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Life History Attributes of Arizona Grasshopper Sparrow (Ammodramus savannarum ammolegus) and Comparisons with Other North American Subspecies

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ABSTRACT.—*Ammodramus savannarum ammolegus*—commonly referred to as the Arizona Grasshopper Sparrow—occurs in the desert and plains grasslands of southeastern Arizona, southwestern New Mexico, and northern Sonora, Mexico. Although a subspecies of conservation concern, this is the first intensive study of its life history and breeding ecology, providing baseline data and facilitating comparisons with other North American Grasshopper Sparrow subspecies. Specifically, I found *A. s. ammolegus* males generally weighed less than other subspecies (16.0 ± 0.8 g) but with intermediate exposed culmen length (11.6 ± 0.5 mm) and wing chord length similar to the other two migratory subspecies (62.7 ± 1.5 mm). Territory size for *A. s. ammolegus* was 0.72 ± 0.37 ha, with some variation between sites and among years, possibly indicating variation in habitat quality across spatial and temporal scales. The return rate for *A. s. ammolegus* males was 39.2%. Nest initiation for *A. s. ammolegus* was early to mid-July after the monsoons had begun. Domed nests were constructed on the ground, primarily under native bunch grasses, and frequently with a tunnel extending beyond the nest rim, with nest openings oriented north. Clutch size was 3.97 ± 0.68, with no evidence of Brown-headed Cowbird (*Molothrus ater*) nest parasitism. Extreme climate factors in the arid Southwest may have affected the life history and morphology of *A. s. ammolegus* as compared to other subspecies, influencing body size and mass, culmen length, breeding phenology, and nest orientation. Other geographic variation occurred in return rates, clutch size, and nest parasitism rates. The baseline data for *A. s. ammolegus* obtained in this study will inform future taxonomic and ecological studies as well as conservation planning. Comparisons of *A. s. ammolegus* morphometrics with those of other subspecies will assist field biologists in distinguishing among subspecies where they overlap, especially on wintering grounds.

INTRODUCTION

Grasshopper Sparrow (*Ammodramus savannarum*) is a widely distributed grassland bird, breeding throughout the grasslands of North America, Central America, and the Caribbean. However, across its entire range and in many biogeographic regions, this species has experienced long-term population declines (Sauer *et al.*, 2014). As such, this species has been designated a Common Bird in Steep Decline (Berlanga *et al.*, 2010; NABCI, 2014) and has been designated as a focal species by the U.S. Fish and Wildlife Service (USFWS; Ruth, 2015). Within North America four subspecies have been recognized, with an additional four from southern Mexico to northern Ecuador, and another four resident in the Caribbean (Vickery, 1996).

Ammodramus savannarum ammolegus (commonly referred to as the Arizona Grasshopper Sparrow) occurs in the desert and plains grasslands of southeastern Arizona, southwestern New Mexico, and northern Sonora, Mexico (Oberholser, 1942; AOU Checklist, 1957; Strong, 1988; Williams, 1991). The largest numbers and densities of *A. s. ammolegus* are

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found in the Sonoita and San Rafael valleys in Arizona and the Animas Valley in New Mexico, with additional small or remnant populations in the Altar, San Pedro, San Bernardino, Santa Cruz, and Sulphur Springs valleys in Arizona and in Sonora, Mexico (Mills, 1982; Strong, 1988; Ruth, 2008). It seems likely breeding *A. s. ammolegus* may also be found in small remnant populations in northwestern Chihuahua, Mexico (Manzano-Fischer *et al.*, 1999; Ruth, 2015). The current winter range of *A. s. ammolegus* extends from southern Arizona south to Sinaloa and Morelos, Mexico, and Guatemala (Vickery, 1996; Corman and Wise-Gervais, 2005).

Despite being listed as a Bird of Conservation Concern for USFWS Region 2 (USFWS, 2008) and as endangered in the state of New Mexico, *A. s. ammolegus* is arguably the least studied of the North American subspecies, with current research limited to roadside surveys and associated basic habitat work (Meents, 1979; Mills, 1982; Strong, 1988; Williams, 1991; Ruth, 2008). Obtaining baseline data for *A. s. ammolegus* would assist future taxonomic and ecological studies as well as conservation planning. Therefore, the primary objective of this study was to provide baseline data that would address the information gap for this subspecies of conservation concern. Specifically, I estimated basic life history attributes of *A. s. ammolegus* including male mass and morphometric measurements, territory size, and return rates, as well as breeding phenology, nest placement and orientation, nest and egg dimensions, clutch size, and nest parasitism rates.

The secondary objective of this study was to compare *A. s. ammolegus* morphometric and mass estimates with available data for other Grasshopper Sparrow subspecies. Given the notable variation in grassland types and climate experienced by the different subspecies, and their different migratory status, it is reasonable to expect differences in morphometrics or other life history characteristics among Grasshopper Sparrow subspecies. Such differences would assist scientists in distinguishing among subspecies (especially in winter when distributions of *A. s. ammolegus* and *A. s. perpallidus* overlap; JMR, pers. obs.), as plumage differences (*see* Oberholser, 1942; Phillips *et al.*, 1964; Rising, 1996; Vickery, 1996; Pyle, 1997) often overlap, making separation in the field by plumage alone difficult, if not impossible.

Methods

Study Area

This study was conducted during 2009–2014 on two sites in the semidesert and plains grasslands of Santa Cruz County, southeastern Arizona: the Audubon Appleton-Whittell Research Ranch (Audubon) (lat: 31°36′4″N; long: −110°30′40″W; elev: 1497 m) located south of the town of Elgin and the Davis pasture on the Bureau of Land Management (BLM) Las Cienegas National Conservation Area (Davis) (lat: 31°41′42″N; long: −110°35′46 ″W; elev: 1430 m) located east of the town of Sonoita. In this region long-term mean annual precipitation is ∼450 mm (Arguez *et al.*, 2012; Audubon, 2016), with ∼60% occurring as monsoonal rains between July and September (McClaran and Van Devender, 1995). Mean temperature in summer is ∼23.8 C but can range from 16–31.6 C (Arguez *et al.*, 2012).

