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Authors: Titulaer, Mieke, Melgoza-Castillo, Alicia, Macías-Duarte, Alberto, and Panjabi, Arvind O.

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Seed size, bill morphology, and handling time influence preferences for native vs. nonnative grass seeds in three declining sparrows

Mieke Titulaer,[1,4]* Alicia Melgoza-Castillo,[1] Alberto Macías-Duarte,[2] and Arvind O. Panjabi[3]

ABSTRACT—The invasion of exotic grasses is a potential threat to the winter habitat of migratory grassland birds by reducing native sources of seed food. We compared seed preferences among 3 native (blue grama [*Bouteloua gracilis*], sideoats grama [*Bouteloua curtipendula*], and green sprangletop [*Leptochloa dubia*]), and 3 exotic (Lehmann lovegrass [*Eragrostis lehmanniana*], buffelgrass [*Pennisetum ciliare*], and natal grass [*Melinis repens*]) grass seeds in captive Baird's (*Ammodramus bairdii*), Grasshopper (*A. savannarum*), and Savannah (*Passerculus sandwichensis*) sparrows to investigate factors that determine vulnerability of grassland passerines to exotic grasses in the Chihuahuan Desert. We hypothesized that seed handling time would determine the ability of sparrows to exploit exotic grass seeds, and that larger-billed birds would be able to better exploit a larger variety of seeds, including exotic seeds. We offered seeds in choice and nonchoice trials and determined handling times for the different seed and bird species. The results indicate that handling time in relation to seed size determined seed preferences. Sparrows preferred seeds they could handle more efficiently to maximize energy intake over time. Baird's and Savannah sparrows, with intermediate and small bill sizes, respectively, preferred natal grass seeds of intermediate size and short handling time, and Grasshopper Sparrows, with the largest bill, preferred the larger sideoats grama seeds. Lehmann lovegrass, the smallest seed with intermediate handling time, was avoided by the 3 sparrows. Buffelgrass, the largest seed with the longest handling time, was avoided by Baird's and Savannah sparrows. Blue grama, the second-smallest seed with relative short handling time, was neither preferred nor avoided, and green sprangletop, an intermediate-sized seed with a relatively longer handling time, was avoided in the choice trials but consumed in the nonchoice trials. These results indicate that exotic grass seeds may be a source of food for 3 sparrows wintering in the Chihuahuan Desert, provided they can be handled efficiently. Our results also show, however, that wintering grassland sparrows are probably unable to consume sufficient buffelgrass and Lehmann lovegrass seeds to meet daily energy requirements, indicating that these grasses may be a threat by reducing exploitable sources of seed food. *Received 6 January 2017. Accepted 7 January 2018.*

Key words: *Ammodramus* spp., buffelgrass, food selection, handling efficiency, Lehmann lovegrass, natal grass, *Passerculus sandwichensis*.

Tamaño de semilla, morfologia del pico y tiempo de manipulación influyen sobre las preferencias de semillas de pastos nativos vs. exóticos en tres gorriones en declive

RESUMEN (Spanish)—La invasión de pastos exóticos es una amenaza potencial para el hábitat invernal de las aves de pastizal migratorias por la disminución en fuentes nativas de alimentación de semillas. Comparamos preferencias de semillas entre tres semillas nativas (navajita (*Bouteloua gracilis*), banderita (*Bouteloua curtipendula*) y gigante (*Leptochloa dubia*)) y tres semillas exóticas (africano (*Eragrostis lehmanniana*), buffel (*Pennisetum ciliare*) y rosado (*Melinis repens*)) en *Ammodramus bairdii*, *A. savannarum* y *Passerculus sandwichensis* en cautiverio para investigar factores que determinan la vulnerabilidad de los passerinos de pastizal a pastos exóticos en el Desierto Chihuahuense. Hipotetizamos que el tiempo de manipulación determinaría la habilidad de los gorriones para aprovechar semillas de pastos exóticos y que aves con picos más grandes podrían aprovechar mejor una mayor variedad de semillas, incluyendo semillas exóticas. Ofrecimos semillas en pruebas de opción simple y múltiple y determinamos el tiempo de manipulación para las diferentes semillas y especies de aves. Los resultados indican que el tiempo de manipulación en relación a tamaño de la semilla determina las preferencias de semilla. Los gorriones prefirieron semillas que pudieron manipular más eficientemente para maximizar el consumo de energía sobre el tiempo. *Ammodramus bairdii* y *P. sandwichensis*, con tamaño de pico intermedio y pequeño, respectivamente, prefirieron semillas de zacate rosado, de tamaño intermedio y tiempo de manipulación menor, y *A. savannarum*, con el pico más grande, prefirió las semillas más grandes de zacate banderita. El zacate africano, la semilla más pequeña y con tiempo de manipulación intermedio, fue evitado por los tres gorriones. El zacate buffel, la semilla más grande con el tiempo de manipulación mayor, fue evitado por *A. bairdii* y *P. sandwichensis*. El zacate navajita, la segunda semilla más pequeña con un tiempo de manipulación relativamente corto, no fue preferido ni evitado y el zacate gigante, una semilla de tamaño intermedio con un tiempo de manipulación relativamente mayor, fue evitado en las pruebas de opción múltiple pero consumido en las pruebas de opción simple. Estos resultados indican que las semillas de pastos exóticos pueden ser una fuente de alimento para tres gorriones invernales en el Desierto Chihuahuense, siempre que las semillas pueden ser manipuladas eficiente. Sin embargo, nuestros resultados también muestran que gorriones de pastizal invernales probablemente no pueden consumir suficiente semilla de zacate buffel y africano para satisfacer sus requisitos diarios de energía, lo que indica que estos pastos podrían ser una amenaza a través de la reducción de fuentes aprovechables de alimento de semillas.

