter accumulations in burn class one longleaf pine savannas throughout much of the species' winter range contrasts with the sparrow's preference for breeding habitat characterized by dense, tall grass and thick litter accumulations due to fire return intervals of two or more years (Cully and Michaels 2000, Reinking et al. 2000, Powell 2006, 2008).

In the treeless Florida dry prairie, litter accumulates differently in dry-mesic and wet-mesic communities. In the dry-mesic prairie, litter composed of saw palmetto fronds (*Serenoa repens*), oak leaves (*Quercus minima*), and other woody shrubs (e.g. *Lyonia lucida*, *L. fruticosa*, *Ilex glabra*, *Hypericum reductum*, *Bejaria racemosa*) accumulates more quickly than litter from the dead grasses and forbs in the wet-mesic prairie, which lacks woody shrubs. Therefore, wet-mesic prairie, with minimal litter accumulation (<0.5 cm, M. Korosy, pers. obs.) in burn classes two and three, provides habitat structure for ground-foraging sparrows comparable to that in burn class one within longleaf pine savannas.

The winter 2007-08 sampling period followed below-normal rainfall conditions during the spring and summer growing season of 2007 which may have inhibited regrowth and fruiting of cespitose grasses in burn class one prairie. The sparse vegetation may have provided inadequate cover or forage for Henslow's Sparrow; however, this inference conflicts with

findings by previous researchers working in southern Louisiana, who found that maximum densities of wintering Henslow's Sparrows were predicted most accurately by low-density habitat structural characteristics rather than by seed composition or density (Johnson et al. 2011). In Florida dry prairie, however, prey abundances (seeds and arthropods) may be associated differently with burn class, habitat structure, and plant community type than elsewhere in the species' winter range. Given the natural, historic fire return interval of approximately two years, on average, the one to three year rotations applied to benefit the Florida Grasshopper Sparrow will support overwintering Henslow's Sparrows in the wet-mesic prairie in burn classes two and three.

2.5.1.4 Bachman's Sparrow

In contrast to the other three species of sparrows sampled in this study, Bachman's Sparrows strongly preferred dry-mesic prairie patches. Bachman's Sparrows predominantly occupy the understory of longleaf pine savannas and pine flatwoods in the southeastern United States, which have understory conditions similar to that of the dry-mesic patches within the Florida dry prairie (Abrahamson and Hartnett 1990, USFWS 1999). The species' affinity for treeless, dry mesic prairie at our study location is consistent with use of similar understory plant communities in longleaf pine savannas and pine flatwoods ecosystems elsewhere in the species' breeding range.

Bachman's Sparrow was most abundant in burn class one, but abundance declined progressively through burn class two, three, and four prairie, notwithstanding year effects between sample years. Our results are consistent with previous research on relative winter abundance and time since fire for this resident species (Tucker et al. 2004, 2006, Cox and Jones 2007), but this is the first study to establish this pattern in peninsular Florida. Management strategies for this species should emphasize frequent burn cycles (every one to three years) and

the maintenance of dry-mesic grassland. Importantly, this strategy would equally benefit the Endangered Florida Grasshopper Sparrow, which appears to utilize both wet and dry-mesic prairie habitats.

Across all four sparrow taxa sampled in this study, prairie plant community association and time since fire strongly affected relative abundance. Nevertheless, we found no linear relationship between sparrow abundance and plant community or burn class. The effect of time since fire on sparrow abundance is not consistent among species or across plant communities within the Florida dry prairie, and management strategies should account for these differences (Fig. 2.1). We recommend that land managers maintain a diversity of plant communities and burn rotations within grasslands, as suggested by our results and previously published studies, as opposed to managing exclusively for dry or wet-mesic communities and regular, one or two year burn cycles. Managers should also generally strive for heterogeneous burns that mimic lightning fires, as opposed to the more common homogeneous or “clean” prescribed fires, because a patchy vegetation structure promotes higher overall native species richness (Keeley et al. 2009, Myers and Harms 2011, Noss 2013). Managing for a diverse prairie landscape also may allow species to shift their habitat associations in response to the increasingly variable climate in Florida (Von Holle et al. 2010). Future research on wintering sparrows in peninsular Florida should examine associations between relative abundance of sparrows, time since fire, fire seasonality, plant community type, and winter diets across multiple years to improve understanding of winter sparrow occupancy in dry prairie and other grassland communities. Longer-term studies may reveal how sparrow-plant community associations change with annual variation in climate and provide a basis for refining predictions of winter sparrow distributions given scenarios of global climate change.

Table 2.1: Sampling strategy for burn classes, each sampled in six plots of between four and five ha. Three of the six plots in each group covered predominantly wet-mesic prairie and three plots covered predominantly dry-mesic prairie. An unscheduled burn of Five Mile Prairie occurred in the latter part of the first sampling year preventing resampling of those six plots. The total number of plots sampled (including replicate samples) in each year was 36.

	Sampling Area	Burn Class	# of Plots	Times Sampled	# of Plot Samples
Year 1					
	Corridor Prairie	2	6	1	6
	Five Mile Prairie	2	6	1	6
	Audubon Prairie	2	6	2	12
	Duck Slough East Prairie	4	6	2	12
Year 2					
	5 Mile Prairie	1	6	3	18
	Audubon Prairie	3	6	3	18

Table 2.2: Results of 4 x 2 chi-square tests ($p = 0.0001$) demonstrate a lack of independence between sparrow abundance (birds/100 ha) and the two habitat categories within each burn class. FGSP: Florida Grasshopper Sparrow (*A. s. floridanus*), GRSP: Grasshopper Sparrow (*A. s. pratensis*), HESP: Henslow's Sparrow, BACS: Bachman's Sparrow.

Burn class	Sparrow	Wet mesic	Dry mesic	X^2	df
1	FGSP	4	4	58.543	3
	GRSP	56	12		
	HESP	14	1		
	BACS	22	63		
2	FGSP	3	2	45.961	3
	GRSP	18	8		
	HESP	25	2		
	BACS	13	51		
3	FGSP	0	0	62.758	2
	GRSP	55	6		
	HESP	53	5		
	BACS	25	44		
4	FGSP	0	0	24.314	2
	GRSP	2	0		
	HESP	9	0		
	BACS	11	40		

Table 2.3: Model results of plant community habitat association and burn class regressed against relative abundances of three sparrows in Florida dry prairie. Candidate models are ranked according to Akaike's information criteria corrected for small sample size (AIC_c) for each species. Akaike weights (w_i), relative likelihood (L_i), and number of model parameters (K) are also shown.

Model	AIC_c	ΔAIC_c	w_i	L_i	K
Henslow's Sparrow					
habitat + burn	22.80	0.00	1.00	0.36	2
habitat	23.71	0.92	0.63	0.23	1
habitat*burn + habitat	23.87	1.07	0.59	0.21	2
habitat*burn + habitat + burn	23.98	1.19	0.55	0.20	3
habitat*burn	32.79	10.00	0.01	0.00	1
habitat*burn + burn	32.87	10.07	0.01	0.00	2
burn	76.80	54.01	0.00	0.00	1
Grasshopper Sparrow					
habitat	22.37	0.00	1.00	0.56	1
habitat + burn	24.42	2.04	0.36	0.20	2
habitat*burn + habitat	26.08	3.71	0.16	0.09	2
habitat*burn + habitat + burn	26.17	3.79	0.15	0.08	3
habitat*burn	28.23	5.85	0.05	0.03	1
habitat*burn + burn	28.28	5.91	0.05	0.03	2
burn	64.57	42.20	0.00	0.00	1
Bachman's Sparrow					
habitat	27.05	0.00	1.00	0.42	1
habitat + burn	28.00	0.95	0.62	0.26	2
habitat*burn + habitat	28.96	1.91	0.38	0.16	2
habitat*burn + habitat + burn	29.01	1.96	0.38	0.16	3
habitat*burn	37.64	10.59	0.01	0.00	1
habitat*burn + burn	37.67	10.62	0.00	0.00	2
burn	55.78	28.73	0.00	0.00	1

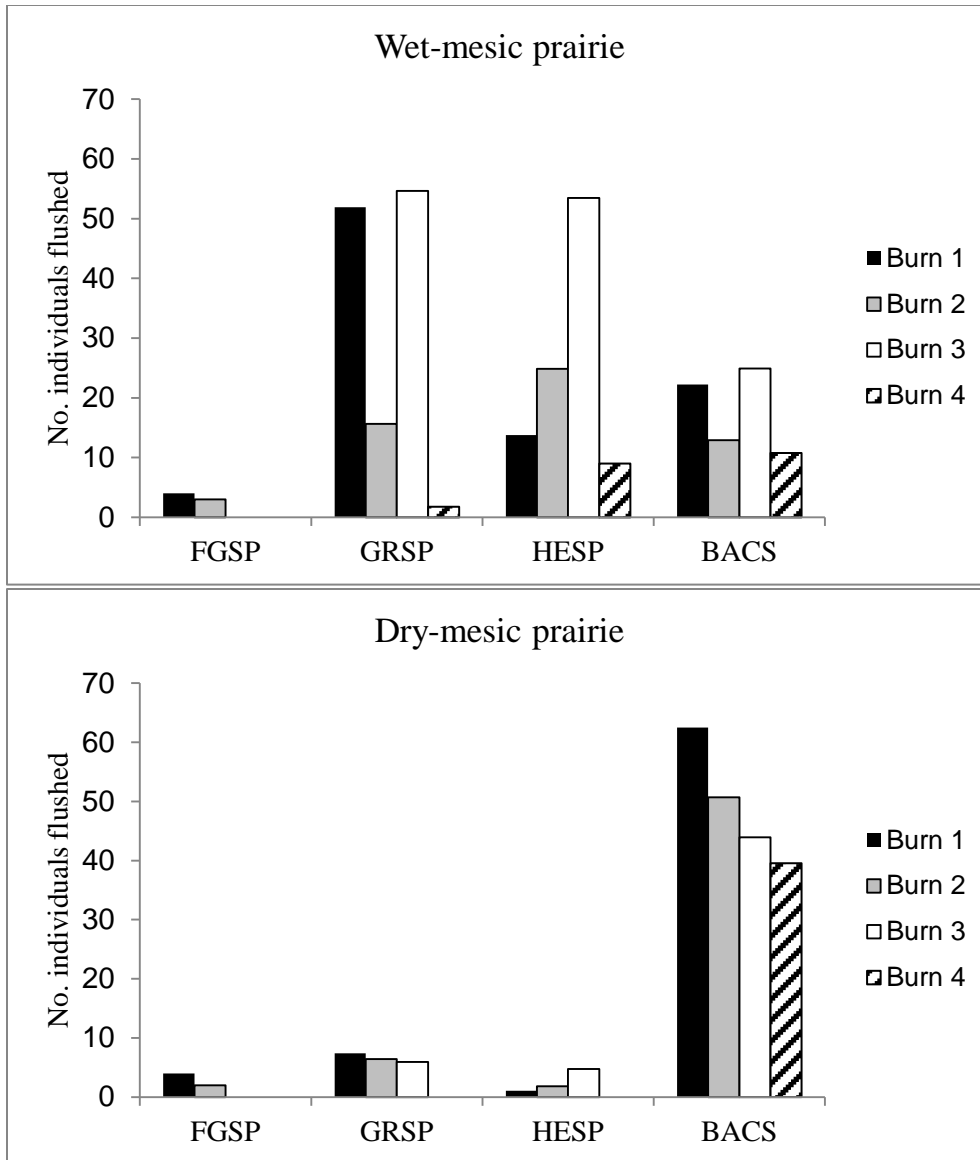


Figure 2.1: Relative abundance of sparrows per 100 ha in wet-mesic and dry-mesic prairies. Burn class 2 and 4 prairies were sampled in winter 2006-07; burn class 1 and 3 were sampled in winter 2007-08. FGSP: Florida Grasshopper Sparrow, GRSP: Grasshopper Sparrow, HESP: Henslow's Sparrow, BACS: Bachman's Sparrow.

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CHAPTER 3: STABLE ISOTOPES DELINEATE ESTIMATED FALL MOLT PERIOD DIETS AND DIET OVERLAP BETWEEN RESIDENT FLORIDA GRASSHOPPER SPARROW AND BACHMAN'S SPARROW IN FLORIDA DRY PRAIRIE

3.1 Abstract

Diet niches are integral characteristics of food webs that may vary temporally with food availability. In grassland ecosystems food may not be limited except during periods of drought or freezing temperatures and, in these periods, closely related species with overlapping diet niches may compete for more limited food resources. Florida Grasshopper Sparrow has shown recent, dramatic, and unexplained population declines on publicly managed dry prairie lands. Little is known of the potential for diet overlap between the federally-Endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) and other Florida dry prairie residents such as the sympatric Bachman's Sparrow (*Peucaea aestivalis*). We used stable carbon and nitrogen isotope ratios of bird feathers and potential food sources, e.g., arthropods and seeds, to estimate diets and isotopic niche breadth for the two resident sparrows during the annual feather molt period, August to mid-October 2007. Grasshoppers (Orthoptera, including a variety of species foraging on both C₃ and C₄ herbs), spiders, dragonflies, flies, beetles and weevils comprised the majority of the diets of adult and juvenile Florida Grasshopper Sparrows and Bachman's Sparrows, but in differing proportions. The C₃ and C₄ sedge and grass seeds sampled in our study did not appear to be significant food sources during the fall molt period. Despite the similarity in reconstructed diets for the two sparrow species, analysis of diet overlap suggested that approximately half of the Florida Grasshopper Sparrows had diets consisting of higher trophic level prey than Bachman's Sparrows. In particular, some adult male Florida Grasshopper Sparrows may be foraging more on higher order consumers and/or on larger arthropods (e.g.

spiders, dragonflies, and adult grasshoppers), with unknown consequences for survival and reproduction especially during periods in which these foods may be more limited.

3.2 Introduction

Niche partitioning allows potentially competing animal species to coexist through differing resource use, for example, by diet or habitat partitioning (Di Bitetti et al. 2010, Ahrestani et al. 2012, Shiels et al. 2013). Sympatric bird species may partition available food resources by consuming different prey, using different foraging behaviors, or exploiting different microhabitats to avoid direct competition (MacArthur 1958, Wiens 1969, Snow and Snow 1971, Allaire and Fisher 1975, Wiens and Rotenberry 1979).

Diet overlap is a necessary condition for competition to occur between closely related, sympatric taxa with similar foraging habits. In species-rich grassland ecosystems such as Florida dry prairie diet niches of closely related species may overlap significantly without adverse consequences for survival or reproductive success provided that food availability is not limited. If prey were limited in abundance during the fall molt period by extended drought, for example, competition for scarce food resources could adversely affect survival or physiological condition of the less abundant Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) and particularly the inexperienced juveniles.

Food availability for grassland birds is usually not considered to be limited during the breeding season so grassland ecosystems can support bird species with overlapping diets (Wiens and Rotenberry 1979, Pulliam and Dunning 1987). However, given recent, dramatic declines in reproductively isolated, non-migratory Florida Grasshopper Sparrow populations (Tucker et al. 2010) on publicly managed lands (Florida Grasshopper Sparrow working group, unpubl. data), there is greater interest in factors that may affect survival and breeding success, such as diet

overlap and the potential for food resource competition among sympatric, ground-foraging bird species.

Published records of prey consumed by Florida Grasshopper Sparrows are limited to data on stomach contents of breeding-season adults and nestlings. Identified stomach contents of two nestlings included 87.5% arthropods and 12.5% seeds (Delany et al. 2000). Arthropods comprised 69% of the stomach contents of 9 adult and one “young” Florida Grasshopper Sparrow with seeds comprising the remainder (Howell 1932). Orthopterans and larvae composed 73.7% and 22.6%, respectively, of prey items delivered to nestling Grasshopper Sparrows (*A. s. pratensis*) in Kentucky (Adler and Ritchison 2011). Lepidopteran larvae composed 16 and 20% of Grasshopper Sparrow (*A. s. pratensis*) diets in South Dakota and Oklahoma, respectively (Wiens 1973).

Bachman’s Sparrow resides in longleaf pine savannas and pine flatwoods of the southeastern United States and in the Florida dry prairie near the southern edge of its geographic range where it co-occurs with the Florida Grasshopper Sparrow. Grass seeds comprised more than 90% of the stomach contents of Bachman’s Sparrows in Texas in summer (n = 5), fall (n = 11), and winter (n = 44) (Allaire and Fisher 1975). In Alabama and Texas, however, animal matter comprised 58% (n=10) and 68% (n = 7), of stomach contents, respectively, with grass and sedge seeds comprising the remainder (Dunning 2006).