The upland grasslands on these sites were dominated by a variety of native annual and perennial bunchgrasses including gramas (*Bouteloua* sp.), cane beardgrass (*Bothriochloa barbinodis*), threeawns (*Aristida* sp.), wolftail (*Lycurus setosus*), curly mesquite (*Hilaria belangeri*), and plains lovegrass (*Eragrostis intermedia*), as well as exotic grasses, predominantly Lehmann lovegrass (*Eragrostis lehmanniana*) and some Boer lovegrass (*E. chloromelas*). The sites also supported varying densities of shrubs, succulents, and low trees, predominantly

velvet mesquite (*Prosopis velutina*; McClaran and Van Devender, 1995); however, this study focused in the relatively open grasslands at both sites.

<center>FIELD METHODS</center>

During the breeding seasons in 2009–2013, field work was initiated between late June and mid-July, beginning gradually earlier over the period of the study, and continued until late August each year (25 July–18 August 2009; 6 July–26 August 2010; 27 June–31 August 2011; 26 June–25 August 2012; and 26 June–31 August 2013). In addition, a short week of winter field work was conducted to document year-round site fidelity (6–10 January 2011; 25–29 January 2012; 8–12 January 2013; and 15–19 January 2014).

Capture and marking.—In 2010–2013, known territorial males were captured by luring them into a single mist net placed near the center of their territory using digital recordings of conspecific songs and playback devices (Jones *et al.*, 2007). Each captured individual (territorial males, as well as the occasional female) was marked with a numbered U.S. Geological Survey (USGS) aluminum band, plus a unique combination of three color bands. Adult sex was assigned based on cloacal protuberance and observed singing behavior for males, or brood patch for females. Standard measures were taken on all captured birds including mass, wing chord, and exposed culmen. All capture and handling procedures were approved by the Institutional Animal Care and Use Committee of the USGS Fort Collins Science Center.

Territory mapping.—The flushing territory mapping protocol (Wiens, 1969) was used to document the territories of male Grasshopper Sparrows from 2009–2013. Male territories were mapped once per year by following a territorial male and recording each location it perched (singing and nonsinging) or flushed using a handheld GPS (global positioning system) unit until 20–30 observation points were compiled. In most cases, all observation points were recorded on a single day; if fewer than 20 observations were compiled in one day, the observer returned as soon as possible to complete the mapping.

Returns.—Calculations of return rates to breeding areas were based on mostly opportunistic resightings of banded individuals while observers conducted other activities (*e.g.*, capture and banding, territory mapping, nest searches and monitoring, and nest and vegetation measurements) on the study sites. Early in the season, observers also specifically searched study sites for previously banded Grasshopper Sparrows. These activities were conducted 6 d per week, alternating between the two study sites, from late June through the end of August. Data on color banded males in 2010–2012 and resightings in 2011–2013 were used. Like Jones *et al.* (2007), it was assumed there were no significant effects of capture, handling, or bands on return rates, as similar studies on other species found no negative effects of color bands on return rates (Watt, 2001; Perkins *et al.*, 2004).

To document year-round site fidelity, the flush mist netting protocol described in Ruth *et al.* (2014) was used for 2 d during the winter on each site. Here, six or seven 7 ha plots were sampled that covered as much of the study area in the summer as possible. During flush mist netting, volunteers flushed sparrows from both sides of the 7 ha hourglass shaped plot into a 100 m line of multiple mist nets (*see* Fig. 2; Ruth *et al.*, 2014).

Nest searching.—To locate active nests, sites were searched three to five times per week from early July through the end of August in 2011–2013. Search techniques included rope dragging (Davis, 2003; Dieni and Jones, 2003), behavioral observation (Martin and Geupel, 1993), opportunistic foot flushing, and occasional visual sightings of nests. Rope dragging involved two people who systematically pulled a single weighted 28 m length of heavy rope with aluminum or tin cans attached at 1 m intervals across the study site; if a third person was

available, that person walked immediately behind the rope at the middle to help in sighting flushed birds. During behavioral observations one person observed individual Grasshopper Sparrows until they returned to their nest. Because of the cryptic behavior of Grasshopper Sparrows when approaching or leaving their nest, this method was most effective once adults became more active when feeding chicks.

Once a nest was found, it was marked for relocation by attaching a small piece of colored flagging to vegetation four paces from the nest in the direction of the nest entrance and another at four paces in the opposite direction. Nest site location was recorded with a handheld GPS unit in case flagging markers were lost. Incubation period was calculated assuming incubation starts with the penultimate egg (Vickery, 1996). Nest initiation date (date of the onset of incubation) for each nest was based on date when the nest was found, length of incubation and nestling periods, and hatch and fledge dates. In 2013, the dimensions (length × width) of one to two eggs were measured in a randomly selected subset of nests as soon after the nest was found as possible.

Nest site measurements.—Nest measurements were taken typically within a week of nest failure or fledgling. However, in 2011, the first year of nest monitoring, 17 nests were measured more than 7 d after nest completion. Measurements included: inside (cup) diameter, inside depth, nest height (height of nest rim above ground surface), orientation of nest opening (relative to true north using a magnetic compass), length of tunnel (distance of dome cover beyond nest rim), nest concealment, and identification of the plant species under which the nest was located. Percent nest concealment was estimated visually from directly above the nest and from 1 m away from the nest at ground level in the four cardinal directions. The arithmetic mean of those five measurements was used as the mean nest concealment value for each nest (Jones and Dieni, 2007).

Population and subspecies comparisons.—To compare morphometric and life history attributes among *A. s. ammolegus* populations and to other Grasshopper Sparrow subspecies, information was compiled from: (1) previously published studies, (2) unpublished data provided by several colleagues (A. Boyle, *A. s. perpallidus* in Kansas; S. Jones, *A. s. perpallidus* in Montana; E. Hewett Ragheb, *A. s. floridanus* in Florida), and (3) museum specimens from the Museum of Southwestern Biology (MSB; MSB8843-8848, accessed 5 November 2015).

As some sources measured bill length using exposed culmen while others used tip-to-nares, a correction factor that could be applied in order to achieve comparable results was estimated. To do this, the mean difference between these measurements taken from 26 male Grasshopper Sparrow specimens in the MSB collection (a mix of *A. s. ammolegus*, *A. s. perpallidus*, and unknown subspecies) was first estimated. Then this difference (3.19 mm) was added to all tip-to-nares measurements to estimate the exposed culmen length. Subspecies were combined in this estimate, as the mean ± SD difference did not differ substantially between the known *A. s. ammolegus* (3.24 ± 0.53 mm; n = 8) and *A. s. perpallidus* (3.13 ± 0.59 mm; n = 7) measurements.