Palabras clave: *Ammodramus* spp., eficiencia de manipulación, *Passerculus sandwichensis*, selección de alimento, zacate africano, zacate buffel, zacate rosado.

North American grassland birds are among the most threatened groups of birds worldwide (Brennan and Kuvlesky 2005) as a result of long-term habitat loss and alterations (Vickery et al. 1999, Askins et al. 2007). Most species of grassland birds are migratory and overwinter in the grasslands of northern Mexico (Macías-Duarte et

[1] Universidad Autónoma de Chihuahua, Chihuahua, Mexico
[2] Universidad Estatal de Sonora, Hermosillo, Sonora, Mexico
[3] Bird Conservancy of the Rockies, Fort Collins, CO, USA
[4] Current address: Borderlands Research Institute, Sul Ross State University, Alpine, TX, USA
* Corresponding author: mieke.titulaer@sulross.edu

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al. 2011). Reduction in suitable winter habitat is probably a key factor in grassland bird declines (Vickery and Herkert 2001, Pool et al. 2014). Main threats to grassland bird winter habitat include large-scale agricultural conversions (Pool et al. 2014), overgrazing (Curtin et al. 2002, Desmond et al. 2005), shrub encroachment (Desmond et al. 2005), invasion of exotic grass species (Van Devender et al. 2005, Ortega-S et al. 2013), and conversion to exurban developments (Bock et al. 2008).

Changes in vegetation characteristics due to invasive grass species negatively influence breeding grassland bird abundance (Flanders et al. 2006, George et al. 2013). Limited attention has been focused on the effects of exotic grass invasions on wintering grassland bird populations, but Bock et al. (1986) suggest that exotic grasslands are less suitable for grassland specialists during winter. Exotic grass invasions change structural characteristics of the vegetation and may reduce plant species richness and diversity (Steidl et al. 2013), which could lead to a reduction in food availability for seed-eating birds if birds prefer native seeds or if they are unable to use exotic grass seeds. The most widespread invasive grass species in the Chihuahuan Desert grasslands of northern Mexico are natal grass (*Melinis repens* [Willd.] Zizka), Lehmann lovegrass (*Eragrostis lehmanniana* Nees), and buffelgrass (*Pennisetum ciliare* [L.] Link) (Ortega-S et al. 2013). Natal grass and Lehmann lovegrass are aggressive competitors of native grasses that already dominate large areas of northern Mexican grasslands and continue to spread (Melgoza-Castillo and Morales-Nieto 2013, Melgoza-Castillo et al. 2014). Buffelgrass has been planted extensively in northern Mexico and southern USA to improve forage production of rangelands (Franklin et al. 2006) and remains popular among landowners because of its high forage quality and drought tolerance (Brenner 2010). However, buffelgrass may have similar negative effects on native vegetation characteristics (Sands et al. 2009) and bird communities (Flanders et al. 2006). The extent to which exotic grasses have invaded the Chihuahuan Desert has not yet been quantified; however, Sánchez-Muñoz (2009) found that in Chihuahua, Lehmann lovegrass expanded cover by 200% over a 20-year period, displacing 80% of native forbs and 50% of native grasses. Natal grass invasions are more recent, but this grass is estimated to represent 5–10% of the vegetation cover in the state of Chihuahua (Melgoza-Castillo et al. 2014).