Bachman’s Sparrow, Florida Grasshopper Sparrow, and Eastern Towhee (*Pipilo erythrophthalmus*) are the only three species within the family Emberizidae that are resident in Florida dry prairie. Eastern Towhee inhabits the more dense, shrubby patches within dry mesic prairie, patches unburned for >3 years, and shrubby patches in mesic flatwoods, in contrast to Bachman’s and Florida Grasshopper Sparrows (Korosy et al. 2013), which use habitat with low

shrubs (especially saw palmetto [*Serenoa repens*] and dwarf live oak [*Quercus minima*]), with abundant open ground, and a graminoid-rich herbaceous layer dominated by wiregrass (*Aristida beyrichiana*). Bachman's Sparrow is, therefore, the most closely related, year-round potential diet competitor with the Florida Grasshopper Sparrow.

Although animal diets can be estimated using conventional methods such as observational studies under optimal conditions and from stomach contents, these methods have inherent limitations (Inger and Bearhop 2008). Adult animals, such as ground-dwelling sparrows that forage in dense herbaceous vegetation, are often difficult to locate and impossible to observe for more than a few seconds at a time. Diet reconstruction based on stomach contents is subject to underestimation of quickly digested, soft-bodied prey items such as lepidopteran larvae and overestimation of hard-bodied prey items such as beetles (Hobson and Clark 1992).

Stable isotope analysis of bird feathers is a suitable tool for reconstructing diets of imperiled avian populations, obviating the need to extract blood, muscle, or organ tissues from individual birds (Hobson and Clark). Once formed, keratin comprising a bird's feathers is metabolically inactive so that stable isotope ratios reflect diet at the time the feather was formed (Hobson). Comparing isotopic signatures in feathers with potential foods ingested during feather growth allows estimation of the proportion of these foods assimilated by each species. Diets estimated using stable isotope analysis can be used as a proxy to draw inferences about ecological niches of co-occurring animals that may be potential competitors (Newsome et al. 2007).

In a species-rich ecosystem such as Florida dry prairie many potential foods exist for ingestion by ground-dwelling sparrows including a broad array of arthropod taxa and seeds. To estimate diets using mixing models, however, one must reduce the number of potential food

sources by grouping taxonomically related samples or by other means (Phillips et al. 2005) so that calculated group mean isotope ratios of food sources and consumer tissues are statistically distinct (Layman et al. 2011). If multiple food source groups do not differ it may be more informative to investigate demographic sub-groups or the range of individual diets within each species. Individual variability in prey preferences can have important consequences for fledgling and adult survival and for reproductive success (Inger et al. 2006, Jackson et al. 2012). For sympatric, generalist consumers that eat comparable proportions of the same food groups, considerable diet overlap may occur (Flaherty and Ben-David 2010).

Based on published accounts of diets of both sparrows we predicted significant overlap between diets of resident Florida Grasshopper Sparrows and Bachman's Sparrows during the fall feather molt period. We also predicted that, given the high abundance and diversity of arthropod prey at the study location, diets of both sparrows would be predominantly arthropods with seeds a less significant part of the diet. To test these predictions we reconstructed average diets and tested for diet overlap for both sparrows during the fall feather molt period using stable carbon and nitrogen isotope ratios of arthropod and seed reference samples together with feather samples collected from individual sparrows. We also tested for diet differences based on age and sex of Florida Grasshopper Sparrows.

3.3 Methods

3.3.1 Study Site

Our research was conducted at Kissimmee Prairie Preserve State Park, which encompasses approximately 10,200 ha of dry prairie within the 22,500 ha Preserve (USFWS 1999). During our 2006-2008 field research, the Preserve was believed to support one of the

largest extant populations of the endemic, non-migratory Florida Grasshopper Sparrow (Pranty and Tucker 2006) and an abundant breeding population of Bachman's Sparrow (P. Miller and M. Korosy, unpublished data).

The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*), a non-migratory subspecies of Grasshopper Sparrow, is endemic to Florida dry prairie, a treeless, pyrophytic mosaic of plant communities comprising 302 species of vascular plants (Orzell and Bridges 2006b). Less than 10% remains of an estimated 5,000 km² of pre-settlement Florida dry prairie (Noss 2013). Annual point count surveys on public lands, where most of the remaining individuals are thought to reside, produced the lowest historic population count on record in 2012 (n = 74 males; Florida Fish and Wildlife Conservation Commission, unpubl. data).

Arthropod richness and abundance are positively correlated with native grasses and forb cover in grasslands (McIntyre and Thompson 2003, McMellen 2006). Arthropod inventories in Florida dry prairie at Kissimmee Prairie Preserve State Park have, to date, documented a variety of taxa: 89 butterfly species (Lepidoptera) (Florida Park Service 2012); 10 species of damselflies and 30 species of dragonflies (Odonata); 54 species of ants (Formicidae); 108 spider species (Araneae); and more than 600 species of moths (Kissimmee Prairie Preserve State Park; L. Atherton and C. Wolf, pers. comm.).

3.3.2 Feather Samples

Florida Grasshopper Sparrows and Bachman's Sparrows resident at the study site undergo a complete annual molt of all body feathers, flight feathers, and tail feathers between mid- August and late October (M. Korosy and P. Miller, unpubl. data). Hatch-year (i.e., juvenile) birds of both species also undergo a complete molt during this time period, so that after early

November, when the majority of our winter flush-net sampling occurred, juveniles usually could not be distinguished from adults (Pyle 1997).

Singing male Florida Grasshopper Sparrows were target-captured in single 18 m long, 30 mm mesh mist nets between 8 March 2007 and 31 August 2007 and between 16 February 2008 and 24 June 2008 using tape-playback of male territorial songs. Adult females and juveniles were captured incidentally during the same periods in 2007 and 2008. In non-breeding periods when males do not perch or sing, we used flush-netting, an active sampling method in which grassland birds are systematically driven toward a stationary line of mist nets for mark and recapture of Florida Grasshopper Sparrows and Bachman's Sparrows. Flush-net sampling occurred between 5 November 2007 and 11 March 2008 at two sites approximately 5 km apart at the study location. Both sampling sites were approximately 4-5 ha and were sampled three times each during the winter. Sampling terminated in early March due to federal permit conditions prohibiting flush-netting in the breeding season of the Endangered Florida Grasshopper Sparrow. All captured birds received a uniquely-numbered, aluminum leg band issued by the U. S. Geological Survey's Bird Banding Lab to enable subsequent identification when recaptured.

Three large-scale, volunteer-supported mist-netting events also were conducted during winter 2007-2008 at a single location that was 1 km and 4.5 km, respectively, from the two sites at which sparrow flush-netting occurred during winter 2007-2008. At each event, volunteers dragged a 90-meter rope across the dry prairie vegetation flushing birds into a 300-350 meter long mist net array. Sampling events occurred on 28 October 2007, 12 January 2008, and 16 February 2008.

Florida Grasshopper Sparrow feathers incidentally shed during handling and banding were prepared for stable isotope analysis. Feathers analyzed from individual birds ($n = 22$)

included single rectrices (tail feathers; $n = 14$) or multiple body contour feathers from the same individual ($n = 8$) (Fig. 3.1). Tail and body feather samples from individual Florida Grasshopper Sparrows were limited to those that were incidentally shed during capture or banding procedures due to permitting restrictions for this endangered species. All body contour feathers collected from the same individual bird were homogenized to obtain a single sample for stable isotope analysis. One tail feather, the right fourth rectrix, was removed for stable isotope analysis from each Bachman's Sparrow at the time of its initial capture ($n = 29$). Bachman's Sparrows were captured only during the nonbreeding season and could not be aged or sexed reliably.

Feathers collected at the time of capture were assumed to reflect food ingested during the previous annual molt period when growing feathers were blood-supplied. We assumed that carbon and nitrogen stable isotope ratios of incidentally-lost tail feathers from juvenile Florida Grasshopper Sparrows reflected foods consumed prior to each bird's first complete molt, i.e., during the juvenile growth period. Juvenile tail feather growth occurs post-fledging, when adults are providing supplemental food but juveniles are beginning to capture and consume prey independently. Body contour feathers grow in completely prior to fledging, when all of a nestling's diet is provided by its parents.

3.3.3 Seed and arthropod food reference samples

Seeds of common grasses and sedges were collected from fruiting stalks during the fall and winter months of 2006-2007 and 2007-2008 from four different locations at the study site separated by distances ranging from one to five kilometers. We assumed that sampling plants in asynchronous time periods with feather sample collection would not affect analysis because temporal variation in $^{13}\text{C}/^{12}\text{C}$ ratios in plants is minimal compared with the effects of differing photosynthetic method on $^{13}\text{C}/^{12}\text{C}$ ratios (i.e., in that C_3 plants are significantly more depleted in

^{13}C than C_4 grasses) (Fry 2006). The $^{15}\text{N}/^{14}\text{N}$ ratio in plant tissue is influenced temporally and spatially by soil decomposition of particulate nitrogen, which results in progressive increases in the $^{15}\text{N}/^{14}\text{N}$ ratio with soil depth (Fry 2006) so we assumed isotopic analysis would show greater variability of the $^{15}\text{N}/^{14}\text{N}$ within groups of taxonomically related plants and arthropods.

Seed samples were stored in zip-lock plastic bags and frozen within six hours to prevent mold growth. Grass seeds analyzed for stable carbon and nitrogen isotope signatures included: *Ctenium aromaticum*, *Sorghastrum secundum*, *Andropogon virginicus*, *Dichanthelium portoricense*, *Aristida beyrichiana*, and *Panicum anceps*. Sedge seeds analyzed included: *Scleria reticularis*, *Cyperus* sp., and *Rhynchospora* sp (Fig. 3.1).

Arthropod sampling was conducted from 20 December 2006 to 20 February 2007 in canvas sweep nets within 10 m diameter plots ($n = 84$) centered at sparrow flush locations marked with a numbered flag during flush-net sampling. Twenty net-sweeps were made along each margin of the sample plot and twenty sweeps were made across each of the two plot diagonals for a total of 120 sweeps per plot. Arthropods were stored in zip lock plastic bags and were frozen within four to six hours to prevent sample degradation.

From 6 November 2007 to 9 January 2008 arthropods were collected using sticky traps constructed of plywood boards measuring 2.5 x 20 x 30 cm, covered with a 15 x 30 cm Sticky Strip sheet (BioQuip, Inc.). Traps were placed under grass or shrub cover at sparrow flush locations and arthropods removed after 24 hours. Arthropod samples were removed from sticky traps with stainless steel tweezers, placed in zip-lock plastic bags and frozen within four to six hours to prevent degradation. Arthropod body parts directly in contact with the Sticky Strip sheets were not included in samples for isotopic analysis. Arthropod samples collected in both winters were identified to taxonomic order at a minimum and to a finer classification when possible.

Seven taxonomic orders were represented in arthropod samples analyzed for stable carbon and nitrogen isotope signatures: Araneae, Coleoptera, Diptera, Homoptera, Hymenoptera, Lepidoptera, Odonata, and Orthoptera. Orthopteran nymphs in five genera were identified in samples collected in the shrub-dominated dry-mesic prairie plots: *Dicromorpha* spp., *Chortophaga* spp., *Aptenopedes* spp., *Melanoplus* spp., and *Achurum carinatum*. Isotopic signatures of unidentified grasshopper nymphs were grouped with samples identified in the genera *Dicromorpha* spp. and *Chortophaga* spp. based on similarity of isotope ratios. A second group of orthopterans included nymphs in the genera *Aptenopedes* and *Melanoplus*. Two additional groups of orthopterans were composed of nymphs and adults, respectively, of the toothpick grasshopper (*Achurum carinatum*) a species collected only in sampling of the graminoid-dominated wet-mesic prairie plots.

A group of odonates included three small, common dragonflies: blue dasher (*Pachydiplax longipennis*); eastern pondhawk (*Erythemis simplicicollis*); and blue dragonlet (*Erythrodiplax minuscula*). The Diptera group included two houseflies (*Musca domestica*) and two unidentified flies. A single group (Homoptera) was composed of leafhoppers (Cicadellidae), treehoppers (Membracidae), and planthoppers (Fulgoroidea). The remaining three groups included moth larvae (Geometridae), beetles and weevils (Coleoptera), and small wasps (Hymenoptera) (Fig. 3.2).

3.3.4 Stable isotope analysis

Feather and arthropod samples were cleaned, freeze-dried, and homogenized prior to stable isotope analysis. Lipids were extracted from arthropods in a Soxhlet apparatus with petroleum ether as a solvent, since variations in lipid concentration are known to influence stable carbon isotope ratio measurements (Rau et al. 1992). The stable isotope ratios in all samples

were measured using an isotope ratio mass spectrometer (Finnigan MAT Delta Plus XL), calibrated with internal standards, at the Odum School of Ecology, University of Georgia, Athens. The international standards for ^{13}C and ^{15}N are Vienna Peedee Belemnite (VPDB) and atmospheric N_2 (AIR), respectively.

Stable-isotope signatures of feather and food reference samples are expressed in standard delta (δ) notation as parts per thousand (‰):

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3 \quad (1)$$

where X is ^{13}C or ^{15}N and R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) in the sample and standard, respectively (Bond and Hobson 2012).

3.3.5 Data Analysis

3.3.5.1 Feathers

Carbon and nitrogen isotope ratios of individual food reference samples were aggregated into groups for analysis by similarity in taxonomic classification. Initially, we evaluated assumptions to which MANOVA is sensitive including the presence of outliers, normality, multicollinearity, and equality of covariance matrices. Statistical analyses were conducted with IBM® SPSS® version 21.0.0.0 (2012). Significance was tested at $\alpha = 0.05$ unless otherwise indicated. We used multivariate analysis of variance (MANOVA) to test for differences among group mean delta values for feather groups and for differences among food reference samples.

No univariate outliers were identified for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for Florida Grasshopper Sparrow feather samples; however, two univariate outliers for $\delta^{13}\text{C}$ values and two outliers for $\delta^{15}\text{N}$ were identified for Bachman's Sparrow feather samples. Using boxplots of Mahalanobis

distances we identified three multivariate outliers for Florida Grasshopper Sparrow feather samples and five multivariate outliers for Bachman's Sparrow feather samples. Outliers were not removed from data sets because we assumed they represented individual variation within these resident populations. We evaluated normality of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values using the Shapiro-Wilks test and found that only $\delta^{13}\text{C}$ values for Bachman's Sparrow were not normally distributed ($p = 0.01$). The MANOVA assumption of equality of covariance matrices was satisfied (Box's M , $p = 0.90$). Using a one-way MANOVA, we found that feather sample group means for the two sparrows differed for $\delta^{15}\text{N}$ values ($F = 5.39$, $p = 0.02$) but not for $\delta^{13}\text{C}$ values ($F = 1.42$, $p = 0.24$).

Eleven of the Florida Grasshopper Sparrow feather samples were males, and four samples were from females. There were no univariate outliers of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in either group but two multivariate outliers were identified in the male sample group. Outliers were not removed from data sets because these values likely represent individual variation within resident populations. The assumption of equality of covariance matrices of the two sample groups was satisfied (Box's M , $p = 0.28$). Multivariate group means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were not significantly different ($F_{(2,12)} = 1.72$, Pillai's trace = 0.22, $p = 0.22$).

Five of the 22 Florida Grasshopper Sparrow feather samples were composed of body contour feathers from birds captured in juvenal plumage (22-31 August 2007) prior to their first prebasic molt. The remaining 17 samples were rectrices (i.e, tail feathers) collected from birds that had completed prebasic molt ("adults"). Outliers were not removed from data sets based on the assumption that they represented individual variation within resident populations and that this variation may be muted given a larger sample size. Covariance matrices were not equal between the two age groups (Box's M , $p = 0.016$), likely due to the small sample of juvenile feathers and

outlier delta values within the group. There was a statistically significant difference between multivariate group means ($F_{(2,19)} = 10.02$, Pillai's trace = 0.51, $p < 0.01$) and the feather group means differed for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (both $p < 0.01$).

Interpretation of the effects of age differences may be confounded by the effects of the difference in feather tract origins of the two sample sets. However, analysis of feather samples taken from each of three different feather tracts – body contour, tail, and wing – on a single adult Florida Grasshopper Sparrow provided the following $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values: rectrix/tail (-18.5‰, 5.2‰), body/contour (-18.5‰, 5.8‰), and secondary/wing (-19.6‰, 5.4‰). Similarity in isotope ratios between the body contour feather sample and the rectrix sample from this single individual, although anecdotal, suggests that differing feather tracts may not explain the difference in isotopic signatures between the adult and juvenile feather groups. Additional sample sets of feathers from different tracts on the same individual birds would be needed to resolve these isotopic relationships.