In comparisons of *A. s. ammolegus* measurements to other subspecies of Grasshopper Sparrow, some decisions were required about which subspecies was represented in the region of the Midwest where *A. s. pratensis* and *A. s. perpallidus* are thought to overlap (AOU, 1957; Vickery, 1996). For comparison purposes, after consulting with local ornithologists (C. Ribic, S. Dinsmore, and A. Boyle, pers. comm.), birds in Wisconsin, Iowa, Missouri, eastern Oklahoma, and northeastern Texas were considered to be *A. s. pratensis*; and anything west of there to be *A. s. perpallidus*. This assumption, however, requires further study to confirm.

STATISTICAL ANALYSES

Morphometric comparisons among populations and subspecies.—For comparisons of *A. s. ammolegus* morphometric measurements (mass, wing chord, and exposed culmen length) from this study to other *A. s. ammolegus* data and to those of the other subspecies, two-sample *t*-tests were conducted using means and standard deviations with the In-Silico calculator (In-Silico, 2016). Tests were performed by comparing male *A. s. ammolegus* data from this study with any dataset that had a sample size >100; if no datasets for a subspecies had a sample size >100, then the dataset with the largest sample size was used (Table 1).

Information about other Grasshopper Sparrow life history attributes (*e.g.*, territory size, return rate, nest and egg dimensions, clutch size, parasitism rate) are available in the literature (Table 3). However, given the different ways this information was collected, calculated, and presented, it was not appropriate to conduct any formal comparative analyses; therefore, their metrics are qualitatively compared in the discussion.

Territory size calculations.—Mapped locations for each individual bird were used to generate a two dimensional kernel density estimate (Seaman and Powell, 1996; Anich *et al.*, 2009) for each individual territory in each year using R v. 3.2.5 (R Core Team, 2015) with the library ks (Duong, 2016). Here, least-squares cross-validation was used to estimate bandwidth, with final territory size calculated based on the 95% contour. Given the possibility territory size may vary between the two sites or among years, the potential influences of site, year, and their interaction on territory size were evaluated using an analysis of variance in Systat 13 (Systat, 2009).

Nest opening orientation.—The nest orientation compass readings were adjusted for 10° E declination. R v. 3.2.0 (R Core Team, 2015) with package "circular" (Agostinelli and Lund, 2013) was used to examine the orientation of nest openings descriptively and Rayleigh's test for directionality was used. Unless stated otherwise, estimates are provided as mean ± SD throughout.

RESULTS

Morphometric measurements.—Mean mass of male *A. s. ammolegus* was 16.0 ± 0.8 g, mean wing chord was 62.7 ± 1.5 mm, and mean exposed culmen was 11.6 ± 0.5 mm (Table 1). Only two females were captured; mean mass (range) was 15.8 g (14.8–16.7 g), mean wing chord was 59.5 mm (59–60 mm), and mean exposed culmen was 10.5 mm (9.7–11.4 mm).

When compared to the New Mexico specimens of *A. s. ammolegus*, there was no significant difference in mean mass of males between the two *A. s. ammolegus* populations ($t = 0.00$, P > 0.999; Table 1). However, mean male wing chord in this study was significantly smaller than the New Mexico population ($t = -3.19$, P = 0.008; Table 1), while mean exposed culmen length was significantly longer ($t = 4.55$, P = 0.003; Table 1). For all three morphometric measures in this study, the standard deviation around the mean and the range of values were larger than for the small sample from New Mexico, indicating more variation in these traits in the *A. s. ammolegus* subspecies than previously known.

The mean mass of male *A. s. ammolegus* was consistently and significantly less than the mass of all other Grasshopper Sparrow subspecies: *A. s. perpallidus* (Kansas, $t = -9.51$, P < 0.001; Table 1), *A. s. pratensis* (Illinois, $t = -10.84$, P < 0.001; West Virginia, $t = -12.24$, P < 0.001; Table 1), and *A. s. floridanus* ($t = -7.12$, P < 0.001; Table 1). However, mean *A. s. ammolegus* wing chord for males was significantly longer than the resident *A. s. floridanus* ($t = 14.81$, P < 0.001; Table 1) but was not significantly different than measurements for the migrant *A. s. pratensis* (Kansas; $t = 0.50$; P = 0.62; Table 1) or *A. s. perpallidus* (Illinois; $t = 0.55$; P = 0.58; West Virginia; $t = 0.88$; P = 0.38). Mean exposed culmen length for male *A. s. ammolegus* was significantly shorter than *A. s. floridanus* ($t = -10.11$, P < 0.001; Table 1) but longer than *A. s. perpallidus* (Montana, $t = 4.78$, P < 0.001; Table 1). Comparisons with *A. s. pratensis*, however,

TABLE 1.—Comparison of male Grasshopper Sparrow (*Ammodramus savannarum*) measurements among populations and subspecies