Wintering grassland passerines, especially Emberizids, feed almost exclusively on seeds (Desmond et al. 2008); therefore, habitat quality for these seed-eating birds may be strongly influenced by the presence of seeds that can be profitably exploited (Pulliam 1986). Granivorous passerines are selective in their diet in that they do not consume seeds relative to their abundance (Pulliam 1985, Desmond et al. 2008). Seed selection may be influenced by handling time, which is a function of the relationship between seed size or form and bill characteristics (Willson 1971, Díaz 1996, Hrabar and Perrin 2002, Van der Meij et al. 2004). Additionally, seed selection may be influenced by seed nutritional value such as energy (Valera et al. 2005), protein (Johansen et al. 2014), fat (Thompson et al. 1987, Molokwu et al. 2011), carbohydrate (Ríos et al. 2012), water content (Carillo et al. 2007), or the presence of toxic components (Molokwu et al. 2011, Ríos et al. 2012).

Because invasive grass species tend to become dominant and reduce native plant species richness and diversity (Sands et al. 2009, Lyons et al. 2013), invasive grass species are a potential threat to granivorous grassland birds. Grassland bird abundance and species diversity was reduced at a winter habitat site in Arizona dominated by Lehmann lovegrass compared to a site where native grasses and Lehmann lovegrass were mixed (Méndez-González 2010), which could indicate that birds are not able to exploit Lehmann lovegrass seeds or, alternatively, may be explained by poor quality seeds. However, more detailed information on seed selection by wintering grassland birds in relation to invasive grasses is lacking.

The objective of this research was to investigate factors that determine the vulnerability of grassland birds to invasions of exotic grasses in the Chihuahuan Desert. We hypothesized that (1) seed preferences would be determined by seed handling time, regardless of the nature of the seeds (native or exotic), and (2) that differences in bill volume between bird species would result in different handling times for at least some seeds, and, consequently, in different seed preferences. In this regard, we investigated seed selection by Baird's

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(*Ammodramus bairdii*), Grasshopper (*A. savannarum*), and Savannah (*Passerculus sandwichensis*) sparrows comparing consumption of seeds from the 3 main invasive grass species in northern Mexico (natal grass, Lehmann lovegrass and buffelgrass) to consumption of seeds from 3 native grasses. Baird's and Grasshopper sparrows are grassland obligates (Vickery et al. 1999) that overwinter in northern Mexico (Panjabi et al. 2010). Savannah Sparrow has been listed as a grassland obligate (Vickery et al. 1999) as well as a grassland associate (Desmond et al. 2005) and a grassland generalist (Ruth et al. 2014) and often co-occurs with *Ammodramus* species during winter (Grzybowski 1983, Gordon 2000, Ruth et al. 2014). Widespread population declines have been documented for these 3 species over the last 45 years (Sauer et al. 2014). Because Baird's, Grasshopper, and Savannah sparrows overwinter in (semi-) open grasslands with tall, dense grass cover (Macías-Duarte et al. 2009), where they presumably feed almost exclusively on seeds, these species may be particularly vulnerable to invasions by exotic grasses. These 3 sparrows have similar body sizes but differ in bill morphology, which allows us to explore the role of bill morphology in seed selection, controlling for energetic needs (i.e., metabolic rate). As per our hypothesis, we predict that Grasshopper Sparrows, with the largest bill, will be able to better exploit a larger variety of seeds (including exotic seeds) than Savannah Sparrows, with the smallest bill.

Methods

Subjects and housing

We captured Baird's Sparrows (8 individuals), Grasshopper Sparrows (7 individuals), and Savannah Sparrows (8 individuals) using mist nets on 15–16 November 2013 at the Teseachi research ranch of the Autonomous University of Chihuahua, located in the municipality of Namiquipa, Chihuahua, Mexico (28°32′38″N, 107°26′45″W). We measured bill length (exposed culmen), width, and depth to the nearest 0.1 mm with a caliper and body mass to the nearest 0.1 g with a Jennings CJ-300 digital scale. We housed birds in indoor facilities on the ranch in individual $1 \times 0.5 \times 0.5$ m cages with 4 perches, a nest, and dried bean plant and grass (without seeds) as substrate. Vitamin-enriched water was provided ad libitum. Diet consisted of a mixture of the experimental seeds (specified later) supplemented with commercial seeds (canary grass and millet). The experimental birds were given a 3 to 4 d adaptation period to acclimate to captivity and the experimental seeds. We followed this procedure because the introduced seed species are not present at the ranch where the birds were captured, and birds might initially avoid them due to unfamiliarity. We provided commercial seeds only after a bird had sampled all the different experimental seeds.



Figure 1. Experimental seeds in order of seed mass (from left to right; from smallest to largest): Lehmann lovegrass (exotic), blue grama (native), green sprangletop (native), natal grass (exotic), sideoats grama (native), and buffelgrass (exotic).