3.3.5.2 Food reference samples

Univariate and multivariate outliers of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values identified for each arthropod and seed sample group were removed from their respective groups prior to further analysis because of implicit taxonomic variation given the high species richness at the study site. Removal of outliers resulted in 16 arthropod and seed sample groups of 2 to 29 samples each and two single samples of sedge seeds.

Using a one-way MANOVA, the within-group means of food sources were statistically unequal among groups by Pillai's trace, a statistic robust for the assumption of multivariate normality (1.825, $F = 107.00$, $p < 0.001$, eta squared = 0.92), and by Wilk's lambda (0.006, $F = 95.14$, $p < 0.001$). We used the Tukey post hoc test to determine which potential food groups were statistically inseparable for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 3.2). The group means for

spiders (Araneae), dragonflies (Odonata), and flies (Diptera) did not differ ($\delta^{13}\text{C}$: $p = 1.00$; $\delta^{15}\text{N}$: $p = 0.22$). Group means for wasps (hymenoptera) and adult toothpick grasshoppers (*Achurum carinatum*, Orthoptera) did not differ ($\delta^{13}\text{C}$: $p = 0.44$; $\delta^{15}\text{N}$: $p = 0.07$). Group means for moth larvae (Geometridae), and a combined group of C_4 grass seeds (*Sorghastrum secundum*, *Aristida beyrichiana*, *Panicum anceps*, *Ctenium aromaticum*) did not differ ($\delta^{13}\text{C}$: $p = 1.00$; $\delta^{15}\text{N}$: $p = 0.27$).

3.3.6 Diet Reconstruction and Diet Overlap

We used the Stable Isotope Analysis in R (SIAR) model (R Development Core Team 2012; Parnell et al. 2010) to estimate proportions of grass and sedge seeds and arthropod taxa that comprised each sparrow species' diet during the prebasic molt period and the feather regrowth period. In order to reconstruct animal diets, it is necessary to adjust the isotope ratios of animal tissues for stepwise enrichment of the heavier ^{15}N and ^{13}C isotopes from the lower values in potential food sources. These correction factors are known as trophic enrichment factors or trophic discrimination factors. Trophic enrichment factors (TEFs), represented by the $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ notations, have been estimated experimentally in a growing number of mammals, fish, invertebrates, and birds (Caut et al. 2009), primarily for aquatic-foraging species in several taxonomic orders (Mizutani et al. 1992). We used $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ values from two published sources to estimate sensitivity of diet estimates to varying TEFs: 1) values obtained from feathers of Garden Warblers (*Sylvia borin*) fed diets of mealworms or elderberries (Hobson and Bairlein 2003) and 2) values from feathers of the Yellow-rumped Warbler (*Setophaga coronata coronata*) fed arthropod-rich diets (Pearson et al. 2003; 49% insect diet). For Yellow-rumped Warbler, $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ TEFs were reported for 20%, 49%, 73%, and 97% insect diets (Pearson 2003).

Initially, model input included isotopic group means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all arthropod and seed sample groups analyzed ($n = 18$; Fig. 3.1). Use of the MANOVA reduced the number of potential food groups from 18 to 12 (Fig. 3.2). Because SIAR model performance improves substantially with fewer source inputs (Parnell et al. 2010), we further reduced the number of likely sources (potential food groups) using *a priori* knowledge of food sources from published literature, a sensitivity analysis with two published sources of trophic enrichment factors (TEFs) and iterative model runs with progressive removal of sources comprising $<5\%$ of proportional isotopic contribution to each mixture (group mean of feather samples).

We estimated diet overlap between Florida Grasshopper and Bachman's sparrows by constructing a Bayesian Standard Ellipse Area (SEA_b) for each sparrow on a bivariate plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individual feather samples using a script within SIAR known as Stable Isotope Bayesian Ellipses in R (SIBER)(Jackson et al. 2011). A standard ellipse includes the core 40% of the data set for which it is calculated and, in this use, is a means of comparing isotopic niche widths between the two sparrow species. Using SIBER, we calculated 10,000 posterior draws of SEA_b for the stable isotope ratios of feather samples from each sparrow species using normal prior distributions. For each sparrow, we also plotted a convex hull, a polygon constructed by connecting the most divergent isotopic signatures among feather samples collected from each species, which represents the diet breadth of sampled sparrows during the prebasic molt period. We used niche metrics – nitrogen range, carbon range, total area of the convex hull and SEA_b (Bayesian standard ellipse area) – to estimate the extent of dietary overlap during the feather molt period (Layman et al. 2007).

3.4 Results

3.4.1 Sparrow diet reconstruction

The sensitivity analysis, varying only the trophic enrichment factors ($\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$) for diet reconstruction, resulted in selection of the same food sources for each pair of $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ values but assigned different proportions of those food sources to the estimated average diets of Florida Grasshopper Sparrow and Bachman's Sparrow. Using TEFs of 2.7 ± 0.1 (SD) for $\Delta^{13}\text{C}$ and 4.0 ± 0.3 (SD) for $\Delta^{15}\text{N}$ (Hobson and Bairlein 2003) modeling converged on a solution of three major diet components at a 95% credibility interval: mean Florida Grasshopper Sparrow diets were estimated to be 20-32% C_3 -foraging grasshoppers (Orthoptera), 33-44% C_4 -foraging grasshoppers (Orthoptera) and 30-42% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera). Using the same TEFs, mean Bachman's Sparrow diets were estimated to be 20-30% C_3 -foraging grasshoppers (Orthoptera), 42-51% C_4 -foraging grasshoppers (Orthoptera) and 23-34% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera).

Using TEFs of 4.3 ± 0.1 (SD) for $\Delta^{13}\text{C}$ and 3.5 ± 0.1 (SD) for $\Delta^{15}\text{N}$ (Pearson et al. 2003; 97% insect diet) and selecting diet proportions at the 95% credibility interval, mean Florida Grasshopper Sparrow diets were estimated to be 30-42% C_3 -foraging grasshoppers (Orthoptera), 17-28% C_4 -foraging grasshoppers (Orthoptera) and 36-47% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera). Using the same TEFs, mean Bachman's Sparrow diets were estimated to be 30-40% C_3 -foraging grasshoppers (Orthoptera), 26-35% C_4 -foraging grasshoppers (Orthoptera) and 29-39% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera).

The sensitivity analysis of estimated average diets of adult and juvenile Florida Grasshopper Sparrows also resulted in selection of the same food sources but in differing proportions for the two age groups. Using TEFs of 2.7 ± 0.1 (SD) for $\Delta^{13}\text{C}$ and 4.0 ± 0.3 (SD) for $\Delta^{15}\text{N}$ (Hobson and Bairlein 2003) modeling converged on a solution of three major diet components at the 95% credibility interval: mean adult Florida Grasshopper Sparrow diets were estimated to be 20-32% C_3 -foraging grasshoppers (Orthoptera), 33-44% C_4 -foraging grasshoppers (Orthoptera) and 30-42% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera). Using the same TEFs, mean juvenile Florida Grasshopper Sparrow diets were estimated to be 6-30% C_3 -foraging grasshoppers (Orthoptera), 42-67% C_4 -foraging grasshoppers (Orthoptera) and 11-43% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera).

Using TEFs of 4.3 ± 0.1 (SD) for $\Delta^{13}\text{C}$ and 3.5 ± 0.1 (SD) for $\Delta^{15}\text{N}$ (Pearson et al. 2003; 97% insect diet) and selecting diet proportions at the 95% credibility interval, mean adult Florida Grasshopper Sparrow diets were estimated to be 30-42% C_3 -foraging grasshoppers (Orthoptera), 17-28% C_4 -foraging grasshoppers (Orthoptera) and 36-47% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera). Using the same TEFs, mean diets of juvenile Florida Grasshopper Sparrows were estimated to be 18-39% C_3 -foraging grasshoppers (Orthoptera), 30-50% C_4 -foraging grasshoppers (Orthoptera) and 19-44% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera). The higher within-group variability in diet estimates for the juveniles may be a function of the small sample size ($n = 5$) but also may result from in vivo diet variability among juvenile birds inexperienced at foraging or due to diet supplementation by their parents.

Use of the Pearson (2003) TEF for $\Delta^{13}\text{C}$ shifted the resulting diet proportions toward C_3 foods for both Florida Grasshopper and Bachman's sparrows as well as for adult and juvenile Florida Grasshopper Sparrows, resulting in higher proportional contributions of C_3 -foraging grasshoppers and lower proportions of C_4 -foraging grasshoppers as compared with estimated diet proportions of these two foods when using the Hobson and Bairlein (2003) TEF for $\Delta^{13}\text{C}$. Use of the Pearson (2003) TEF for $\Delta^{15}\text{N}$ increased the estimated diet proportions of higher trophic level food sources – spiders, dragonflies, and flies in the estimated diets of both sparrows and also in the estimated diets of adult and juvenile Florida Grasshopper Sparrows as compared with use of the larger Hobson and Bairlein (2003) TEF for $\Delta^{15}\text{N}$.

3.4.2 Diet overlap

We used SIBER to calculate standard ellipses and convex hulls from individual feather samples of Florida Grasshopper Sparrow and Bachman's Sparrow (Fig. 3.3). The range of $\delta^{15}\text{N}$ values within the convex hull calculated for Bachman's Sparrow feather samples (3.37 ‰) was greater than that for Florida Grasshopper Sparrow feather samples (2.7 ‰) whereas the difference between the ranges of $\delta^{13}\text{C}$ values within the convex hulls for the two species was negligible (0.06 ‰) (Table 3.1).

Total area of the convex hulls for each of the two sparrows differed by 0.21‰^2 which represents 2.3% of the total area of each hull (Table 3.1). The hull overlap area, 4.71‰^2 , represents 52.2% and 50.0% of the individual convex hull areas for Florida Grasshopper Sparrow and Bachman's Sparrow, respectively. Comparing the area of standard ellipses calculated for the two feather groups, we found a 44.3% probability that the isotopic niche width of Florida Grasshopper Sparrow molt period diets was smaller than that for Bachman's Sparrow, indicating that the isotopic niche widths of the two sparrows do not differ.

3.5 Discussion

We found that grasshoppers (Orthoptera) foraging on both C₃ and C₄ herbs comprised the majority of the diets of adult and juvenile Florida Grasshopper Sparrows and Bachman's Sparrows at the study location. Additional diet components included spiders (Araneae), small dragonflies (Odonata), flies (Diptera), and beetles and weevils (Coleoptera). Although the coleoptera source group was estimated to be the fourth largest estimated diet contribution for both Florida Grasshopper and Bachman's Sparrows with SIAR, published research documents that beetles and weevils comprise a relatively minor diet component.

Our results with SIAR diet reconstruction indicated that neither C₃ nor C₄ grass or sedge seeds sampled were a significant food source during the fall molt period, a time when arthropods remain plentiful in the warm climate of south-central Florida. Homopterans (i.e. leafhoppers, planthoppers, and treehoppers) were not identified as a significant diet source. Due to their small size, about 5 mm in length, hoppers would be difficult prey to capture for a low energetic yield. Hymenoptera (small wasps) also did not appear to be a significant diet source.

Lepidopteran larvae are listed as common in the diets of juvenile and adult Grasshopper Sparrow subspecies according to published literature (Wiens and Rotenberry 1979, Delany et al 2000, Adler and Ritchison 2011) but the term "larvae" does not differentiate between butterfly larvae and moth larvae. Our sampling methods of sweep-netting and sticky traps did not capture butterfly larvae; however, we did capture moth larvae using sweep nets. Our modeling results did not reveal moth larvae as a significant food source but this does not preclude butterfly larvae as a significant food source since the latter forage on a wide variety of grasses, forbs, and shrubs. Similarity among group means of isotopic ratios for moth larvae, C₄ grasshopper nymphs, and C₄ seeds precluded separate analysis of these food sources. Larger sample sizes and proper sampling

to capture a diversity of butterfly larvae could increase the effectiveness of mixing models at distinguishing among larvae, these food sources.

Estimated proportions of the major diet items differed among adult and juvenile Florida Grasshopper Sparrows and Bachman's Sparrows. Diet proportions of grasshoppers foraging on C₃ herbs were similar for adult Florida Grasshopper Sparrows and Bachman's Sparrows but significantly less for juvenile Florida Grasshopper Sparrows. The abundant C₄ "toothpick" grasshopper nymphs (*Achurum carinatum*) composed a larger percentage of Bachman's Sparrow diets than adult Florida Grasshopper Sparrow diets but an even larger percentage of juvenile Florida Grasshopper Sparrow diets. Adult Florida Grasshopper Sparrows consumed more from the mixed arthropod group of spiders, flies, and small dragonflies than either Bachman's Sparrows or juvenile Florida Grasshopper Sparrows. Beetles and weevils (Coleoptera) likely compose a portion of the diets of both sparrows but the model results indicated relatively high uncertainty for solutions that included both coleopterans and C₃-foraging orthopterans, and we could not discern the relative importance of both arthropod groups simultaneously.

There are aspects of sampling design for food sources that may influence the accuracy and precision of mixing model results. In a species-rich ecosystem such as the dry prairie, a sample design that is based on collecting large sample sizes of a large number of distinct, taxonomically related food groups may produce so many food source groups that mixing models cannot converge on meaningful solutions because of isotopic similarity between numerous food source groups. Alternatively, small sample sizes and within-group taxonomic complexity may produce groups with indistinct isotopic ratio means, complicating resolution of diet estimates. Omission of major food sources as model input may or may not be recognized in modeling results because of isotopic similarity between the omitted food sources and the included sources.

Sampling of arthropods with sweep nets biased our arthropod sample collection against ground-dwelling insects that would be captured more efficiently by other sampling methods (e.g. pitfall traps) such as larger beetles and spiders, mole crickets, and beetle larvae, and against capture of an abundance or diversity of lepidopteran larvae, which are generally sampled by visual inspection of harvested plant biomass (Standen 2000). Arthropod forms vary throughout their individual life histories and some are more suitable for capture in sweep nets (e.g. grasshopper nymphs, small spiders and beetles, and planthoppers as opposed to large, adult grasshoppers and larger spiders). However, we sampled arthropods during the prebasic molt period of our two focal sparrow species so the arthropods used for food reference samples were temporally representative of the prey base. Future research on sparrow diets in dry prairie should include isotopic analysis of hemipterans, butterfly larvae, and larger samples of beetles and weevils separated into isotopic value groups based on family or finer classification.

Although we predicted that diets of the two sparrow species at the study location would be similar to the species' diets as documented in published literature, we predicted that molt period diets of both sparrows would be predominantly arthropods due to abundance and availability in the dry prairie during the fall feather molt period. Our sampling of C₃ and C₄ grass and sedge seeds, although not exhaustive in terms of the species richness at the study location, was representative of seeds available to foraging, ground-dwelling birds at the study location. Analysis showed that seeds were a minor source of forage; we infer, therefore, that arthropods comprised the majority of the diets of Florida Grasshopper Sparrow and Bachman's Sparrow in native Florida dry prairie during the fall molt period.

Despite the similarity in reconstructed diets for the two sparrow species using SIAR, the Layman metrics from SIBER showed a dietary overlap of 50-52.2% indicating that

approximately half of the Florida Grasshopper Sparrows had mean diets consisting of higher trophic level prey than Bachman's Sparrows during the feather molt period. The convex hulls, constructed by linking the outlying isotopic ratios of individual feather samples for each sparrow, were similar in total area, but the carbon and nitrogen isotopic values differed in their respective ranges. Adult male Florida Grasshopper Sparrows identified by isotopic ratios enriched in ^{15}N may be foraging on diets more abundant in secondary consumers or on a diet composed of larger arthropods (e.g. spiders, dragonflies, and adult grasshoppers) than Bachman's Sparrows. The similarity in isotopic niche widths for $\delta^{13}\text{C}$ between the two sparrows indicates that their diets incorporate a similar range of C_3 and C_4 plants and arthropods foraging on C_3 and C_4 plants. The 25% larger $\delta^{15}\text{N}$ niche width for Bachman's Sparrow suggests that individual birds may have diets with larger proportional contributions of C_4 grasshoppers than the majority of Florida Grasshopper Sparrows.

Alternatively, the greater $\delta^{15}\text{N}$ niche width for Bachman's Sparrow may result from incorporation of a larger number of juveniles with diets either adult-supplemented with C_4 based foods or diets that included C_4 seeds that were not identified as a significant overall diet contribution for Bachman's Sparrows due to model averaging effects. Because the data set for the resident Florida Grasshopper Sparrow included both juveniles and adults, and given that Bachman's Sparrow is also resident at the study site, it can be inferred that juvenile Bachman's Sparrows also were included in the sample data. The extent to which diet variability of juvenile Bachman's Sparrows contributed to the greater range of $\delta^{15}\text{N}$ values within the convex hull calculated for Bachman's Sparrow could not be quantified.