Location	Mass (g)			Wing chord (mm)			Exposed culmen (mm)			Reference
	n	Mean ± SD	Range	N	Mean ± SD	Range	n	Mean ± SD	Range	
A. s. ammolegus										
Arizona	100	16.0 ± 0.8	12.5–17.7	106	62.7 ± 1.5	58–66	105	11.6 ± 0.5	10.5–12.8	this study
Arizona				unk	64.8	62–67	unk	12.2	12.0–12.5	Oberholser (1942)
unk.				10	65[a]	62–68	unk[a]	11.75[a]	11.0–12.5	Pyle (1997)[a]
New Mexico	6	16.0 ± 0.5	15.3–16.8	6	63.5 ± 0.5	62.5–64.0	6	11.0 ± 0.3	10.6–11.4	Mus. of SW Biology[b]
A. s. perpallidus										
Kansas	105	17.0 ± 0.7	15.4–19.1	105	62.6 ± 1.4	60.0–66.5				A. Boyle (unpub. data)
Montana	42	17.9 ± 1.6	14.2–21.2	42	62.1 ± 2.2	59–70	42	7.9 ± 0.6[c]	6.5–9.6[c]	S. Jones (unpub. data)
unk.				77	62[a]	58–66	unk[a]	10.8[a]	10.0–11.6	Pyle (1997)
California	16	16.8 ± 1.3		34	61.7 ± 1.8	57.2–66.3				Collier (1994)
western U.S.				12	62.5		12	10.9	10.2–11.7	Ridgway (1901)[e]
A. s. pratensis										
Illinois	212	17.3 ± 1.3	12.5–22.5	212	62.6 ± 1.6	54.0–68.0	212	11.9 ± 1.0	5.8–15.9	Wenny (2005)
West Virginia	131	17.3 ± 0.8[d]	15.0–20.0	131	62.5 ± 2.0[d]	57.5–67.0	131	8.06 ± 0.3[c,d]	7.1–8.9[c]	Ammer et al. (2008)[d]
Maine	42	17.3 ± 1.3[d]	14.5–20.0	42	59.8 ± 1.3[d]					JVWells in Vickery (1996)[d]
Connecticut	8	17.8 ± 0.9[d]		8	62.0 ± 0.9[d]		8	11.9 ± 0.3[d]		Crossman (1989)[d]
unk.				67	61.5[a]	58–65	unk[a]	11.35[a]	10.5–12.2	Pyle (1997)
eastern U.S.				9	61.0	58.7–62.2	9	11.4	10.7–12.2	Ridgway (1901)[e]
A. s. floridanus										
Florida	84	16.9 ± 0.9	14.2–19.7	99	59.7 ± 1.4	57–64	98	12.3 ± 0.5	11–14.2	E. Hewett Ragheb and K. Miller (unpub. data)
Florida	25	17.2 ± 0.2[b]		25	60.7 ± 0.3[b]					Delany et al. (1994)
Florida				60	61[a]	58–64	unk[a]	11.7[a]	10.9–12.5	Pyle (1997)

[a] Pyle (1997) provides ranges representing 95% confidence intervals, making the mean the midpoint between the extremes; although he provides wing chord by sex, he does not provide a sample size or separate exposed culmen measures by sex (presumably pooled)

[b] Specimens # 8843–8848; collected in Hidalgo County, NM on 17 July 1987 (SO Williams III); Museum of Southwestern Biology (accessed 5 Nov 2015)

[c] Source used nares-to-tip culmen measure rather than exposed culmen; addition of 3.19 mm (mean difference between exposed culmen and nares-to-tip measurements explained in text) gives an estimate of mean exposed culmen for these data

[d] Source provided SE and not SD; transformed to SD for comparison

[e] Ridgway (1901) described the Grasshopper Sparrow as *Coturniculus savannarum* with four subspecies with only two in North America—*C. s. passerinus* in the eastern U.S. and *C. s. bimaculatus* in the western U.S. and Mexico; he does not specifically note locations where specimens were collected

TABLE 2.—Annual return rates of adult territorial male Arizona Grasshopper Sparrows (*Ammodramus savannarum ammolegus*) to the same sites in subsequent years

	Audubon			Davis			Total (sites merged)		
Year	Number of banded adult males[a]	Number of returns observed in subsequent year	Percentage	Number of banded adult males[a]	Number of returns observed in subsequent year	Percentage	Number of banded adult males[a]	Number of returns observed in subsequent year	Percentage
2010	18	7	38.9	19	8	42.1	37	15	40.5
2011	21	10	47.6	31	12	38.7	52	22	42.3
2012	23	8	34.8	22	7	31.8	45	15	33.3

[a] In 2011 and 2012, this value includes males banded that year plus banded males resighted from previous year

showed contradictory patterns, with mean exposed culmen for *A. s. ammolegus* in this study being significantly shorter than *A. s. pratensis* in Illinois ($t = -3.56$, $P < 0.001$; Table 1) but longer than *A. s. pratensis* in West Virginia ($t = 5.42$, $P < 0.001$, Table 1).

Territory size.—Pooled across years and sites, male *A. s. ammolegus* territory size was 0.72 ± 0.37 ha (n = 230, 95% kernel density estimate); number of sample points per individual territory for calculation was 25.5 ± 4.0 points. There were significant effects of year ($F_{4,220} = 8.24$; $P < 0.001$) and site on territory size ($F_{1,220} = 4.69$; $P = 0.03$) but no significant effect of the year*site interaction term ($F_{4,220} = 1.75$; $P = 0.14$). Territory size was greater in 2010 (0.90 ± 0.38 ha; n = 41) and 2011 (0.85 ± 0.39 ha; n = 52) as compared to 2009 (0.64 ± 0.35 ha; n = 47), 2012 (0.61 ± 0.28 ha; n = 43), and 2013 (0.58 ± 0.32 ha; n =47). Territory size was larger at Audubon (0.77 ± 0.37 ha; n = 110) than Davis (0.67 ± 0.36 ha; n = 120).

Return rates.—Thirty-eight adult males (39.2%) exhibited breeding site fidelity in at least one subsequent year, while 13 of the 38 were resighted in two subsequent years (Table 2). Additionally, several males exhibited year-round site fidelity, with five males recaptured in at least one subsequent winter on the same site (four on Davis and one on Audubon), while three of these five were also resighted during the subsequent breeding season, and one was recaptured in two subsequent winters and breeding seasons on the same site.

Nests and eggs.—Earliest nest initiation dates ranged from 8–13 July at Audubon and 9–17 July at Davis (2011: 12 July at Audubon, 17 July at Davis; 2012: 8 July at Audubon, 9 July at Davis; and 2013: 13 July at Audubon, 16 July at Davis). Across sites and years, nest initiation peaked on 17 July (Fig. 1). The incubation period for *A. s. ammolegus* was 11–12 d and time from hatching to fledging was 8–9 d (n = 128).