Experimental seeds

The experimental seeds were collected throughout the state of Chihuahua in September and October 2013. We used blue grama (*Bouteloua gracilis* [Kunth] Lag. ex. Griffiths), sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), and green sprangletop (*Leptochloa dubia* [Kunth] Nees) as native seed species (Fig. 1). Blue grama and sideoats grama have been found to occur in Baird's, Grasshopper, and Savannah sparrow habitat in Chihuahua (Desmond et al. 2005). Green sprangletop seed is intermediate in size between blue and sideoats grama and is also present in the winter habitat of the birds, although less common. We used natal grass, Lehmann lovegrass, and buffelgrass as exotic seed species (Fig. 1) because they are the most widespread invasive grasses in northern Mexico. For both native and exotic seed species, we used a range of species that differed in seed mass; therefore, seed size and origin (i.e., native vs. exotic) were not related. Seed mass is correlated with seed energy content (Willson 1971); therefore, we determined seed to the nearest 0.01 mg for 50 seeds of each species to calculate average seed mass per species

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as an index of seed energy content. We offered unhusked seeds (Fig. 1) to the birds without removal of any seed structures as representative of how birds would encounter the seeds in the field.

Experimental procedure

The experiment was conducted from 19 to 27 November 2013. The evening before experimental days, we removed all seeds from the cages at sunset (~1730 h, UTC−7). We removed all spilled seeds from trays that were placed under the cages to leave no seeds available to the birds. At sunrise the next morning (~0700 h), we placed the experimental seeds in the cages. Birds were allowed 1 h to feed, after which we removed the experimental seeds. Feeders were 10 cm high with a diameter of 15 cm, which allowed birds to enter inside the feeder to minimize spillage. Spilled seeds were recovered from the trays after each trial. We then fed the birds with a mixture of the experimental seeds supplemented with commercial seeds until sunset, after which the same procedure was followed. We weighed seeds to the nearest 0.01 mg before and after the trial to determine the amount consumed.

Following recommendations by Cueto et al. (2001), we tested preferences in choice trials and nonchoice trials. In choice trials, we presented the 6 seed species simultaneously to the birds in individual feeders positioned in random order during day 1 to 3. Seed order presentation was randomized among birds and among days using random number tables to determine the order for each individual bird species for each day of the choice trials. During nonchoice trials (from day 4 to 9), only 1 of the 6 seed species was presented at a time. We assigned numbers from 1 to 6 to the seeds and then used random number tables to determine the order in which the seeds were offered to each individual bird. We imposed the restriction that each bird received all the different seed species, and each seed species was presented to at least one individual of every bird species on each day of the experiment. For example, if individual 1 received seed 4 on day 1 then the next day seed 4 was no longer an option, and if 2 individual birds of one species received seed 4 on day 1, then seed 4 is was no longer an option for any of the other individual birds of that species that day. We provided 2 g of each seed in choice trials and 4 g of each seed in nonchoice trials. These amounts were much higher than the birds consumed to avoid a preferred seed species being depleted, which would force the experimental birds to consume a less-preferred species in the choice trials. We filmed one bird of each species every day during both the adaptation and experimental phase, but not all recordings showed the bird husking and consuming the seeds. We first selected the parts of each recording in which we were able to identify seed consumption from the moment the seed was picked up to the moment the bird dropped the husk and consumed the seed. We then randomly selected a starting point and from there determined seed handling time for 40 seeds, the average maximum number of seeds represented by high quality recordings across the different seed and bird species. Savannah Sparrow handling times could not be estimated for buffelgrass and Lehmann lovegrass seeds, however, because these seeds were never visibly consumed during recording periods.

Statistical analysis

All statistical analyses were performed in R 3.3.1 (R Core Team 2016). To verify the assumption that the 3 bird species in the experiment differ in bill morphology but not in body size, we analyzed differences in bill volume ($l \times w \times h$) and body mass (as an indicator of body size) using multivariate analysis of variance (MANOVA) with bird species as a factor and bill volume and body mass as response variables, and Wilk's lambda as a test statistic. Differences among bird species were determined with a Tukey test. To test the assumption that differences in bill morphology lead to differences in handling time, we analyzed the handling times of 40 seeds per seed species and bird species using a linear mixed model from the *lme4* package (Bates et al. 2015) with bird species and seed species as fixed factors and individual bird as a random factor to control for the effect of multiple measurements on the same bird. The handling time (s) response variable was log-transformed to fulfil the model assumption of linearity. The model assumption of normal distribution of error was checked graphically and using a Shapiro-Wilk normality test on the residuals. The final model was selected by backward elimination of variables (Fox and

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Weisberg 2011). We calculated the 95% confidence intervals (CI) of the linear combinations of model estimates representing the comparisons between bird and seed species using the delta method from the *msm* package (Jackson 2011).