Individual variability in prey preferences can have important consequences for adult survival and reproductive success (Inger et al. 2006, Jackson et al. 2012). Because pesticide

toxicity has been identified as a likely contributor to grassland bird declines (Mineau and Whiteside 2013) and consumers at higher trophic levels are generally more vulnerable due to biomagnification of toxins, the consumption of higher trophic level prey by Florida Grasshopper Sparrows may be a factor in their decline. Unfortunately, data to test this hypothesis explicitly are not yet available.

The published literature suggests greater variation of plants in the diet of Bachman's Sparrow than for Florida Grasshopper Sparrow (*A. s. floridanus*) and Grasshopper Sparrow (*A. s. pratensis*). Our results support a similar inference in that the range of $\delta^{15}\text{N}$ values for the 29 Bachman's Sparrow feathers analyzed was 24.8% greater than the range of $\delta^{15}\text{N}$ values for the 22 Florida Grasshopper Sparrow feathers analyzed, indicating a wider range of significant contributions from primary producers to secondary or higher-order consumers for Bachman's Sparrow. This diet diversity trait has adaptive value for the Bachman's Sparrow, a species not known to migrate southward during the North American winter months when arthropod abundance declines with decreasing ambient temperatures and especially with the occurrence of freezes. The ability of Bachman's Sparrow to switch the bulk of its diet to plant-based sources also has adaptive value during drought periods when arthropod abundance declines.

By contrast, Florida Grasshopper Sparrow, for which arthropods comprise a much greater and less variable proportion of their diet, may be less tolerant of drastic reductions in arthropod prey due to droughts and persistent freezing temperatures than Bachman's Sparrow. If global climate change brings greater variability in temporal rainfall abundance and ambient temperatures, a more significant challenge to the prey base of the declining, and severely range- and habitat-restricted Florida Grasshopper Sparrow may result than to the far more abundant

Bachman's Sparrow, which resides in a greater range of latitudes and within a wider range of plant communities.

Stable carbon and nitrogen isotope ratios have not been used previously to reconstruct diets and evaluate dietary overlap of sympatric species that have a potential arthropod and seed prey base as diverse as that found in Florida dry prairie. We found the complementary diet reconstruction analysis provided by SIAR and the trophic niche width and diet overlap analysis provided by SIBER useful for elucidating trophic relationships between two closely related, sympatric sparrows. Future research in Florida dry prairie using isotopic analysis should focus on obtaining larger and more diverse arthropod and seed sample sizes to investigate potential competition between the federally Endangered Florida Grasshopper Sparrow and other sympatric avian species, as well as the potential risk to Florida Grasshopper Sparrows from consuming higher trophic level prey in an agricultural region where pesticides are used.

Table 3.1: Layman metrics for Bayesian ellipses constructed on a bivariate plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from individual feathers of Florida Grasshopper Sparrow ($n = 22$) and Bachman's Sparrow ($n = 29$). The total area metric is for the convex hull, a polygon drawn by connecting the most divergent sample data points for each sparrow.

Layman metric	Florida Grasshopper Sparrow	
	Florida Grasshopper Sparrow	Bachman's Sparrow
Nitrogen range (‰)	2.7	3.37
Min.	3.85	2.35
Max.	6.55	5.72
Carbon Range (‰)	4.98	5.04
Min.	-21.39	-20.85
Max.	-16.41	-15.81
Total area (‰ ²)	9.03	9.24
SEA _B (‰ ²)	2.98	2.91

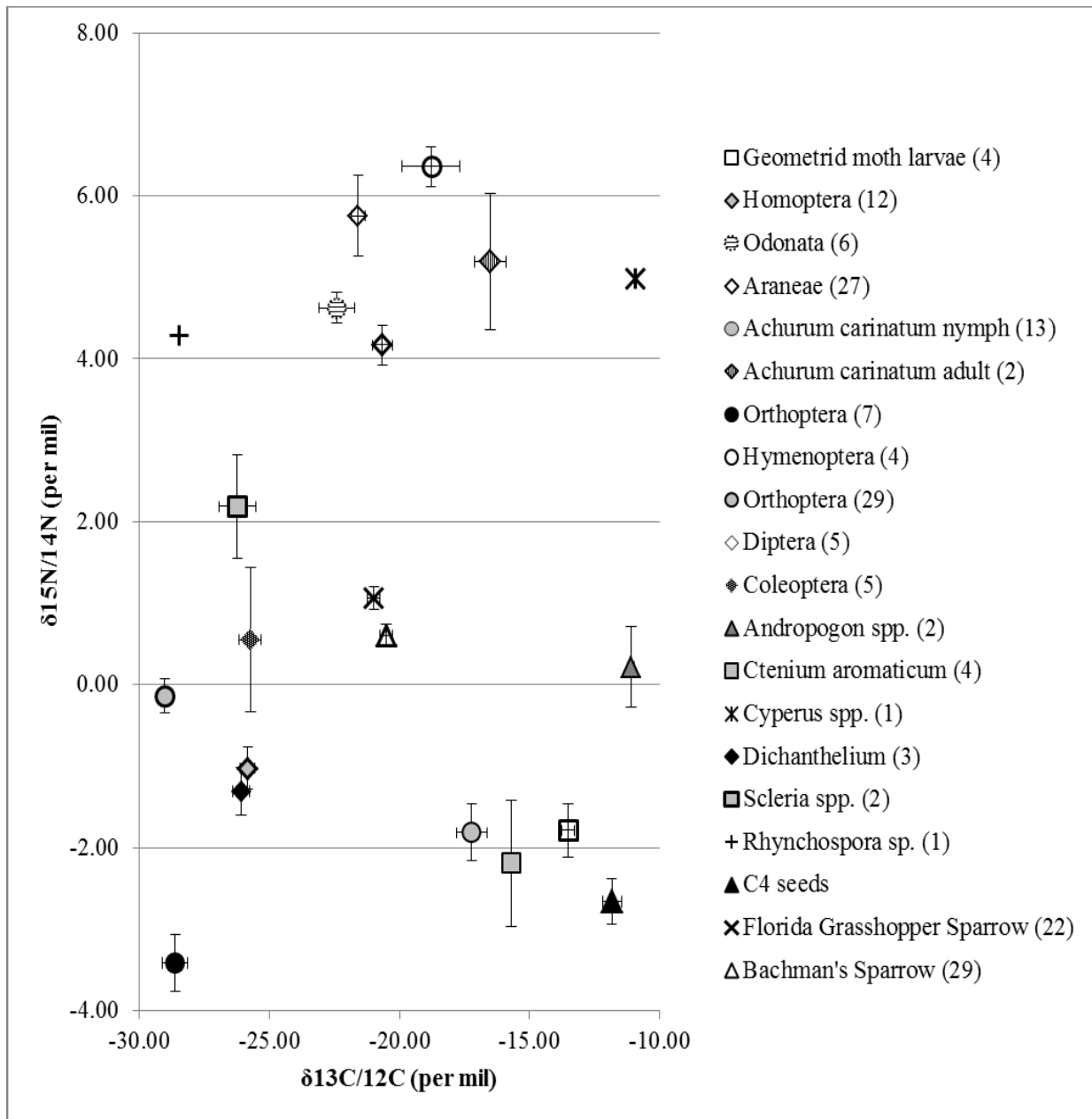


Figure 3.1: Group mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values \pm SE for Florida Grasshopper Sparrow and Bachman's Sparrow feather samples and for arthropod and seed groups. The number of sample replicates for each group is shown in parentheses.

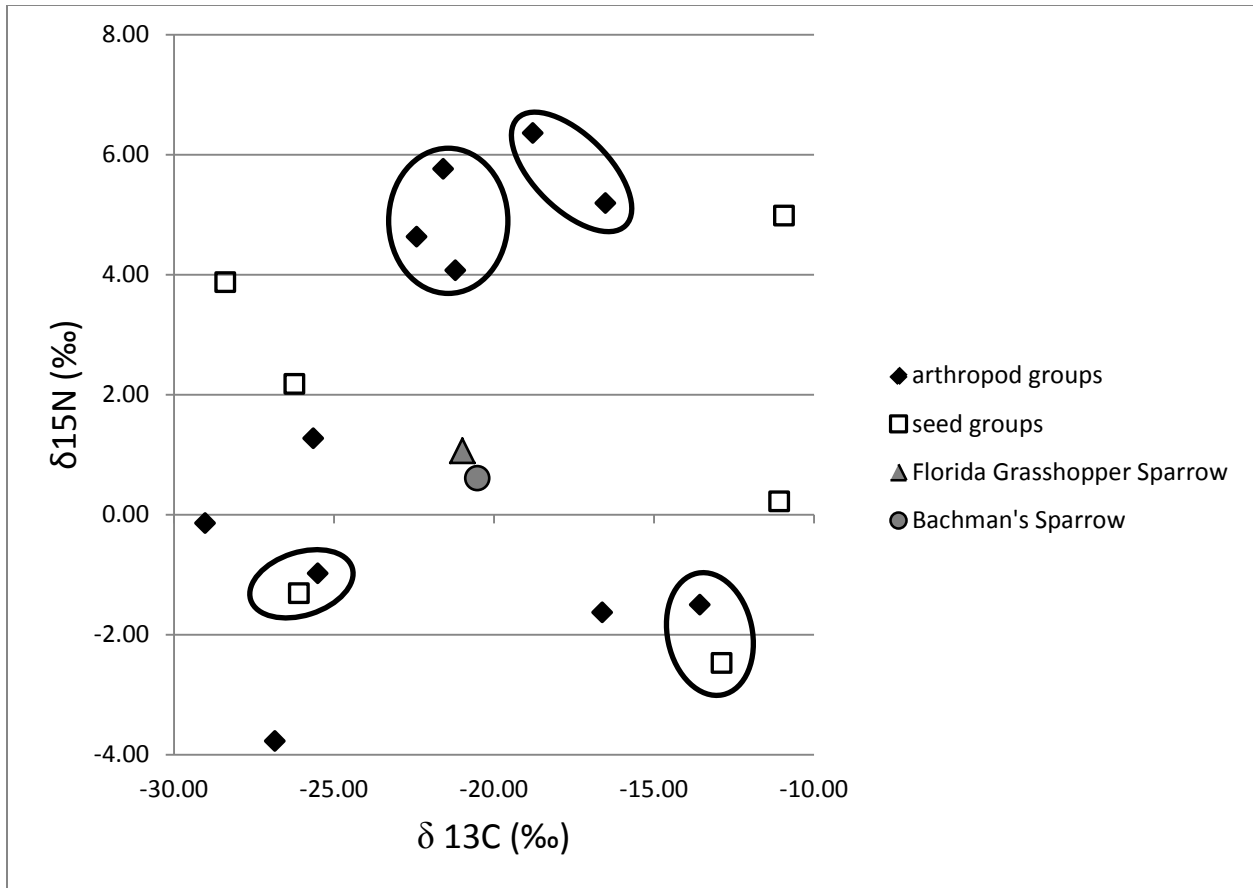


Figure 3.2: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for groups of potential arthropod and seed food sources and for feather samples (i.e., diet-derived isotopic mixtures) from Florida Grasshopper Sparrow ($n = 22$) and Bachman's Sparrow ($n = 29$). Mean delta values for feather sample groups were corrected for trophic enrichment (2.7 ± 0.1 (SD) for $\Delta^{13}\text{C}$ and 4.0 ± 0.3 for $\Delta^{15}\text{N}$) (Hobson and Bairlein 2003). Food groups that did not differ significantly for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are surrounded by oval shapes.

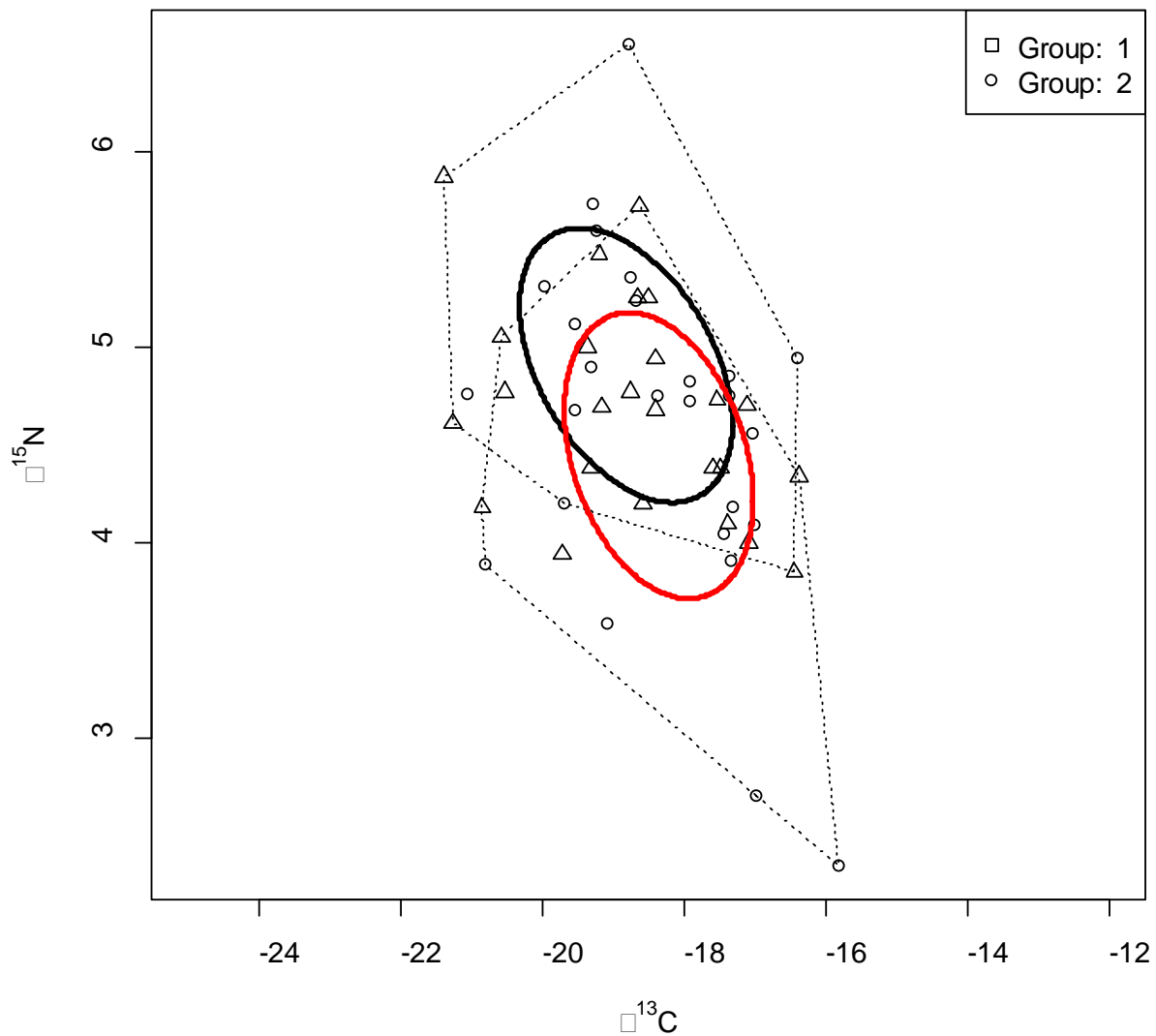


Figure 3.3: SIBER-generated convex hulls and standard ellipses for Florida Grasshopper Sparrows (Group 1) and Bachman's Sparrows (Group 2). Data points are $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of all individual feather samples. Polygons are convex hulls constructed by connecting the most extreme isotopic values for each species and represent the range of individual diets for each species. Standard ellipses are the minimum calculated to contain 40% of the data points for each species.

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CHAPTER 4: STABLE CARBON AND NITROGEN ISOTOPE RATIOS REVEAL WINTER DIET ESTIMATES AND DIET OVERLAP FOR THREE GRASSLAND SPARROWS IN FLORIDA DRY PRAIRIE

4.1 Abstract

Animal community assemblages change seasonally at all latitudes due to seasonal dispersals and migrations. Avian communities increase in diversity in subtropical grassland ecosystems during migratory passage and winter months due to an influx of migratory birds that augment resident avian populations. We used stable carbon and nitrogen isotope ratios of bird feathers and potential arthropod and seed food sources to investigate diet overlap among resident Bachman's Sparrow (*Peucaea aestivalis*) and migratory Henslow's (*Ammodramus henslowii*) and Grasshopper Sparrow (*Ammodramus savannarum pratensis*) in Florida dry prairie, a species-rich, subtropical grassland ecosystem. We captured and recaptured sparrows in winter 2007-2008 using systematic flush-netting, removing a tail feather at first capture and the regrown feather when birds were recaptured. Henslow's and Grasshopper Sparrow winter diets did not differ, but both species' winter diets differed from Bachman's Sparrow winter diets. Winter diets of all three sparrows included a variety of arthropods, grass seeds, and sedge seeds, but Bachman's Sparrow winter diets spanned greater trophic diversity than either of the migratory sparrows.