Across sites and years, 81% (n = 112) of nests were constructed under native grasses; in a few cases (n = 19) nests were constructed under clumps that had more than one grass species. There were some differences in the plants under which Grasshopper Sparrow nests were constructed on the two sites. At Audubon nests were found under a limited number of grass species; 91% (n = 52) were located under three species: cane beardgrass (63%), plains lovegrass (13%), and Lehmann lovegrass—an exotic (15%). At Davis nests were located under a broader range of grass species; 96% (n = 60) were located under six species: cane beardgrass (13%), Lehmann lovegrass—exotic (28%), blue grama (*Bouteloua gracilis*) (23%), sideoats grama (*B. curtipendula*) (5%), threeawn (22%), and wolftail (5%). Only one nest was not located under a grass clump, but rather under a semishrub—burroweed (*Isocoma tenuisecta*).
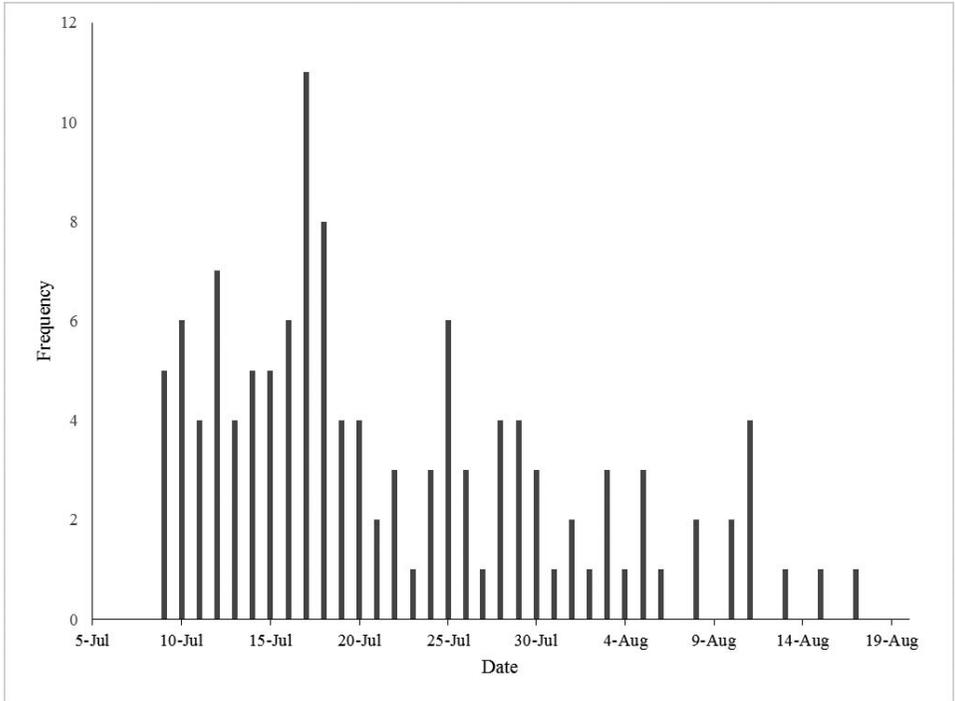
FIG. 1.—Frequency distribution of Arizona Grasshopper Sparrow (*Ammodramus savannarum ammolegus*) nest initiation dates (n = 128) pooled across sites and years (2011–2013)

The majority of nest openings were oriented towards north, with orientation toward 353.8 ± 41.6° (n = 115; Fig. 2). Nest orientation data met the Rayleigh test assumptions against multimodal data, and the test statistic showed strong departure from a uniform distribution in favor of directionality in nest orientation (Rayleigh $z_{67.97}$, P < 0.001). Ninety-three percent of nests were oriented between 290° and 70°; no nests were oriented to the south between 110° and 245° (Fig. 2).

Nest dimensions were as follows: inside diameter of nest was 65.2 ± 4.6 mm (n = 115), mean inside depth was 28.4 ± 6.1 mm (n = 115), mean height of nest rim above ground level was 25.4 ± 10.4 mm (n = 114), and entrance opening was 38.8 ± 7.0 mm (n = 114). Some but not all nests had a tunnel extending out from the dome beyond the nest rim; for those nests with tunnels (n = 82), tunnel length was 25.5 ± 15.8 mm (range 8–75 mm). Nest concealment was 87.7 ± 8.1% (n = 79) from 2012–2013.

Mean egg dimensions were 18.9 × 14.4 mm (n = 53); extremes were 17.0 × 13.8 mm, 20.9 × 14.5 mm, 17.0 × 13.5 mm, and 19.0 × 15.3 mm. Clutch size for *A. s. ammolegus* was 3.97 ± 0.68 eggs (n = 74; range: three to six eggs). No Brown-headed Cowbird (*Molothrus ater*) eggs were observed in any nests.

DISCUSSION

This study provides previously unavailable information about life history attributes for the *A. s. ammolegus* subspecies of the Grasshopper Sparrow, as well as a larger sample size of

TABLE 3.—Comparison of Grasshopper Sparrow (*Ammodramus savannarum*) life history attributes among subspecies. Given the different ways that attributes were collected, calculated, and presented, apparent differences among subspecies should be viewed with caution