To assess seed preferences in the choice trials, we calculated Manly's selectivity index as described by Chesson (1983) for each seed species and individual bird. We used the equation that assumes no food depletion because we provided a sufficient amount of each seed species to prevent depletion of a preferred seed. Therefore, the preference index was calculated as:

$$\hat{\alpha}_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j}, i = 1, \ldots, m,$$

where $\hat{\alpha}_i$ is the estimated seed preference, r_i is the amount of seed type i that was consumed, and n_i the total amount of seed type i that was offered. This preference index ranges from 0 (seed type i is not consumed) to 1 (the diet consists entirely of seed i); its advantage is that it does not depend on food density (Chesson 1983).

Because the different seed species were offered simultaneously in the choice trials, they are not independent (Roa 1992). Therefore, following Cueto et al. (2013), we performed a 2-way ANOVA with repeated measures to analyse differences in Manly's selectivity index for factors seed species and bird species and their interaction using the *car* package (Fox and Weisberg 2011). We used the Greenhouse-Geisser corrected test to adjust the degrees of freedom for the averaged tests of significance when symmetry assumptions were violated. We then used a post hoc test with Bonferroni correction for multiple comparisons to test whether the preference index of each seed species was significantly different from 0.167, the value of $\hat{\alpha}_i$ attained when the birds would be completely unselective. Rejection of the null hypothesis H_0: $\alpha_i = 0$ indicates that a seed is either preferred or rejected.

We also used a 2-way ANOVA with repeated measures to analyse differences in the amount consumed in the nonchoice trials because each seed species was tested with the same individual bird and therefore constitutes a repeated measure. In the nonchoice trials the response variable was amount consumed instead of Manly's selectivity index because here we offered only one seed at a time, and therefore the diet would always consist entirely of seed species i. In addition, the nonchoice trials were performed to determine whether the 3 bird species are able to consume the different seeds and not to determine preferences. We performed pairwise comparisons with the Bonferroni correction method to determine which seeds were consumed significantly differently by each bird species.

In addition to the statistical analysis, we used a graphical approach suggested by Cueto et al. (2001) to integrate the results of the choice and nonchoice trials. For each bird species, we constructed a 2-dimensional scatterplot in which the average percentage of each seed consumed in the nonchoice trials is depicted on the x-axis and in the choice trials on the y-axis. In this plot, preference is indicated by a high percentage of consumption in both choice and nonchoice trials, and avoidance is indicated by a low percentage of consumption in both types of trials. Seeds with a high consumption in nonchoice trials but low consumption in choice trials are less-preferred seeds.

Ethical note

The experiments were approved by SEMARNAT (the Mexican ministry of environment and natural resources, permit number SGPA/DGVS/09559/13). Cages were adjusted as much as possible to the needs of the birds. We measured fat score on a scale from 0 (no fat) to 5 (bulging) as an indication of body condition. At the end of the experiment we repeated the measurement of weight and fat score to compare body condition before and after the experiment. Of the 22 birds, 15 increased their body weight and fat score during their time in captivity, 4 remained the same, and 3 lost weight. There was no pattern among species. On 27 November 2013 we released the birds in the same location where they were caught.

Results

The overall effect of bird species on a combination of bill and body measurements was significant (MANOVA: $F_{4,40} = 49.69$, $P < 0.001$), indicating that bird species differed in the overall measurement of body size. Between-subject tests

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Table 1. Body mass and bill measurements of grasshopper (GRSP; $n = 7$), Baird's (BAIS; $n = 8$) and Savannah (SAVS; $n = 7$) sparrows: mean (SD). Letters indicate significant differences at $P < 0.05$ (Tukey test).

Bird species	Body mass (g)	Bill length (mm)	Bill width (mm)	Bill depth (mm)	Bill volume (mm^3)
GRSP	16.6 (1.0) a	10.6 (0.4) a	5.8 (0.4) a	6.0 (0.3) a	368.1 (35.9) a
BAIS	17.5 (1.2) a	10.2 (0.3) b	5.8 (0.2) a	5.6 (0.1) b	327.6 (16.1) b
SAVS	16.5 (1.7) a	10.0 (0.2) b	5.1 (0.2) b	5.0 (0.3) c	252.2 (20.3) c

showed that bird species differed significantly in bill volume ($F_{2,21} = 49.69$, $P < 0.001$) but not in body mass ($F_{2,21} = 1.53$, $P = 0.24$), the latter an indicator of body size (Table 1). Grasshopper Sparrow had the largest bill volume, followed by Baird's Sparrow, and finally Savannah Sparrow (Table 1). Handling time (Fig. 2) was best explained by the model with the interaction between bird species and seed species (likelihood-ratio test: $\chi^2 = 25.94$, df = 8, $P = 0.001$). The 95% CIs (Fig. 2) indicate that Grasshopper Sparrow had a shorter handling time for natal grass compared to Lehmann lovegrass, green sprangletop, and buffelgrass and a longer handling time for buffelgrass compared to all other seeds except green sprangletop. Baird's Sparrow and Savannah Sparrow had a shorter handling time for natal grass compared to all other seeds, and Savannah Sparrow had a longer handling time for sideoats grama compared to the other seeds (Fig. 2).