4.2 Introduction

Animal assemblages undergo seasonal changes following post-breeding dispersal and semiannual latitudinal or altitudinal migrations. Food webs change seasonally within communities due to growth and dormancy cycles and influx or departure of migrants. In the Florida dry prairie ecosystem resident avian populations are augmented annually by passage and overwintering species that may alter food web dynamics.

Arthropod richness and abundance are positively correlated with native grasses and forb cover in native grassland habitats (McIntyre and Thompson 2003, McMellen 2006). Food availability for grassland birds is not usually considered to be limited during breeding season and, provided that food resources remain abundant, grassland ecosystems can support bird species with overlapping diets (Wiens 1973, Rotenberry and Wiens 1979). The species-rich dry prairie ecosystem exemplifies food abundance with 302 species of vascular plants (Orzell and Bridges 2006), 89 butterfly species (Lepidoptera) (Florida Park Service 2012), 10 species of damselflies and 30 species of dragonflies (Odonata), 54 species of ants (Formicidae), 108 spider species (Araneae), and more than 600 species of moths (Kissimmee Prairie Preserve State Park; L. Atherton and C. Wolf, pers. comm.) identified currently.

Florida dry prairie also harbors the range-restricted, federally Endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) which has undergone recent, dramatic population declines on publicly managed lands (Florida Grasshopper Sparrow working group, unpubl. data). The abundance of arthropods and plants in dry prairie comprise a species-rich prey base for resident grassland birds including Florida Grasshopper Sparrow and Bachman's Sparrow (*Peucaea aestivalis*) and migratory sparrows.

In addition to the treeless dry prairie, which is near the southern edge of its geographic range, Bachman's Sparrow occupies longleaf pine savannas and pine flatwoods of the southeastern United States. Grass seeds comprised more than 90% of the stomach contents of Bachman's Sparrows during winter in Texas (n = 44) (Allaire and Fisher 1975). In Alabama and Texas, however, animal matter comprised 58% (n=10) and 68% (n = 7), of stomach contents, respectively, with grass and sedge seeds comprising the remainder (Dunning 2006).

Resident Bachman's and Florida Grasshopper sparrows are sympatric with migratory Grasshopper Sparrows (*Ammodramus savannarum pratensis*) and Henslow's Sparrows (*Ammodramus henslowii*) during their annual nonbreeding periods. Henslow's Sparrows, which rarely occur south of Lake Okeechobee, have been documented in Florida from 7 October (Stevenson and Anderson 1994) to 18 June (Pranty and Scheuerell 1997). Grasshopper Sparrows (*A. s. pratensis*) have been documented in Florida from 27 September to 17 May (Stevenson and Anderson 1994). No published records of Grasshopper Sparrow winter diets were found during literature searches.

Based on fecal samples, Henslow's Sparrows overwintering in southeastern Louisiana pine savannas consume a predominantly seed-based diet including an array of sedges in the genera *Scleria* and *Rhynchospora* and grasses in the genera *Dichanthelium*, *Panicum*, *Andropogon*, *Schizachyrium*, and *Aristida* with minor quantities of arthropods (DiMiceli 2006, Johnson et al. 2011). In southern Mississippi, *Rhynchospora* spp. seeds and *Scleria* spp. seeds were the most abundant and second most abundant diet items, respectively, in flushed crops of Henslow's Sparrows (n = 67) in two winters. Beetles and weevils (Coleoptera), flies (Diptera), springtails (Collembola), and spiders (Araneae) were the most common arthropods identified in crop samples but constituted a minor proportion of diet biomass along with grass seeds in the genera *Panicum*, *Paspalum*, and *Andropogon* (Fuller 2004).

Although animal diets can be estimated using conventional methods such as observational studies under optimal conditions, stomach contents, fecal samples, and crop contents, these methods have inherent limitations (Inger and Bearhop 2008). Adult animals, such as ground-dwelling sparrows that forage in dense herbaceous vegetation, are often difficult to locate and impossible to observe for more than a few seconds at a time. Diet estimation based on

crop contents provides a temporal snapshot of prey taken but is valuable given large sample sizes (e.g., Fuller 2004). Diet reconstruction based on stomach contents or fecal samples is subject to underestimation of quickly digested, soft-bodied prey items such as lepidopteron larvae and overestimation of hard-bodied prey items such as beetles (Hobson and Clark 1992).

Stable isotope analysis of bird feathers is a suitable tool for reconstructing diets of imperiled avian populations, obviating the need to extract blood, muscle or organ tissues from individual birds (Hobson and Clark 1993). Once formed, keratin comprising a bird's feathers is metabolically inactive so that stable isotope ratios reflect diet at the time the feather was formed (Hobson 1999). Comparing isotopic signatures in feathers with potential foods ingested during feather growth allows estimation of the proportion of these foods assimilated by each sparrow species. For sympatric, generalist consumers that eat comparable proportions of the same food groups, considerable diet overlap may occur (Wiens and Rotenberry 1979, Pulliam and Dunning 1987, Flaherty and Ben-David 2010).

In a species-rich ecosystem such as Florida dry prairie there are many potential foods for ground-dwelling sparrows including a wide array of arthropods and seeds. In order to estimate diets using mixing models it is necessary to reduce the number of potential food sources by grouping samples or by other means (Phillips et al. 2005). Use of calculated group mean stable isotope ratios to represent food sources and consumer tissues can be informative if they are statistically distinct (Layman et al. 2011). However, where isotopic group means are indistinct, individual variability in prey preferences can have important consequences for fledgling and adult survival and for reproductive success (Inger et al. 2006, Jackson et al. 2012). Diets estimated using stable isotope analysis can be used to draw inferences about ecological niches of co-occurring animals that may potentially compete (Newsome et al. 2007).

Diet overlap is a necessary condition for competition to occur between closely related, sympatric taxa with similar foraging habits. If prey were limited in abundance during the mid-winter period and diet overlap was significant, competition for scarce food resources could adversely affect survival or physiological condition of sympatric sparrows (Pulliam and Dunning 1987).

Based on published diet research and winter habitat associations for these three sparrows at the study location (Korosy et al. 2013) we predicted significant overlap between mid-winter diets of Grasshopper and Henslow's sparrows and less overlap between diets of these two sparrows and Bachman's Sparrows. We predicted that Bachman's Sparrow winter diets would include a greater percentage of seed-based foods than during their fall molt period diet (Chapter 2). We also predicted that arthropods would comprise a significant proportion of Grasshopper Sparrow and Henslow's Sparrow diets in contrast to published research on these species' winter diets in Louisiana and Mississippi (Fuller 2004, DiMiceli 2006, Dimiceli et al. 2007).

4.3 Methods

4.3.1 Study Site

Kissimmee Prairie Preserve State Park encompasses the largest remaining contiguous tract of dry prairie in Florida, approximately 10,200 ha of dry prairie within the 22,500 ha Preserve (USFWS 1999). During our 2006–2008 field research, the Preserve supported one of the largest extant populations of the endemic, non-migratory Florida Grasshopper Sparrow (Pranty and Tucker 2006), an abundant breeding population of Bachman's Sparrows, and several species of overwintering and migratory sparrows including Henslow's, Grasshopper, Savannah (*Passerculus sandwichensis*), Swamp (*Melospiza georgiana*), Chipping (*Spizella passerina*), and

small numbers of Le Conte's (*Ammodramus leconteii*), Lincoln's (*Melospiza lincolnii*), and Vesper (*Pooecetes gramineus*) sparrows (P. Miller and MGK, unpubl. data).

4.3.2 Feather Samples

We captured sparrows in 120 m long mist net arrays (Fig. 4.1) within six 4-5 ha plots in burn class 1 prairie (i.e. in the first winter post-burn) and in six 4-5 ha plots in burn class 3 prairie distributed equally between dry-mesic and wet-mesic prairie (Korosy et al. 2013). Flush-net sampling occurred between 5 November 2007 and 11 March 2008; sampling terminated in early March to avoid flush-netting in the breeding season of the Endangered Florida Grasshopper Sparrow, which is resident at the study site. All captured birds received a uniquely-numbered, aluminum leg band to enable subsequent identification.

Three large-scale, volunteer-supported mist-netting events also were conducted during winter 2007-2008. In these events, volunteers flushed birds into a 300-350 meter long mist net array. Sampling events occurred on 28 October 2007, 12 January 2008, and 16 February 2008.

Adult and juvenile Bachman's Sparrows resident at the study site undergo a complete annual molt of all body feathers, flight feathers, and tail feathers between mid- August and late October (MGK and P. Miller, unpubl. data). All Henslow's Sparrows and Grasshopper Sparrows captured at Kissimmee Prairie Preserve had completed their annual molts prior to capture and could not be aged reliably (P. Miller and MGK, unpublished data). Bachman's, Henslow's, and Grasshopper sparrows could not be sexed reliably when captured during our non-breeding season research.

One rectrix (usually the right fourth rectrix) was removed for stable isotope analysis from each Bachman's, Grasshopper, and Henslow's sparrow at the time of initial capture during the sampling period. For Bachman's Sparrows, this feather was assumed to contain isotopic

signatures of foods ingested at the study location during the annual molt period, August through October. For the migratory species, the isotopic ratios in the initially-removed feathers were assumed to reflect isotopic signatures indicative of food sources ingested prior to, or during, migration rather than food sources at the study location. Feather removal from the dermal base stimulated re-growth of a new feather, a process known as “adventitious molt” (Pyle 1997). The regrown tail feather was removed from recaptured sparrows and analyzed for stable isotope ratios to permit diet reconstruction for both the annual molt period and the regrowth period.

Initially we divided feather samples, by species, into “sets” of feathers, totaling nine preliminary feather groups. Each “set” included the tail feather removed at the time of initial capture, the regrown tail feather collected when a marked bird was recaptured, and the same regrown tail feather for birds captured a third time within season. Isotopic analysis of feather samples collected was limited to individual birds recaptured at least once within the season. Twenty-three Bachman’s Sparrows were captured a total of 50 times, 10 Henslow’s Sparrows were captured a total of 22 times, and 11 Grasshopper Sparrows were captured a total of 24 times within the 2007-2008 sampling period (Fig. 4.2).

A MANOVA also was used to test for equality of the six feather sample group means for Bachman’s, Henslow’s, and Grasshopper sparrows following prior exploratory statistical tests described above to evaluate these data against assumptions to which MANOVA is sensitive. Statistical analyses were conducted with IBM® SPSS® version 21.0.0.0 (2012).

4.3.3 Food Reference Samples

Seeds of common grasses and sedges were collected from fruiting stalks during the fall and winter months of 2006-2007 and 2007-2008 from four different locations at the study site

separated by distances ranging from one to five kilometers. All seed samples were stored in zip-lock plastic bags and frozen within six hours to prevent mold growth.

Arthropod sampling was conducted from 20 December 2006 to 20 February 2007 in canvas sweep nets within 10 m diameter plots ($n = 84$) centered at sparrow flush locations marked with a numbered flag during flush-net sampling. Twenty net-sweeps were made along each margin of the sample plot and twenty sweeps were made across each of the two plot diagonals for a total of 120 sweeps per plot. Arthropods were stored in zip lock plastic bags and were frozen within four to six hours to prevent sample degradation.

From 6 November 2007 to 9 January 2008 arthropods were collected using sticky traps constructed of plywood boards measuring 2.5 x 20 x 30 cm, covered with a 15 x 30 cm Sticky Strip sheet (BioQuip, Inc.). Traps were placed under grass or shrub cover at sparrow flush locations and arthropods removed after 24 hours. Arthropod samples were removed from sticky traps with stainless steel tweezers, placed in zip-lock plastic bags and frozen within four to six hours to prevent sample degradation. Arthropod body parts directly in contact with the Sticky Strip sheets were not included in sample analysis for isotopic ratios. Arthropod samples collected in both winters were identified to taxonomic order at a minimum and to a finer classification when possible.

Carbon and nitrogen stable isotope ratios of individual food reference samples were aggregated into groups for analysis by similarity in taxonomic classification. Prior to performing the MANOVA, univariate outliers and multivariate outliers were removed from arthropod groups, justifiable because of known taxonomic variation within the species-rich dry prairie ecosystem. Univariate and multivariate outliers also were identified within feather sample groups of Bachman's, Henslow's, and Grasshopper sparrows.

We tested each of the assumptions supporting use of one-way multivariate analysis of variance (MANOVA) prior to calculating the MANOVA on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of arthropod and seed groups. We used Tukey's post-hoc test to determine which pairs of food reference sample group means were statistically inseparable and thereby reduce the number of potential food source groups prior to diet reconstruction and diet overlap assessment. Because SIAR model performance improves substantially with fewer source inputs (Parnell et al. 2010), we further reduced the number of likely sources (potential food groups) using *a priori* knowledge of food sources from published literature within the context of a sensitivity analysis using two published sources of trophic enrichment factors (TEFs) and iterative model runs with progressive removal of sources comprising <5% of proportional isotopic contribution to each mixture (group mean of feather samples).

4.3.4 Stable isotope analysis

Feather and arthropod samples were cleaned, freeze-dried, and homogenized prior to stable isotope analysis. Lipids were extracted from arthropods in a Soxhlet apparatus with petroleum ether as a solvent, since variations in lipid concentration are known to influence stable carbon isotope ratio measurements (Rau et al. 1992). The stable isotope ratios in all samples were measured using an isotope ratio mass spectrometer (Finnigan MAT Delta Plus XL), calibrated with internal standards, at the Odum School of Ecology, University of Georgia, Athens. The international standards for ^{13}C and ^{15}N are Vienna Peedee Belemnite (VPDB) and atmospheric N_2 (AIR), respectively.

Stable-isotope signatures of feather and food reference samples are expressed in standard delta (δ) notation as parts per thousand (‰): $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where X is ^{13}C or

^{15}N and R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) in the sample and standard, respectively (Bond and Hobson 2012).

4.3.5 Data Analysis

4.3.5.1 Feathers

Univariate and multivariate outliers for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were identified using boxplots and Mahalanobis distances calculated for delta values in each of the seven feather groups composed of more than two samples (only two Grasshopper Sparrows and two Henslow's sparrows were recaptured twice following initial feather removal). Feather samples for two Grasshopper Sparrows were removed from data sets because both samples had $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ outliers greater than three times the interquartile range. A bivariate plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the three initial feather groups for each of the three sparrow species reveals the similarity in delta values for Grasshopper and Henslow's sparrow feathers grown on a diet of prey from the study location (Fig. 4.3).

Following removal of feather samples for the two Grasshopper Sparrows, we used the Shapiro-Wilks statistic to test for univariate normality of feather sample groups. The $\delta^{15}\text{N}$ values were normally distributed for all feather groups composed of more than two samples. The $\delta^{13}\text{C}$ values were normally distributed except for the Bachman's Sparrow "R" feather group ($p = 0.022$) and the Grasshopper Sparrow "molt" group ($p = 0.035$), both of which included a single $\delta^{13}\text{C}$ outlier. These samples were not removed from their respective feather groups because the $\delta^{15}\text{N}$ values for those same feathers were not outliers. These outliers on only one of the two dependent variables may signify individual variation that would be muted in a larger sample size. The within-group $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were moderately correlated ($r = 0.30 - 0.69$) except for

the Bachman's Sparrow "molt" feather group ($r = 0.12$) and the Henslow's Sparrow "molt" feather group ($r = 0.05$).

Tukey's post-hoc test following the MANOVA on the initial nine feather groups showed that the "R" and "R2" feather groups for all three sparrow species did not differ from each other (Table 4.1) so these two feather groups were combined for each species (Table 4.2). Combining groups reduced the number of feather groups from nine to six for all further analysis.