Location	Subspecies	n	Mean ± SD or %	Reference
Territory size (mean ± SD) ha[a]				
Arizona	*A. s. ammolegus*	230	0.72 ± 0.37	this study
Wisconsin	*A. s. pratensis*[b]	25	0.81 ± 0.44	Wiens (1969) late May–early June
Wisconsin	*A. s. pratensis*[b]	30	0.81 ± 0.23	Wiens (1969) late June
Pennsylvania	*A. s. pratensis*	22	0.82 (0.49–1.34)[a]	Smith (1963)
Connecticut	*A. s. pratensis*	11	0.66 ± 1.29[c]	Crossman (1989) for 1986
Connecticut	*A. s. pratensis*	10	0.78 ± 0.76[c]	Crossman (1989) for 1987
California	*A. s. perpallidus*	41	0.37 ± 0.16	Collier (1994)
Nebraska	*A. s. perpallidus*	31	0.77 (0.36–1.24)[a]	DeLisle and Savidge (1996)
Montana	*A. s. perpallidus*	26	0.43 ± 0.36	Jones (2011)
Florida	*A. s. floridanus*	30	1.8 ± 0.96	Delany *et al.* (1995)
Adult male return rates (%)[d]				
Arizona	*A. s. ammolegus*	97	39.2	this study
Illinois	*A. s. pratensis*	205	25	Wenny (2003) (adults, hatch year)[d]
Maine	*A. s. pratensis*	42	35	Wells in Vickery (1996)
Kentucky	*A. s. pratensis*	39	15.4	Sutter and Ritchison (2005) (adults)[d]
New York	*A. s. pratensis*	35	29	Balent and Norment (2003)
Connecticut	*A. s. pratensis*	10	50	Crossman (1989) (adults)[d]
Maryland	*A. s. pratensis*	unk[e]	57.3	Gill et al. (2006) (breeding adults)[d]
Kansas	*A. s. perpallidus*	111	19.8	B.K. Sandercock in Jones *et al.* (2007)
Nebraska	*A. s. perpallidus*	85	0	Kaspari and O'Leary (1988) (adults, juveniles)[d]
Montana	*A. s. perpallidus*	45	8.9	Jones *et al.* (2007)
California	*A. s. perpallidus*	35	20	Collier (1994)
Florida	*A. s. floridanus*	49	73	Hewett Ragheb and Miller (2014)
Florida	*A. s. floridanus*	48	52	Delany *et al.* (1995)
Nest dimensions				
Inside nest diameter (mean ± SD) mm[f]				
Arizona	*A. s. ammolegus*	115	65.2 ± 4.6	this study
Texas	*A. s. perpallidus*[b]	unk	(63.5 or 76.2) X 82.6[f]	Simmons (1925)[f]
California	*A. s. perpallidus*	1	63 × 69[f]	Dixon (1916)
Florida	*A. s. floridanus*	15	69 ± 6	Delany and Linda (1998)
Florida	*A. s. floridanus*	11	75–88[f]	Delany in Vickery (1996)[f]
Inside nest depth (mean ± SD) mm[f]				
Arizona	*A. s. ammolegus*	115	28.4 ± 6.1	this study
Texas	*A. s. perpallidus*	unk	31.8–33.0[f]	Simmons (1925)[f]
California	*A. s. perpallidus*	1	30[f]	Dixon (1916)
Nest height to top of rim (mean ± SD) mm[f]				
Arizona	*A. s. ammolegus*	114	25.4 ± 10.4	this study
Texas	*A. s. perpallidus*[b]	unk	50.8–57.2[f]	Simmons (1925)[f]
California	*A. s. perpallidus*	1	43[f]	Dixon (1916)[f]
Florida	*A. s. floridanus*	15	77 ± 5	Delany and Linda (1998)

TABLE 3. Continued

Location	Subspecies	n	Mean ± SD or %	Reference
Florida	*A. s. floridanus*	11	77–105[f]	Delany in Vickery (1996)[f]
Entrance opening (mean ± SD) mm				
Arizona	*A. s. ammolegus*	114	38.8 ± 7.0	this study
Florida	*A. s. floridanus*	15	51 ± 8	Delany and Linda (1998)
Egg dimensions (mean length X mean width) mm				
Arizona	*A. s. ammolegus*	53	18.9 × 14.4	this study
Unknown	*A. s. pratensis*	50	18.6 × 14.4	Smith (1968)
Unknown	*A. s. perpallidus*	32	18.7 × 14.3	Smith (1968)
California	*A. s. perpallidus*	3	18.2 × 15.0	Dixon (1916)
Clutch size (mean ± SD)				
Arizona	*A. s. ammolegus*	74	4.0 ± 0.7	this study
many localities[g]	*multiple*[g]	438	4.3 ± 0.7	McNair (1987)[g]
Kentucky/Tennessee	*A. s. pratensis*	131	4.4	Giocomo *et al.* (2008)
Oklahoma	*A. s. pratensis*[b]	92	4.2 ± 0.7	Reinking and Hendriks in Vickery (1996)
Kentucky	*A. s. pratensis*	46	4.2 ± 0.1	Sutter and Ritchison (2005)
Pennsylvania	*A. s. pratensis*	42	4.4	Smith (1963)
Oklahoma	*A. s. pratensis*[b]	32	4.2 ± 1.1[c]	Rohrbaugh *et al.* (1999)
Montana	*A. s. perpallidus*	123	4.3 ± 1.0[h]	Jones *et al.* (2010)[h]
Florida	*A. s. floridanus*	7	3.3 ± 0.5	Perkins *et al.* (1998) Avon Park site
Florida	*A. s. floridanus*	2	3	Perkins *et al.* (1998) Three Lakes site
Parasitism Rates (%)				
Arizona	*A. s. ammolegus*	128	0	this study
Maryland	*A. s. pratensis*	213	0	Gill *et al.* (2006)
Pennsylvania	*A. s. pratensis*	195	0	Hill and Diefenbach (2013)
Kentucky	*A. s. pratensis*	131	0	Giocomo et al. (2008)
Iowa	*A. s. pratensis*[b]	327	24–28	Hovick *et al.* (2012) (across 2 years)
Montana	*A. s. perpallidus*	123	4	Jones *et al.* (2010)
Manitoba	*A. s. perpallidus*	49	29	Davis and Sealy (2000)
North Dakota	*A. s. perpallidus*	45	22	Koford *et al.* (2000) seeded grasslands
Minnesota	*A. s. perpallidus*	42	7	Johnson and Temple (1990)
North Dakota	*A. s. perpallidus*	13	38	Koford *et al.* (2000) croplands

[a] Where mean or SD were not provided, the range is provided in parentheses

[b] Data from eastern Oklahoma, Texas, and the states of Missouri, Iowa, and Wisconsin are considered *A. s. pratensis* and anything west of there to be *A. s. perpallidus*, although there remain some uncertainties about subspecific identity in this region of potential overlap between *A. s. pratensis* and *A. s. perpallidus*; see text

[c] Source provided SE and not SD; transformed to SD for comparison

[d] Where separate data for adult male return rates were not available, it is noted with the reference

[e] Although sample size for mean return rate of breeding adults is unknown, Gill *et al.* (2006) banded 1985 Grasshopper Sparrows over the 6 y study

[f] Where mean ± SD were not available, nest dimension data are provided as in the citation

[g] McNair (1987) provides a large dataset spanning the range of all North American Grasshopper Sparrow subspecies but does not identify which subspecies were sampled