The interaction between seed species and bird species was significant in the choice trials (repeated measures ANOVA: $F_{5,317} = 8.437$, $P < 0.001$), indicating that the preference index differed among bird species for at least one of the seed species (Fig. 3). For all bird species in the experiment, Manly's selectivity index was significantly different from 0.167 for natal grass, Lehmann lovegrass, green sprangletop, and buffelgrass ($P < 0.05$ for all Bonferroni's tests of differences between cell means). Whereas natal

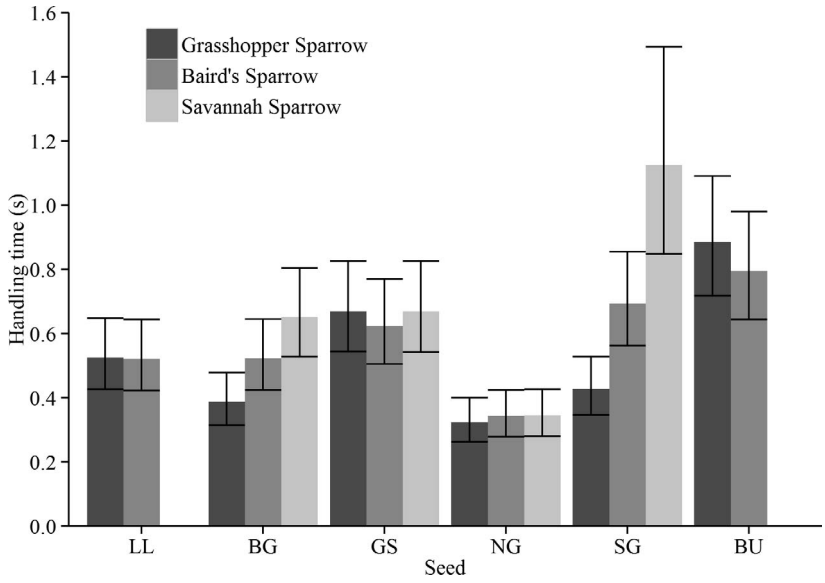


Figure 2. Handling time (s) for the different seed species ($n = 40$ seeds per species), separated by bird species. Data are back-transformed means ± 95% confidence intervals from a random-effects ANOVA with log-transformed response. Seeds are positioned in order of seed mass (from left to right; from smallest to largest): LL = Lehmann lovegrass (0.12 ± 0.03 mg), BG = blue grama (0.32 ± 0.06 mg), GS = green sprangletop (0.60 ± 0.08 mg), NG = natal grass (0.65 ± 0.11 mg), SG = sideoats grama (2.44 ± 0.80), BU = buffelgrass (2.88 ± 0.90). Savannah Sparrow never consumed Lehmann lovegrass and buffelgrass in our video recordings.

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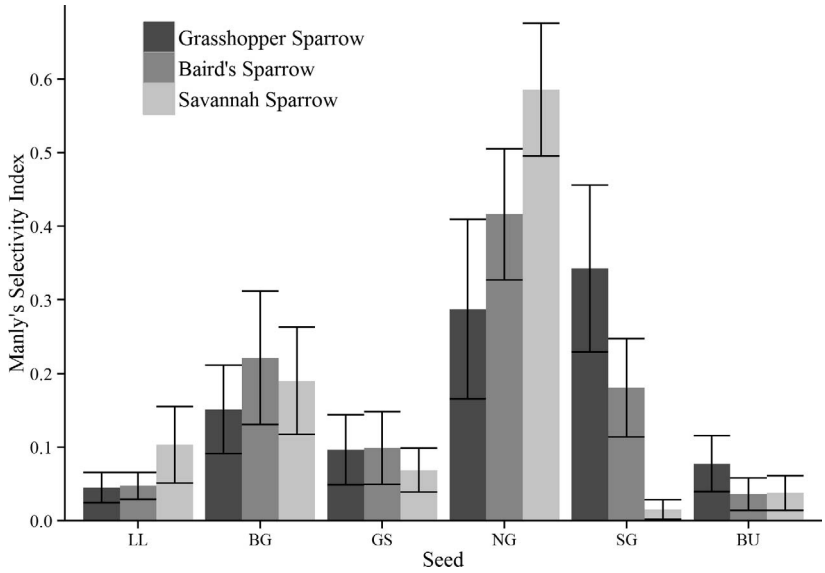