Using the six feather groups, we again tested for outliers, normality, and linearity. There was one univariate outlier for $\delta^{13}\text{C}$ in the Bachman's Sparrow "R" feather group and one outlier for $\delta^{13}\text{C}$ in the Grasshopper Sparrow "R" feather group but no outliers in any group for $\delta^{15}\text{N}$. There were four multivariate outliers in the Bachman's "R" feather group and one in the Grasshopper sparrow "molt" group. None of the outliers in the six feather groups was removed so that individual variation within groups was included in diet estimates. The $\delta^{13}\text{C}$ values for the two feather groups with multivariate outliers were not normally distributed (Shapiro-Wilks, $p = 0.004$, $p = 0.035$, respectively); $\delta^{15}\text{N}$ values were normally distributed for all feather groups. Feather group delta values showed moderate correlation between the dependent variables except for the Bachman's Sparrow molt group ($r = -.120$) and the Grasshopper Sparrow molt group ($r = -0.05$). In the MANOVA, covariance matrices for the two dependent variables were not equal (Box's M , $p < 0.001$) and Levene's test showed that error variances of the dependent variables were not equal across feather groups ($\delta^{15}\text{N}$: $F(5,86) = 9.051$, $p < 0.001$; $\delta^{13}\text{C}$: $F(5, 86) = 2.876$, $p = 0.019$).

Tukey's post-hoc test established significant differences between "molt" feather groups for all three sparrows (Table 4.2). Diets of Henslow's and Grasshopper sparrows during their annual molt periods, prior to arrival at the study location, are unknown but may differ because of

differing pre-migration geographic origins. Their diets would differ, predictably, from that of resident Bachman's Sparrow. The Bachman's Sparrow "molt" and regrown feather groups differed only with respect to $\delta^{13}\text{C}$ values so these groups were analyzed separately in SIAR. The $\delta^{13}\text{C}$ values in both the "molt" and the regrown Bachman's Sparrow feathers differed from the $\delta^{13}\text{C}$ values of the regrown feather groups for both Henslow's and Grasshopper sparrows but $\delta^{15}\text{N}$ values did not differ among these three groups. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of regrown Henslow's and Grasshopper sparrow feathers did not differ and were combined for analysis in SIAR to increase sample size for this feather group (n = 23).

4.3.5.2 Seed and arthropod food reference samples

Seeds analyzed for stable carbon and nitrogen isotope ratios included both C_3 and C_4 grasses - *Ctenium aromaticum*, *Sorghastrum secundum*, *Andropogon virginicus*, *Dichanthelium portoricense*, *Aristida stricta* var. *beyrichiana*, and *Panicum anceps* - and sedges: *Scleria reticularis*, *Cyperus* sp., and *Rhynchospora* sp.

Seven taxonomic orders were represented in arthropod samples analyzed for stable carbon and nitrogen isotope signatures: Araneae, Coleoptera, Diptera, Homoptera, Hymenoptera, Lepidoptera, Odonata, and Orthoptera. Orthopteran nymphs in five genera were identified in samples collected in the shrub and grass dominated dry-mesic prairie plots: *Dicromorpha* spp., *Chortophaga* spp., *Aptenopedes* spp., *Melanoplus* spp., and *Achurum carinatum*. Isotopic signatures of unidentified grasshopper nymphs were grouped with samples identified in the genera *Dicromorpha* and *Chortophaga* based on similarity of isotope ratios. A second group of orthopterans included nymphs in the genera *Aptenopedes* and *Melanoplus*. Two additional groups of orthopterans were composed of nymphs and adults, respectively, of the toothpick grasshopper (*Achurum carinatum*) a species collected only in sampling of the graminoid-dominated wet-mesic prairie plots.

A group of odonates included three small, common dragonflies: blue dasher (*Pachydiplax longipennis*); eastern pondhawk (*Erythemis simplicicollis*); and blue dragonlet (*Erythrodiplax minuscula*). The Diptera group included two houseflies (*Musca domestica*) and two unidentified flies. A single group (Homoptera) was composed of leafhoppers (Cicadellidae), treehoppers (Membracidae), and planthoppers (Fulgoroidea). The remaining three groups included moth larvae (Geometridae), beetles and weevils (Coleoptera), and small wasps (Hymenoptera).

Removal of univariate and multivariate outliers of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values prior to use of one-way MANOVA to evaluate differences among group means resulted in 17 arthropod and seed sample groups of 2 to 29 samples each and two single samples of sedge seeds. Using a one-way MANOVA, the within-group means of food sources were statistically unequal among groups by Pillai's trace, a statistic robust for the assumption of multivariate normality (1.825, $F = 107.00$, $p < 0.001$, eta squared = 0.92), and by Wilk's lambda (0.006, $F = 95.14$, $p < 0.001$).

We used Tukey's post hoc test to determine which potential food groups were statistically inseparable for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, reducing the number of potential food groups from 17 to 12 (Fig. 4.4). The group means for spiders (Araneae), dragonflies (Odonata), and flies (Diptera) did not differ ($\delta^{13}\text{C}$: $p = 1.00$; $\delta^{15}\text{N}$: $p = 0.22$). Group means for wasps (hymenoptera) and adult toothpick grasshoppers (*Achurum carinatum*, Orthoptera) did not differ ($\delta^{13}\text{C}$: $p = 0.44$; $\delta^{15}\text{N}$: $p = 0.07$). Group means for moth larvae (Geometridae), and a combined group of C₄ grass seeds (*Sorghastrum secundum*, *Aristida stricta* var. *beyrichiana*, *Panicum anceps*, *Ctenium aromaticum*) did not differ ($\delta^{13}\text{C}$: $p = 1.00$; $\delta^{15}\text{N}$: $p = 0.27$).

4.3.6 Diet Reconstruction

We used the Stable Isotope Analysis in R (SIAR) model (R Development Core Team 2012; Parnell et al. 2010) to estimate proportions of grass and sedge seeds and arthropod taxa

that comprised each sparrow species' diet during the prebasic molt period and the feather regrowth period. In order to reconstruct animal diets, it is necessary to adjust the isotope ratios of animal tissues for stepwise enrichment of the heavier ^{15}N and ^{13}C isotopes from the lower values in potential food sources. These correction factors are known as trophic enrichment factors or trophic discrimination factors. Trophic enrichment factors (TEFs), represented by the $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ notations, have been estimated experimentally in a growing number of mammals, fish, invertebrates, and birds (Caut et al. 2009), primarily for aquatic-foraging species in several taxonomic orders (Mizutani et al. 1992). We used $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ values from two published sources to estimate sensitivity of diet estimates to varying TEFs: 1) values obtained from feathers of Garden Warblers (*Sylvia borin*) fed diets of mealworms or elderberries (Hobson and Bairlein 2003) and 2) values from feathers of the Yellow-rumped Warbler (*Setophaga coronata coronata*) fed arthropod-rich diets (Pearson et al. 2003; 49% insect diet). For Yellow-rumped Warbler, $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ TEFs are reported for 20%, 49%, 73%, and 97% insect diets (Pearson 2003).

Diet overlap between Bachman's, Grasshopper, and Henslow's sparrows was estimated by constructing a Bayesian Standard Ellipse Area (SEA_b) for each sparrow on a bivariate plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individual feather samples using a script within SIAR known as Stable Isotope Bayesian Ellipses in R (SIBER)(Jackson et al. 2011). A standard ellipse includes 40% of the data set for which it is calculated and, in this use, is a means of comparing isotopic niche widths between the two sparrow species. Using SIBER, we calculated 10,000 posterior draws of SEA_b for the stable isotope ratios of feather samples from each sparrow species using normal prior distributions. For each sparrow, we also plotted a convex hull, a polygon constructed by connecting the most divergent isotopic signatures among feather samples collected from each

species, which represents the diet breadth of sampled sparrows during the prebasic molt period. We used niche metrics – nitrogen range, carbon range, total area of the convex hull, and SEA_b – to estimate the extent of dietary overlap during the feather molt period (Layman et al. 2007).

4.4 Results

4.4.1 Sparrow diet reconstruction

Diets were reconstructed from stable isotopic signatures of two feather groups representing winter diets: the regrown Bachman's Sparrow feathers and the combined group of regrown feathers for Henslow's and Grasshopper Sparrows. Using TEFs of 3.5 ± 0.1 for $\Delta^{13}\text{C}$ and 3.3 ± 0.04 for $\Delta^{15}\text{N}$ (Pearson 2003; 49% insect diet), Bachman's Sparrow winter diets were estimated to comprise 0.0-28% C_3 -foraging grasshoppers (Orthoptera), 16-32% C_4 -foraging grasshoppers (Orthoptera), 17-40% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera), 0.0-38% seeds of *Scleria* spp., and 0.0-32% from a combined group of arthropods (Homoptera) and seeds of *Dichanthelium* spp. at the 95% credibility interval. Using TEFs of 2.7 ± 0.1 for $\Delta^{13}\text{C}$ and 4.0 ± 0.3 for $\Delta^{15}\text{N}$ (Hobson and Bairlein 2003), Bachman's Sparrow winter diets were estimated to comprise 0.0-25% C_3 -foraging grasshoppers (Orthoptera), 27-43% C_4 -foraging grasshoppers (Orthoptera), 7.6-30% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera), 0.0-34% seeds of *Scleria* spp., and 1.0-36% from a combined group of arthropods (Homoptera) and seeds of *Dichanthelium* spp. at the 95% credibility interval. The sensitivity analysis of Bachman's Sparrow winter diets resulted in selection of the same food source groups but in differing proportions. Use of the larger $\Delta^{15}\text{N}$ TEF of Hobson and Bairlein (2003) in the SIAR model assigned a larger percentage of the diet to C_4 -foraging grasshoppers and a smaller percentage of the diet to the combined

group of spiders, flies, and dragonflies. The relatively small difference in $\Delta^{13}\text{C}$ values in the sensitivity analysis produced only slight changes in diet proportions assigned to the food groups of *Scleria* spp., Homoptera and *Dichanthelium* spp., and C_3 -foraging grasshoppers.

For both Henslow's and Grasshopper sparrows, winter diets at the 95% credibility interval using TEFs of 3.5 ± 0.1 for $\Delta^{13}\text{C}$ and 3.3 ± 0.04 for $\Delta^{15}\text{N}$ (Pearson 2003; 49% insect diet) comprised: 1.0-30% C_3 -foraging grasshoppers (Orthoptera), 0.0-35% beetles and weevils (Coleoptera), 9.9-31% from a combined group of arthropods (Homoptera) and seeds of *Dichanthelium* spp., 1.3-38% seeds of *Scleria* spp., and 14-34% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera). Using TEFs of 2.7 ± 0.1 for $\Delta^{13}\text{C}$ and 4.0 ± 0.3 for $\Delta^{15}\text{N}$ (Hobson and Bairlein 2003), Henslow's and Grasshopper sparrow winter diets comprised: 0.0-9.3% C_3 -foraging grasshoppers (Orthoptera), 0.0-22% beetles and weevils (Coleoptera), 44-63% from a combined group of arthropods (Homoptera) and seeds of *Dichanthelium* spp., 0.0-13% seeds of *Scleria* spp., and 23-34% from a combined group of spiders (Araneae), dragonflies (Odonata), and flies (Diptera). Use of the larger $\Delta^{15}\text{N}$ TEF of Hobson and Bairlein (2003) in the sensitivity analysis assigned the bulk of the diet to two food sources – the combined group of Homoptera and *Dichanthelium* spp. and the combined group of spiders, flies, and dragonflies. Use of the smaller $\Delta^{13}\text{C}$ value of Hobson and Bairlein (2003) contributed to the significant increase in percentage of the diet assigned to the combined food source of Homoptera and *Dichanthelium* spp. and reduced diet proportions of beetles and weevils, seeds of *Scleria* spp., and C_3 -foraging grasshoppers.

4.4.2 Diet overlap

Convex hulls and standard ellipses were constructed for four feather groups using SIBER (Fig. 4.5) and used to compare isotopic niche widths between Bachman's Sparrows molt period and winter diets and among isotopic niche widths for winter diets of Bachman's, Henslow's, and Grasshopper sparrows. The range of $\delta^{15}\text{N}$ values for Bachman's Sparrow feathers grown on their winter diets was 78% greater than the range of $\delta^{15}\text{N}$ values for feathers of the same individual Bachman's Sparrows grown on their fall molt period diets and the $\delta^{13}\text{C}$ range was 56% greater than for feathers grown on their fall molt period diets (Table 4.3).

Comparing the standard ellipse areas for the fall and winter Bachman's sparrow feather groups, we found an 89.7% probability that the trophic niche width of the molt diet was smaller than the winter diet, and therefore, Bachman's Sparrow diets are significantly different during the two time periods. The greater trophic niche width for Bachman's Sparrow winter diets suggests exploitation of a more diverse prey base by individual birds to include a greater percentage of sedge and grass seeds. Despite the significant difference in trophic niche width, there was a 48% overlap of the convex hull of the Bachman's molt feather group (representing fall diets) on the convex hull of the Bachman's regrown feather group (representing winter diets), indicating that nearly half the Bachman's Sparrows sampled had similar diets in fall and winter.

Comparing standard ellipses calculated for the three winter-diet feather groups, we found a 96.8% probability that the trophic width of Henslow's Sparrow winter diets is smaller than that for Bachman's Sparrow winter diets and a 98.1% probability that the trophic width of Grasshopper Sparrow winter diets is smaller than that for Bachman's Sparrow winter diets. We found a 59.5% probability that the trophic width of Henslow's Sparrow winter diets is smaller

than that of Grasshopper Sparrow, indicating that the winter diets of Henslow's Sparrows and Grasshopper Sparrow do not differ.

Overlap extent of the convex hulls for the winter diet feathers is < 1 % for Bachman's and Henslow's sparrows and 15% for Bachman's and Grasshopper Sparrows, providing additional support for differences in winter diets between Bachman's Sparrows and the two migratory sparrows. Between Henslow's and Grasshopper sparrow winter diet-feathers, however, convex hull overlap is 59%, validating the statistically insignificant difference between standard ellipses for the two sparrows.

4.5 Discussion

Ground-dwelling Grasshopper, Henslow's, and Bachman's sparrows were found to be diet generalists, foraging on arthropods, sedge, and grass seeds from November 2007 through February 2008 in Florida dry prairie. Arthropods comprising secondary consumers (spiders, flies, and dragonflies), grasshoppers foraging on C₃ herbs, beetles and weevils, seeds of the sedge genus *Scleria*, and grass seeds from species in the genus *Dichanthelium* were estimated to compose the majority of Grasshopper and Henslow's sparrow diets. Bachman's Sparrow winter diets differed from those of Grasshopper and Henslow's sparrows by an isotopically distinct diet component of grasshoppers foraging on C₄ herbs; beetles and weevils may comprise a lesser portion of their winter diets also, but the proportion was difficult to distinguish from the isotopic contribution of *Dichanthelium* spp. seeds. Sedge (*Scleria* spp., *Rhynchospora* spp.) and grass (*Dichanthelium* spp.) seeds may be the dominant forage for all three sparrow species during periods of sub-freezing overnight temperatures when arthropod abundance declines dramatically but seed availability remains relatively abundant at the study location (MGK, unpubl. data).

The wetland obligate and facultative-wet sedge and grass seeds (Wunderlin and Hansen 2011) that our study found to be winter diet components for all three sparrows are associated with wet-mesic prairie (Orzell and Bridges 2006) and therefore would be readily available forage for Grasshopper and Henslow's sparrows that associate strongly with wet-mesic prairie (Korosy et al. 2013). Although Bachman's Sparrows strongly associate with the shrub-and-grass dominated dry-mesic prairie at the study site, they were flushed from wet-mesic prairie in mid-winter and often were found in proximity to ecotones between wet-mesic and dry-mesic prairie (Korosy et al. 2013 and MGK, unpubl. data) where sedge seeds tend to be more abundant. However, two of the five common species of *Dichanthelium* sp. and at least two species of *Rhynchospora* sp. found at the study location are associated predominantly with dry-mesic prairie (Noss et al. 2008) but are also found in the driest portions of wet-mesic prairie, suggesting an ecotone association for these species and availability as forage for wet-mesic associated Grasshopper and Henslow's sparrows as well as dry-mesic associated Bachman's Sparrows.

Given the abundance of C₃-foraging arthropod taxa and C₃ plant seeds available as winter sparrow forage, we found it difficult to reduce the number of potential food sources using the SIAR mixing model and reached solutions characterized by multiple food sources, some with relatively large credibility intervals, and, therefore, uncertain proportions. While we infer that ground-dwelling sparrows are diet generalists based on the variety of available forage, the similarity in carbon and nitrogen isotopic signatures of food sources complicates differentiation among actual interspecific diet differences given the inherent mathematical limitations of mixing models for species-rich food webs such as that characterizing Florida dry prairie.