[h] Jones *et al.* (2010) provided mean and CV; transformed to SD for comparison
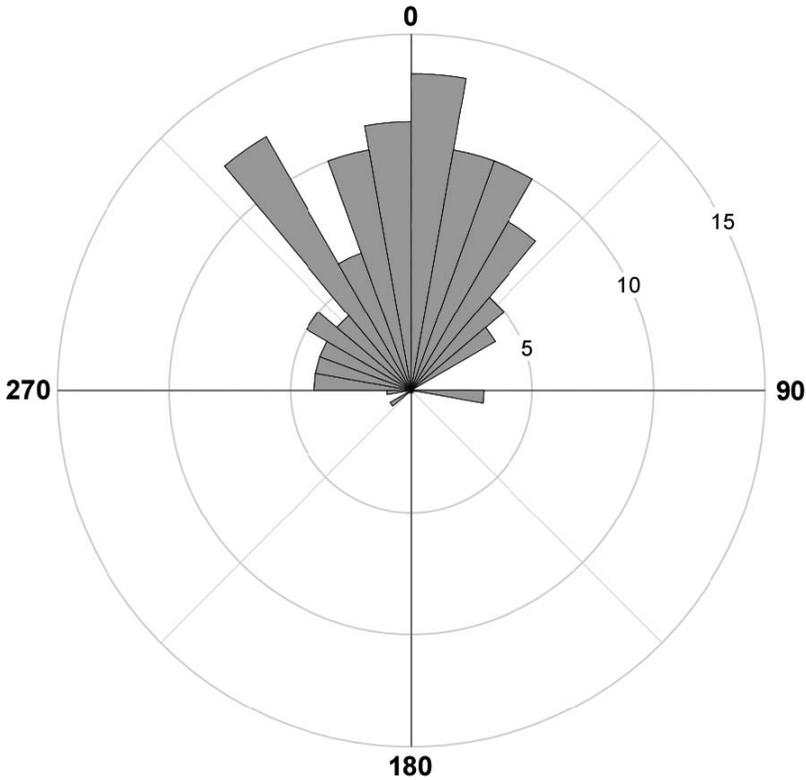
FIG. 2.—Frequency distribution in the orientation of Arizona Grasshopper Sparrow (*Ammodramus savannarum ammolegus*) nest openings (n = 115). Each histogram bar represents 10 degrees; concentric circles designate the number of nests

morphometric measurements than was previously available. Many life history and morphometric traits appear to differ among subspecies or geographically, potentially due to the interrelated factors of climate, migratory strategy, and latitudinal gradients.

Morphometric measurements.—Contrary to previous work that suggests *A. s. ammolegus* is larger than the other Grasshopper Sparrow subspecies (Oberholser, 1942; Pyle, 1997), findings based on mass in this study suggest *A. s. ammolegus* may in fact be smaller than the other subspecies; however, additional research is needed on other measures (*e.g.*, tarsus length) that may be more representative of true body size (Rising and Somers, 1989; Freeman and Jackson, 1990). *A. s. ammolegus* is found in the warmest most arid region of any of these North American subspecies. Such a pattern, if it exists, would be consistent with Bergmann's Rule which states smaller body size occurs in warmer regions where a larger surface area-to-volume ratio would facilitate heat loss. In a related finding, *A. s. ammolegus* nests appear to be qualitatively smaller than other subspecies for which data were available (Table 3), suggesting *A. s. ammolegus* was indeed smaller in size than other subspecies.

Climate may have the opposite effect on bill size. In comparing North American Grasshopper Sparrow subspecies bills, Pyle (1997) describes *A. s. ammolegus* bills as long and slender, *A. s. floridanus* as large and stout, *A. s. pratensis* as medium and stout, and *A. s.*

perpallidus as small. The similar inter-subspecific patterns observed in this study, with longer bills in the two subspecies found in hotter climates (*A. s. ammolegus* and *A. s. floridanus*), are consistent with recent studies documenting a positive association between bill size and high summer temperatures within several sparrow species (Greenberg *et al.*, 2012a; Greenberg *et al.*, 2012b; Greenberg and Danner, 2013). Bird bills consist of a keratin sheath with vascularized tissue beneath. For birds in regions with dry hot summers, relatively mild winters, and habitats with few opportunities to escape direct insolation, these studies propose that selection acts to increase bill size to facilitate dry heat dissipation and reduce respiratory water loss.

In addition to variation in body size and culmen length, there was variation in wing length among subspecies, potentially due to differences in migratory status, as migrant subspecies often exhibit longer wings than resident subspecies (Fitzpatrick, 1998; Förschler and Bairlein, 2011). In this study I found wing chord of *A. s. ammolegus* was no different than the two migratory subspecies (*A. s. pratensis* and *A. s. perpallidus*) but longer than the resident *A. s. floridanus*. However, the migratory status of *A. s. ammolegus* is not clear, as it has been described as both a resident (Rising, 1996; Corman and Wise-Gervais, 2005) and a local or shorter-distance migrant than other migrant subspecies of Grasshopper Sparrow (AOU, 1957; Vickery, 1996). However, recapture of several color-banded *A. s. ammolegus* males on the study site during the winter confirms at least some individuals are resident year-round at sites in Arizona, with one of these males remaining on the same breeding territory for three summers and the two intervening winters.

Territory size.—Territory size of *A. s. ammolegus* appeared qualitatively similar to most *A. s. pratensis* and *A. s. perpallidus* populations but smaller than *A. s. floridanus* (Table 3). There were, however, additional patterns within the region of our study. Variation in *A. s. ammolegus* territory size by year and site may indicate variations in habitat quality (Wiens, 1969) across temporal and spatial scales. Territory size in Bobolink (*Dolichonyx oryzivorus*), another grassland bird, varies inversely with habitat quality, with smaller territories associated with greater prey abundance and more preferred vegetation structure (Diemer and Nocera, 2014). However, exploring possible factors that might have affected *A. s. ammolegus* territory size (*e.g.*, differences in food abundance or density, rainfall, other aspects of habitat quality, or population density) was beyond the scope of this study. It is possible the territory size estimates for *A. s. ammolegus* represent something a bit larger than the normally defined "Type A" territory (*i.e.,* area defended for mating, nesting, and feeding), as locations for singing males, as well as for perched (but not singing) and flushed males, were included. But the estimates almost certainly do not represent the entire home range (area traversed by an individual during normal activities) due to the cryptic nature of Grasshopper Sparrows when not singing (Anich *et al.*, 2009).