Figure 3. Average value of Manly's selectivity index (Chesson 1983) and 95% confidence intervals based on the amount consumed of each seed species by Grasshopper Sparrow ($n = 7$), Baird's Sparrow ($n = 8$), and Savannah Sparrow ($n = 7$) in the choice trials (6 seed species offered simultaneously). Seeds are positioned in order of seed mass (from left to right, from smallest to largest): LL = Lehmann lovegrass (exotic), BG = blue grama (native), GS = green sprangletop (native), NG = natal grass (exotic), SG = sideoats grama (native), BU = buffelgrass (exotic).

grass was preferred by Baird's, Grasshopper, and Savannah sparrows, the other 3 seeds were avoided (Fig. 3). For Grasshopper and Savannah sparrows, Manly's selectivity index was also significantly different from 0.167 for sideoats grama ($P < 0.05$ for all Bonferroni's tests of differences between cell means). Whereas sideoats grama seeds were preferred by Grasshopper Sparrows, they were avoided by Savannah Sparrows (Fig. 3).

The interaction between seed species and bird species was significant in the nonchoice trials (repeated measures ANOVA: $F_{6,737} = 3.239$, $P = 0.006$), indicating that the amount consumed differed among bird species for at least one of the seed species (Fig. 4). Baird's Sparrows consumed significantly less Lehmann lovegrass and buffelgrass than blue grama, sideoats grama, and natal grass ($P < 0.05$ for all Bonferroni's tests of differences between cell means; Fig. 4). Grasshopper Sparrows consumed significantly less Lehmann lovegrass than all other seeds and significantly less buffelgrass compared to sideoats grama ($P < 0.05$ for all Bonferroni's tests of differences between cell means; Fig. 4). Savannah Sparrows consumed significantly less Lehmann lovegrass and buffelgrass than blue grama, green sprangletop, and natal grass ($P < 0.05$ for all Bonferroni's tests of differences between cell means; Fig. 4).

The graphical approach, as suggested by Cueto et al. (2001), shows a clear preference gradient (Fig. 5) from relatively fewer seeds consumed in both choice and nonchoice trials (avoided seeds) toward relatively more seeds consumed in both trials (preferred seeds), with an intermediate of relatively more seeds consumed in the nonchoice trials (i.e., when birds have no other option) than in the choice trials (less-preferred seeds). Because we offered more seeds than birds could consume to avoid depletion, birds never consumed 100% of a seed species. The graphical approach shows that Grasshopper, Baird's, and Savannah sparrows avoided Lehmann lovegrass, and Baird's and Savannah sparrows also avoided buffelgrass, which is consistent with the results of the statistical analysis. Baird's and Savannah sparrows had a clear preference for natal grass, whereas Grasshopper Sparrow's first preference was for sideoats grama with a second preference for natal grass, although the latter is less clear than in the statistical approach.

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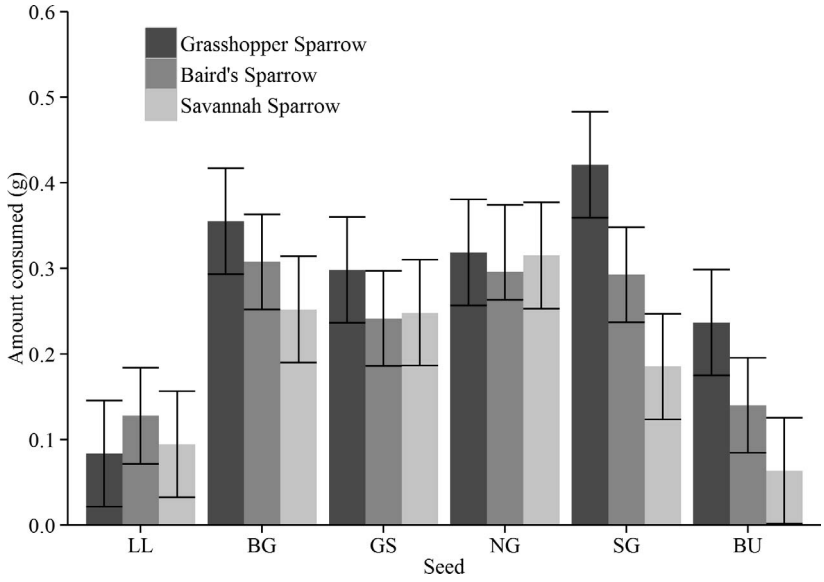


Figure 4. Amount consumed (g) by Grasshopper Sparrow ($n = 7$), Baird's Sparrow ($n = 8$), and Savannah Sparrow ($n = 7$) in the nonchoice trials in which one seed was offered per trial. Data are means ± 95% confidence intervals. Seeds are positioned in order of seed mass (from left to right; from smallest to largest): LL = Lehmann lovegrass (exotic), BG = blue grama (native), GS = green sprangletop (native), NG = natal grass (exotic), SG = sideoats grama (native), BU = buffelgrass (exotic).