We found SIAR useful for analyzing general characteristics of the prey base for our focal species, including trophic levels of probable prey items, and for discerning major C₃ versus C₄

diet components. Due to the large number of potential prey categories with relatively similar isotopic signatures we were unable to differentiate among the array of potential minor diet components for each sparrow.

Using SIBER Layman metrics, we found that winter diets of Grasshopper and Henslow's sparrows occupied comparable isotopic niche widths but that both differed from the isotopic niche width of Bachman's Sparrow winter diets. Our results showed essentially no winter diet overlap between Bachman's and Henslow's sparrows and minor overlap between Bachman's and Grasshopper sparrows, but significant winter diet overlap between Henslow's and Grasshopper sparrows, suggesting the potential for competition if food were to be limited by stochastic, abiotic conditions. We found SIBER analysis useful for comparing isotopic niche widths and diet overlap among focal species, which provided an indication of the potential for competition by ecologically similar sparrows under abiotic conditions that may limit food availability during mid-winter periods. We also found SIBER-generated convex hull metrics useful for comparing Bachman's Sparrow fall molt diets and winter diets for the same birds, with the results suggesting that winter diets are more variable and include more C₃ sedge and grass seeds than diets during the fall molt period.

Grasshopper Sparrow winter-grown feathers were depleted in both ¹³C and ¹⁵N with respect to fall molt period feathers for the same individual birds whereas Henslow's Sparrow winter-grown feathers were depleted in ¹⁵N with no significant change in ¹³C. Winter-grown feathers of Bachman's Sparrows, resident at the study site, were depleted in ¹³C compared with fall molt-period diets of the same individuals but showed no seasonal shift in ¹⁵N. Based on our results for Florida Grasshopper Sparrow in Chapter 2 and the seasonal diet shifts of migratory Grasshopper Sparrows and resident Bachman's Sparrow, resident Florida Grasshopper Sparrows

would be expected to show a winter diet depleted in ^{13}C similar to both Grasshopper Sparrow and Bachman's Sparrow and a diet depleted in ^{15}N to a lesser extent than migratory Grasshopper Sparrows. If research were to bear out this prediction, it would indicate the potential for heightened competition during periods of sub-freezing overnight temperatures and drought periods when arthropod abundance is more limited.

The breeding regions of migratory Grasshopper and Henslow's sparrows overwintering in Florida dry prairie are unknown. Migration of Bachman's Sparrow within Florida or, more broadly, within the southeastern United States has not been documented. Future research should include hydrogen isotope analysis of Grasshopper, Henslow's, and Bachman's sparrow molt feathers to determine approximate latitudes where molt occurred in these species. Migratory sparrows overwintering in dry prairie may represent a diversity of breeding populations throughout each species' breeding range or they may originate from a few, localized regions. Identifying seasonal geographic linkages would provide a basis for investigating relationships between nonbreeding and breeding populations of Henslow's and Grasshopper sparrows and for identifying the existence of a migratory segment of the winter Bachman's Sparrow population at Kissimmee Prairie Preserve.

Table 4.1: Differences between group mean feather sample isotopic signatures for Bachman’s Sparrow (BACS), Henslow’s Sparrow (HESP), and Grasshopper Sparrow (GRSP). Significant differences for $\delta^{15}\text{N}$ only are denoted by p values in cells with gray highlight. Significant differences for $\delta^{13}\text{C}$ only are denoted by p values in cells with white background. Significant differences for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are denoted by p values in black-highlighted cells. Cells with gray highlight denote feather sample group means that did not differ for either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$. Feather groups labeled as “molt” include only tail feathers removed at the time of initial capture. Feather groups labeled “R” and “R2” include regrown tail feathers removed from birds recaptured once or twice, respectively following initial capture and tail feather removal.

	BACS molt	BACS R	BACS R2	HESP molt	HESP R	HESP R2	GRSP molt	GRSP R	GRSP R2
BACS molt				$p < 0.001$	$p < 0.001$	$p = 0.014$	$p = 0.001$; $p = 0.014$	$p < 0.001$	
BACS R				$p = 0.011$; $p < 0.001$	$p = 0.021$; $p < 0.001$		$p < 0.001$	$p < 0.001$	
BACS R2									
HESP molt	$p < 0.001$	$p = 0.011$; $p < 0.001$							
HESP R	$p < 0.001$	$p = 0.021$; $p < 0.001$					$p = 0.024$		
HESP R2	$p = 0.014$								
GRSP molt	$p = 0.001$; $p = 0.014$	$p < 0.001$			$p = 0.024$			$p = 0.031$	
GRSP R	$p < 0.001$	$p < 0.001$					$p = 0.031$		
GRSP R2									

Table 4.2: Differences between group mean feather sample isotopic signatures for Bachman’s Sparrow (BACS), Henslow’s Sparrow (HESP), and Grasshopper Sparrow (GRSP). Significant differences for $\delta^{15}\text{N}$ only are denoted by p values in cells with gray highlight. Significant differences for $\delta^{13}\text{C}$ only are denoted by p values in cells with white background. Significant differences for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are denoted by p values in black-highlighted cells. Cells with gray highlight denote feather sample group means that did not differ for either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$. Feather groups labeled as “molt” include only tail feathers removed at the time of initial capture. Feather groups labeled “R” include only regrown tail feathers from birds recaptured once or twice within season following initial capture and tail feather removal.

	BACS molt	BACS R	HESP molt	HESP R	GRSP molt	GRSP R
BACS molt		$p = 0.200$	$p = 0.045; p < 0.001$	$p < 0.001$	$p < 0.001; p = 0.006$	$p < 0.001$
BACS R	$p = 0.200$		$p = 0.005; p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
HESP molt	$p = 0.045; p < 0.001$	$p = 0.005; p < 0.001$				
HESP R	$p < 0.001$	$p < 0.001$			$p = 0.005$	
GRSP molt	$p < 0.001; p = 0.006$	$p < 0.001$		$p = 0.005$		$p = 0.008$
GRSP R	$p < 0.001$	$p < 0.001$			$p = 0.008$	

Table 4.3: Layman metrics for Bayesian ellipses constructed on a bivariate plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from individual feathers of Henslow's ($n = 12$) and Grasshopper Sparrows ($n = 11$) and Bachman's Sparrow ($n = 23$). The total area metric pertains to the convex hull, a polygon drawn by connecting the most divergent sample data points for each sparrow.

Layman metric	Bachman's Sparrow molt	Bachman's Sparrow winter	Henslow's Sparrow winter	Grasshopper Sparrow winter
Nitrogen range (‰)	1.47	2.62	2.26	1.35
Min.	3.89	2.93	3.77	4.07
Max.	5.36	5.55	6.03	5.42
Carbon Range (‰)	4.48	6.98	1.43	1.52
Min.	-20.85	-21.43	-22.74	-22.38
Max.	-16.37	-14.45	-21.31	-20.86
Total area (‰ ²)	4.72	9.46	1.9	1.56
SEA _B (‰ ²)	1.73	2.71	1.03	0.91

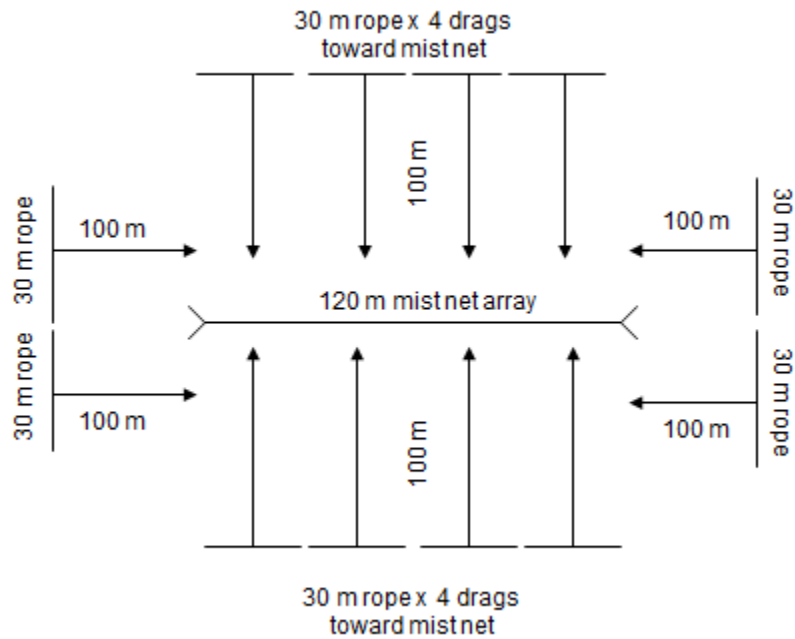


Figure 4.1: Flush-net sampling method used in repeated sampling of 4-5 ha plots. A similar systematic flush method was used in the volunteer-assisted sample plots with a 300-350 m mist net array at the center and a 90 m wide transect flushed on each pass.

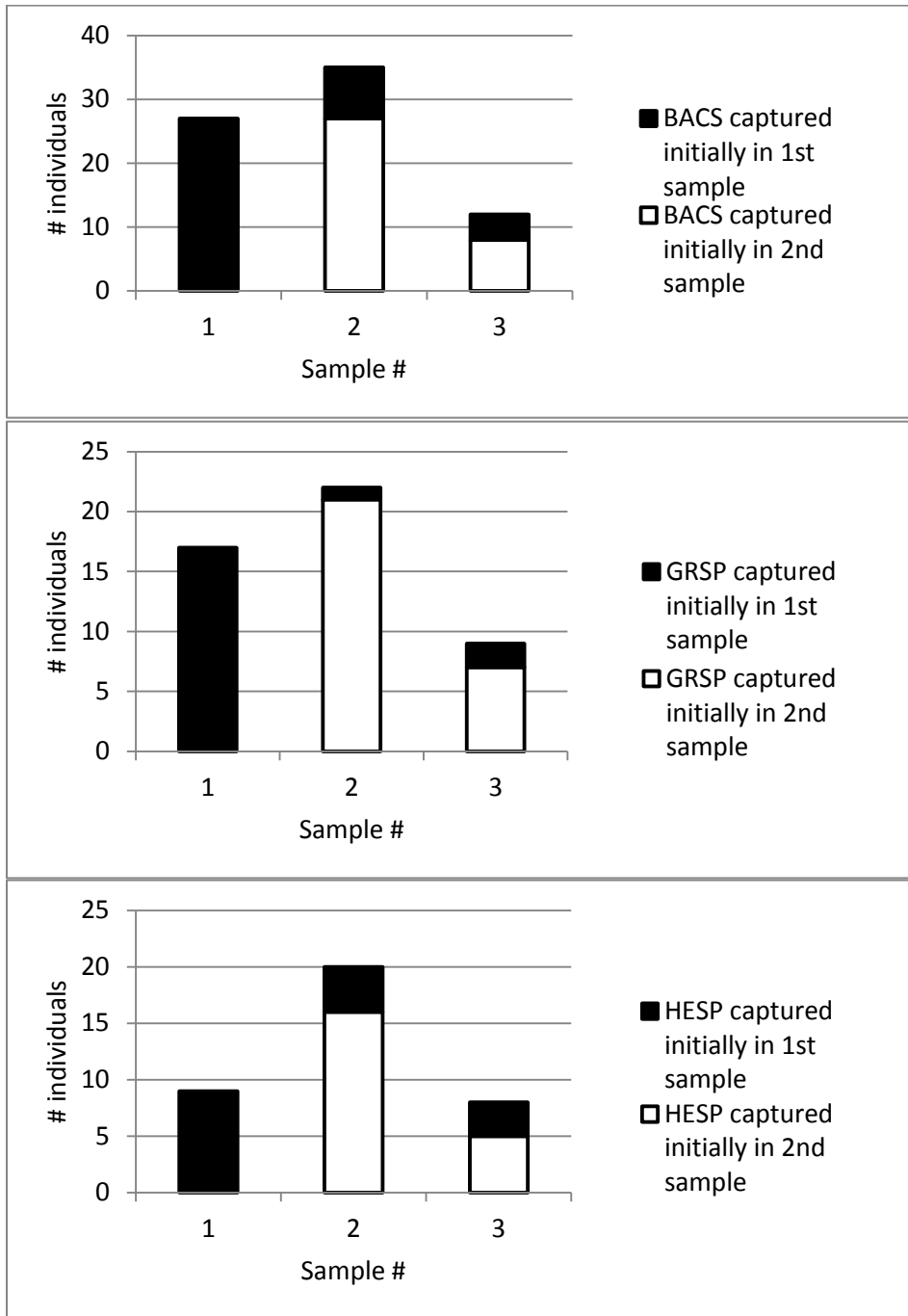


Figure 4.2: Total number of recaptured Bachman’s, Grasshopper, and Henslow’s sparrows in each of three samples of 12 4-5 ha flush-net plots for which feather samples were collected. Plots were resampled a minimum of 5-6 weeks apart to allow for tail feather regrowth. BACS = Bachman’s Sparrow; GRSP = Grasshopper Sparrow; HESP = Henslow’s Sparrow.

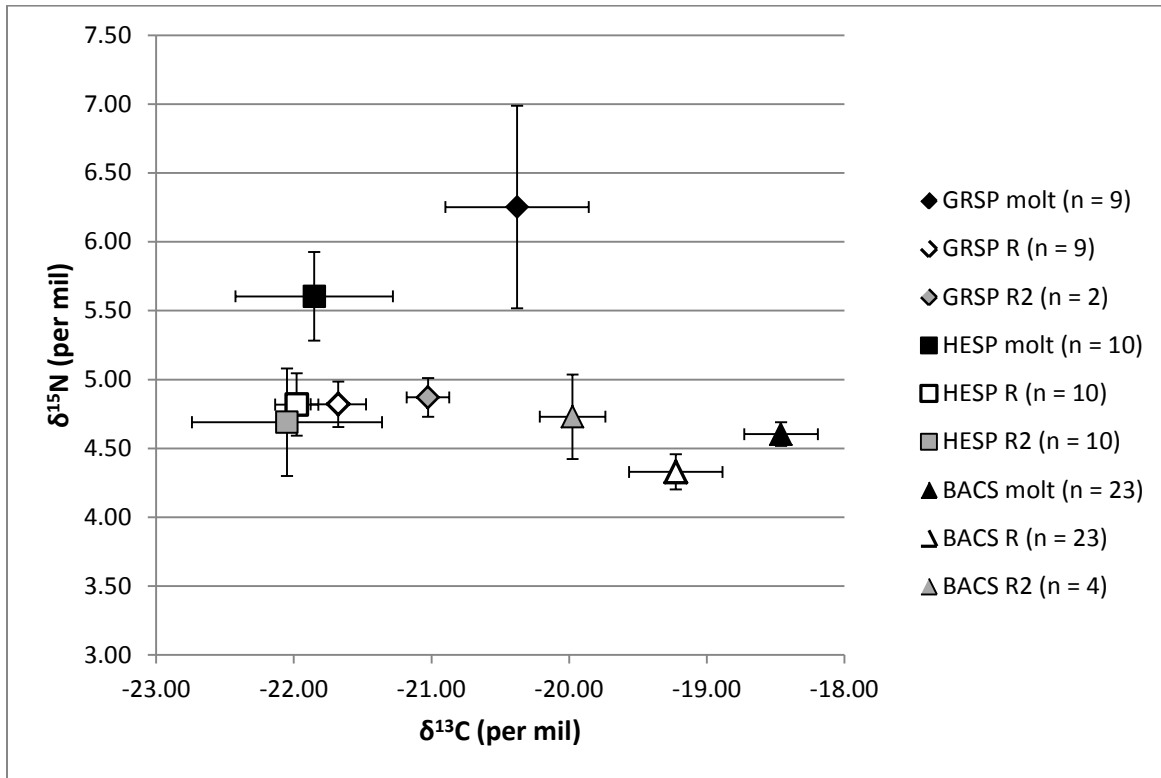


Figure 4.3: Group mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values ($\pm\text{SE}$) of feather samples by species. GRSP = Grasshopper Sparrow; HESP = Henslow's Sparrow; BACS = Bachman's Sparrow. Feather groups labeled as "molt" include only tail feathers removed at the time of initial capture. Feather groups labeled "R" include only regrown tail feathers from recaptured birds. Feather groups labeled "R2" include only regrown tail feathers from birds captured a second time following initial capture and tail feather removal. The "R2" feather groups were not statistically different from the respective "R" groups for each sparrow and the two groups were combined for diet reconstruction.