Return rates.—Jones *et al.* (2007) noted geographic variation in Grasshopper Sparrow return rates across its range, with lower return rates in the Midwest and prairie regions than in the East. Our evidence for *A. s. ammolegus* is consistent with geographic variation in this trait but suggests a more complex pattern, as this subspecies in the Southwest exhibits relatively high return rates that appear more similar to eastern than western populations (Table 3). However, various factors including detectability, survivorship, sex and age differences, site fidelity, and variability and unpredictability in breeding habitats and conditions can affect documented return rates (Wenny, 2003; Gill *et al.*, 2006; Jones *et al.*, 2007). Confounding factors can also include level of effort, dispersal distances, size of study area, and differing methods for calculating and reporting return. Therefore, comparisons of return rates should be viewed with caution.

Nests and eggs.—Breeding phenology for *A. s. ammolegus* in the arid Southwest begins substantially later in the year than other Grasshopper Sparrow subspecies. Breeding initiation is tied to the arrival of the summer monsoons, which, in Arizona, begin in early to mid-July, with the most reliable rainfall in August (McClaran and Van Devender, 1995). Subspecies in more mesic regions initiate breeding earlier: *A. s. pratensis* and *A. s. perpallidus* subspecies begin breeding in May (Vickery, 1996; Gill *et al.*, 2006; Giocomo *et al.*, 2008; Jones *et al.*, 2010), while *A. s. floridanus* exhibits a bimodal season with first peak in March to late June and a second peak in July to September following fires (Shriver *et al.*, 1996). However, the frequency distribution of *A. s. ammolegus* nest initiation dates seems most consistent with a unimodal pattern or a tendency towards a single brood per season (Jones *et al.*, 2010). Smaller peaks later in the season were most likely nests initiated after a first nest failed, although it is certainly possible some individuals who had initiated early successful nests were able to initiate a second nest. Despite differences in timing of nesting, the length of nest stages (incubation and nestling) for *A. s. ammolegus* appears to be fairly similar to other subspecies. For example, in Montana, the incubation period of *A. s. perpallidus* was 10.9 ± 0.14 d (n = 86) and nestling period was 9.7 ± 0.17 d (n = 26) (Jones *et al.*, 2010), while in Pennsylvania, the incubation period of *A. s. pratensis* was estimated at 12–13 d and nestling period at 9 d (Smith, 1963), and in Kentucky, the total nest period (incubation and nestling periods) of *A. s. pratensis* was 19 d (Sutter and Ritchison, 2005).

As compared to other Grasshopper Sparrow subspecies where orientation patterns were less consistent, *A. s. ammolegus* consistently oriented nests toward and around north. For example in Wisconsin, only 64% of *A. s. pratensis* nests (n = 15) faced north or northeast (Wiens, 1969), while in Kentucky, 74% of nests were oriented northwest, north, northeast, or east, and 26% southeast, south, southwest, and west (Sutter and Ritchison, 2005). In contrast orientation of nest openings in *A. s. floridanus* was random (Delany and Linda, 1998). Nesting birds often orient the entrances to their nests in a preferred direction in response to environmental factors such as solar radiation, as well as wind and precipitation (With and Webb, 1993; Burton, 2007). Such selected orientation can optimize the microclimate within the nest in ways that positively affect both adults and nestlings (Mainwaring *et al.*, 2014). The more consistent orientation patterns for *A. s. ammolegus* could be explained by the need to provide protection from the extreme environmental factors that threaten eggs or chicks in this arid habitat. For example direct normal irradiation (*i.e.*, the amount of solar radiation received by a surface per unit area) is much higher in southeastern Arizona (7–8 kWh/sq-m/d) as compared to habitats for other subspecies (*e.g.*, central Florida: 4.5–5 kWh/sq-m/d, Kentucky: 3.5–4.5 kWh/sq-m/d, and Wisconsin: 3.5–4 kWh/sq-m/d; NREL Solar Prospector). Additionally, during the summer in Arizona, prevailing winds are from the south or southeast, bringing moist air from the Gulf of Mexico associated with the monsoon season (Vera *et al.*, 2006), resulting in violent monsoonal storms.

Mean clutch size was generally smaller in *A. s. ammolegus* as compared to a large dataset spanning the range of all North American Grasshopper Sparrow subspecies (McNair, 1987; Table 3). Clutch size in *A. s. ammolegus* was also qualitatively smaller than estimates for *A. s. perpallidus* and *A. s. pratensis* but larger than *A. s. floridanus* (Table 3). The pattern observed in clutch size, with smaller clutch sizes in the southern two subspecies (*A. s. ammolegus* and *A. s. floridanus*) is consistent with one of the well-recognized latitudinal gradients in life history traits of increasing clutch size with increasing latitude (Lack, 1947; Cardillo, 2002). This latitudinal gradient has been attributed to patterns in seasonality of resources, nest predation, and length of breeding season (Griebeler *et al.*, 2010; Rose and Lyon, 2013). Despite geographic variation in clutch size, similar egg dimensions for *A. s. ammolegus* as

compared to other North American subspecies were documented (Table 3). Additionally, no Brown-headed Cowbird parasitism in *A. s. ammolegus* was found, the first assessment for this subspecies. These results are consistent with the general perception that Grasshopper Sparrows are an uncommon host for cowbird parasitism (Friedmann, 1963, 1971), likely because of the concealment offered by dome nests and the secretive behavior of attendant adults. However, a recent literature review (Shaffer *et al.*, 2003) suggests substantial geographic variation in nest parasitism rates in Grasshopper Sparrows, similar to the variation shown in Table 3. The results for *A. s ammolegus* were more similar to the eastern U.S. where there was also no parasitism; parasitism rates in the Midwest and West were higher but also show notable and sometimes significant geographic variation (Table 3). This pattern is consistent with Breeding Bird Survey findings of the highest Brown-headed Cowbird densities in the upper Midwest (Sauer *et al.*, 2014).

Implications.—This study provides much needed baseline data for *A. s. ammolegus*, a rarely studied subspecies of conservation concern. Information about traits such as *A. s. ammolegus* territory size, return rates, breeding phenology, clutch size, and nest parasitism is crucial to resource managers planning grassland bird conservation in desert grasslands. Information about life history traits that may be influenced by precipitation patterns, temperature, and extreme weather will be particularly valuable in developing predictions about how *A. s. ammolegus* populations could be affected by climate change. In addition morphometric measurements are frequently useful in distinguishing among subspecies (Pyle, 1997), and our results suggest this is the case for some morphometric traits in *A. s. ammolegus*. This new information will be useful for informing and directing future taxonomic and ecological studies of Grasshopper Sparrow.

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