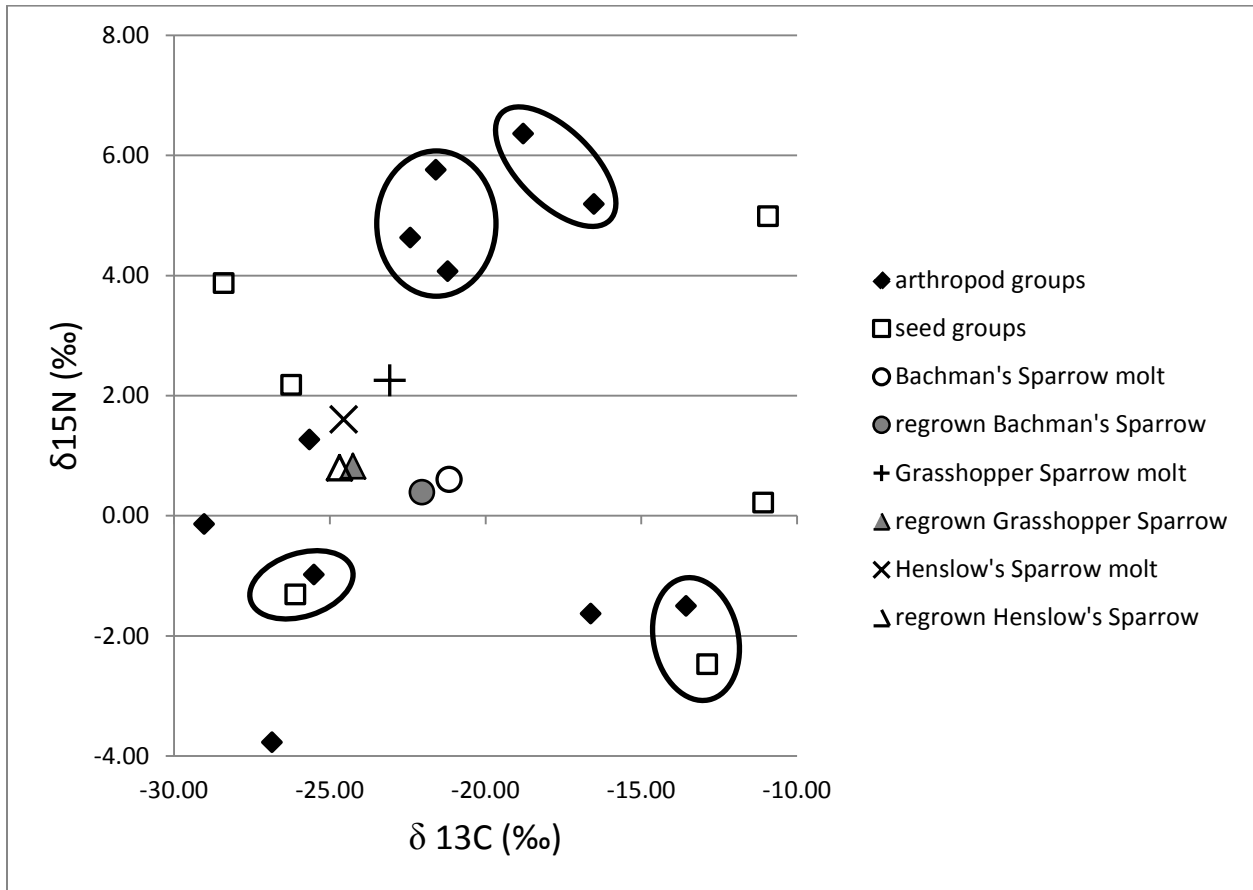


Figure 4.4: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for groups of potential arthropod and seed food sources and for feather samples (i.e., diet-derived isotopic mixtures) from fall molt and winter diets of Bachman's, Grasshopper, and Henslow's sparrows. Mean delta values for feather sample groups were corrected for trophic enrichment (2.7 ± 0.1 (SD) for $\Delta^{13}\text{C}$ and 4.0 ± 0.3 (SD) for $\Delta^{15}\text{N}$) (Hobson and Bairlein 2003). Food groups that did not differ significantly for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are surrounded by oval shapes.

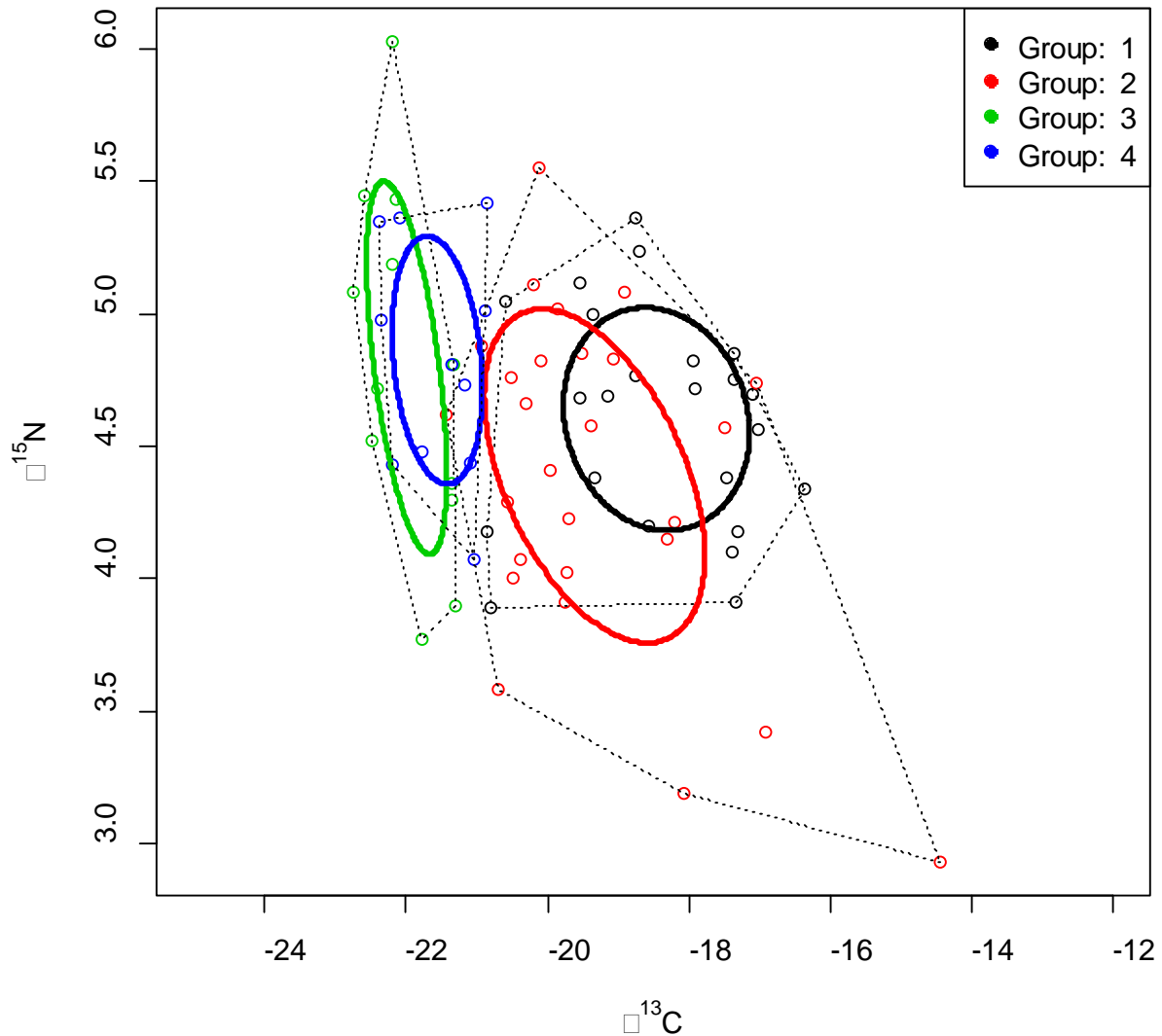


Figure 4.5: Winter diet overlap among Bachman’s Sparrow molt feathers (Group 1), Bachman’s Sparrow regrown feathers (Group 2), Henslow’s Sparrow regrown feathers (Group 3) and Grasshopper Sparrow regrown feathers (Group 4). Convex hulls for each sparrow diet, which allow interspecific diet comparisons that include individual variation, suggest significant winter diet overlap between Henslow’s and Grasshopper sparrows, minimal diet overlap between Grasshopper Sparrow and Bachman’s Sparrow and negligible overlap between Henslow’s Sparrow and Bachman’s Sparrow. Standard ellipses are used to compare trophic niche width among sparrows and reflect comparable results.

4.6 List of References

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CHAPTER 5: CONCLUSION

This dissertation presents results of the first concurrent study in peninsular Florida on winter habitat associations of Florida Grasshopper (*Ammodramus savannarum floridanus*), Bachman's (*Peucaea aestivalis*), Henslow's (*Ammodramus henslowii*), and Grasshopper (*A. s. pratensis*) sparrows, the first concurrent study of fall molt period diets of sympatric Florida Grasshopper and Bachman's sparrows and the first concurrent study of winter diets of Bachman's, Henslow's, and Grasshopper sparrows in Florida.

In Chapter 2 winter habitat associations within two defined plant communities of the dry prairie ecosystem, the dry-mesic and wet-mesic prairie, were established for Florida Grasshopper, Bachman's, Henslow's, and Grasshopper sparrows within four prescribed fire treatments during winter 2006-2007 and winter 2007-2008. Sparrows were flushed systematically, and flush locations marked, in plots split equally between dry-mesic and wet-mesic prairie. Vegetation in plots established at each sparrow flush point was classified as dry-mesic or wet-mesic prairie within the sampled 4-5 ha flush-net plots. Grasshopper and Henslow's sparrows were more abundant in wet-mesic prairie and Bachman's Sparrows were more abundant in dry-mesic prairie across all four fire treatments. Abundances of Grasshopper and Bachman's sparrows were best predicted by habitat association and secondly by time since fire. For Henslow's Sparrow, habitat and time since fire were equally important in predicting abundance.

Florida Grasshopper Sparrows were detected only in small numbers in flush-net plot sampling in each of the two winters and were flushed almost equally from wet-mesic and dry-mesic patches. This non-migratory subspecies was detected in burn class one and burn class two

prairies in winter and was not detected in either burn class three or burn class four plots, despite the fact that all burn class sample plots were located in areas where male Florida Grasshopper Sparrows established breeding territories either before, after, or both before and after winter sampling. Our results confirm the findings of previous research showing that Florida Grasshopper Sparrows are found in low abundance, or are absent, in dry prairie burned more than two years prior (Shriver et al. 1999, Shriver and Vickery 2001) and we recommend continuation of one-to-three-year burn rotations to support optimal habitat conditions for this Endangered subspecies.

Despite the very low number of detections in our winter sampling, there is some indication that Florida Grasshopper Sparrow may be more of a habitat generalist than Bachman's Sparrow, which showed a strong association with dry-mesic prairie. Dry prairie plant community classification of 30 Florida Grasshopper Sparrow nest locations in 2005-2008 showed a nearly equal number of nests in dry-mesic and wet-mesic habitat (Noss et al. 2008), suggesting habitat-generalist behavior in nest site selection. If Florida Grasshopper Sparrow is considered a relative habitat generalist and Bachman's Sparrow is considered a habitat specialist, Florida Grasshopper Sparrow has a wider selection of habitat niches in which to nest and forage than Bachman's Sparrow, potentially providing the former with a range of adaptive options during predicted climate changes in Florida.

Bachman's Sparrows were most abundant in burn class one and least abundant in burn class four, which is consistent with previous research in north Florida and south Alabama (Tucker et al. 2004, Tucker et al. 2006, Cox and Jones 2007) but our study was the first to demonstrate this relationship in peninsular Florida and in the treeless dry prairie habitat. Burn rotations at one to three year intervals in dry prairie will maintain habitat suitable for Bachman's

Sparrows and will be compatible with recommended burn rotations for Florida Grasshopper Sparrows.

Henslow's Sparrow abundance was best predicted by both habitat and burn class whereas Grasshopper Sparrow abundance was best predicted by habitat alone. Henslow's Sparrows were most abundant in the dense grasses of wet-mesic prairie in burn class which conflicts with previous research conducted in longleaf pine savannas in southern Louisiana, Mississippi, and Alabama and northwest Florida in which Henslow's Sparrows were most abundant in burn class one habitat (Carrie et al. 2002, Tucker and Robinson 2003, Palasz et al. 2010). We attribute the difference in burn class association for Henslow's Sparrow to the rapid accumulation of pine needle duff in longleaf pine savannah such that Henslow's prefer habitat burned the previous growing season, compared to the lower rate of litter accumulation in the grass-and-forb dominated wet-mesic prairie habitat where Henslow's were more abundant three years after fire. Based on our results, we find that Henslow's Sparrow is tolerant of, and may prefer, dry prairie three years post-burn, which is a somewhat longer burn rotation than preferred by the Endangered Florida Grasshopper Sparrow.

The migratory Grasshopper Sparrow subspecies was equally abundant in burn classes one and three wet-mesic prairie sampled in the second year of our research which conflicts with results of one other study on Grasshopper Sparrow winter habitat associations in west-central Florida (Butler et al. 2009). There are no other publications on winter habitat associations of the migratory Grasshopper Sparrow. Our results for Grasshopper Sparrow habitat associations suggest that the migratory subspecies can adapt readily to the fire return interval in effect for the Florida Grasshopper Sparrow.

Our research findings with regard to the differences in sparrow species abundances with varying time since fire points to dry prairie habitat management strategies that maximize a landscape with patches of dry-mesic and wet-mesic prairie in burn classes one, two, and three in order to benefit multiple grassland sparrow species. However, given the Endangered status of the resident Florida Grasshopper Sparrow, prescribed burn management may continue to favor biannual fire rotation intervals to which all four of our focal sparrows can adapt.

Results of fall molt-period diet reconstruction and diet overlap modeling for Florida Grasshopper and Bachman's sparrows are presented in Chapter 3. Feathers from captured birds and potential food sources, including an array of arthropods, grass, and sedge seeds were analyzed for stable carbon and nitrogen isotope ratios. The Stable Isotope Analysis in R (SIAR) mixing model was used to estimate diets and diet overlap of the two resident sparrows during the August – October annual molt period. Grasshoppers, including a variety of species foraging on C₃ or C₄ herbs, spiders, dragonflies, flies, beetles and weevils comprised the majority of the diets of adult and juvenile Florida Grasshopper Sparrows and Bachman's Sparrows, but in differing proportions. Moth larvae did not contribute significantly to diets of either sparrow. Butterfly larvae figure prominently in published diet accounts for both sparrows but sampling methods used to collect arthropods in this study were biased against capture of butterfly larvae so results do not include consideration of this probable food source. Despite the similarity in reconstructed diets for the two sparrow species, analysis of diet overlap suggested that approximately half of the Florida Grasshopper Sparrows had diets consisting of higher trophic level prey than Bachman's Sparrows.

Chapter 4 presents results of winter diet reconstruction and diet overlap assessment for Bachman's, Henslow's and Grasshopper sparrows using the SIAR model. Sparrows were

captured and recaptured in winter 2007-2008 using systematic flush-netting, removal of a tail feather at first capture and then removal of the regrown feather when birds were recaptured. Winter diets of all three sparrows included a similar prey base of C₃-foraging grasshoppers, spiders, dragonflies, flies, seeds of *Dichanthelium* spp., and seeds of the sedges *Scleria* spp. Bachman's Sparrow winter diets differed from those of Henslow's and Grasshopper sparrows with a significant estimated proportion of C₄-foraging grasshopper nymphs. Henslow's and Grasshopper sparrow winter diets differed from Bachman's Sparrow winter diets with significant contributions of beetles and weevils. Bachman's Sparrow winter diets occupied a greater isotopic niche width than that of their fall molt period diets and a greater trophic niche width than that of winter diets for migratory Henslow's and Grasshopper sparrows. Estimated winter diets of Henslow's and Grasshopper sparrows differed significantly from that of winter Bachman's Sparrow diets but Henslow's Sparrow winter diets did not differ significantly from Grasshopper Sparrow winter diets.

The chapters in this dissertation make a significant contribution to the body of knowledge pertaining to the federally Endangered Florida Grasshopper Sparrow and the three most abundant sympatric sparrows in Florida dry prairie: resident Bachman's Sparrow, migratory Henslow's Sparrow, and migratory Grasshopper Sparrow. Future research should focus on obtaining larger sample sizes of Florida Grasshopper Sparrows during the nonbreeding period, September through mid-February to quantify habitat associations and diet overlap with sympatric grassland sparrows. Future research should also focus on hydrogen isotope analysis of molt-period feathers of migratory Henslow's, Grasshopper, and other grassland sparrows overwintering in Florida dry prairie to reconstruct the latitudes at which their annual molts occurred prior to arrival in south-central Florida.

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18 September 2013

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