Discussion

We found that seeds of exotic grasses may be a source of food for 3 sparrows wintering in the Chihuahuan Desert, provided their size is adequate for birds' bill morphology and energy requirements (i.e., neither too large to be handled nor too small to provide sufficient energy intake over time). The 3 sparrow species did not differ in body size, and therefore we can fairly assume that their energy requirements are comparable. Preferences differed among bird species, however, in agreement with the expectations based on bill volume and handling time. An efficient handling time means that seed size is large compared to seed handling time, resulting in maximization of energy

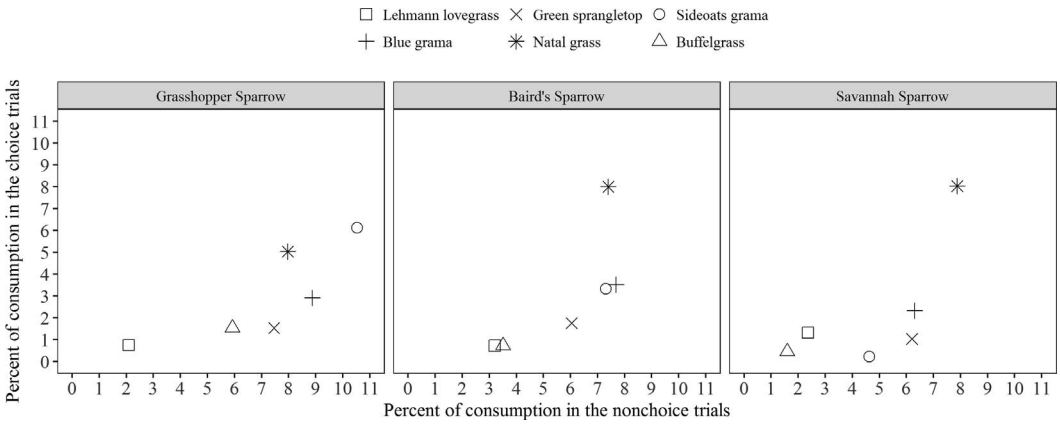


Figure 5. Scatter plots of the average percentage of each seed consumed in the choice and nonchoice trials by Grasshopper Sparrow ($n = 7$), Baird's Sparrow ($n = 8$), and Savannah Sparrow ($n = 7$).

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intake over time (Charnov 1976, Benkman and Pulliam 1988). The 3 sparrows in this experiment preferred seeds they could handle more efficiently; Grasshopper Sparrows, with the largest bill, preferred the larger sideoats grama seeds, with a second preference for natal grass seeds, whereas Baird's and Savannah sparrows preferred the intermediate-sized natal grass seeds over all other seeds. When the 3 sparrows had no other choice, they consumed most of the seeds, but Lehmann lovegrass seeds were avoided by all, and buffelgrass seeds were avoided by Baird's and Savannah sparrows.

Overall, handling times increased with seed size for all bird species, but more so for Savannah Sparrow, the species with the smallest bill. Natal grass was an exception, however. Although this seed is larger than 3 of the other seeds, seed handling time of natal grass was shorter, indicating that natal grass seeds can be handled more efficiently, resulting in a higher energy intake over time. The husk of natal grass seeds is soft and, although they seem to have awns like buffelgrass, the awns are in fact soft hair-like structures, characteristics that likely explain the short handling times. The short handling time may explain preferences for natal grass seeds observed in all birds and suggests that seed selection in grassland passerines is a tradeoff between handling time and energy intake (seed size), which is consistent with predictions from optimal foraging theory (Charnov 1976). Alternatively, birds could simply be choosing seeds with the shortest handling time rather than maximizing energy intake over time (Thompson et al. 1987, Keating et al. 1992). The preference of Grasshopper Sparrows for sideoats grama contradicts the latter explanation, however, because sideoats grama seeds had a longer handling time than some other seeds tested. In addition to handling time, other seed characteristics such as nutrient content could be influencing seed preferences (Molokwu et al. 2011, Ríos et al. 2012); however, nutrient content is generally of secondary importance (Díaz 1996), and the nutrient content of the seeds in our study is unknown.

Seeds from invasive grasses are not necessarily unsuitable for the diets of granivorous birds (Larson et al. 2012), evidenced by the preference for natal grass seeds in this study. The ability of birds to exploit exotic grass seeds could be related to birds being specialists or generalists (Camín et al. 2015). In nature, Savannah Sparrows are able to exploit a wider range of habitat types, whereas *Ammodramus* spp. are restricted to native, intact grasslands on the wintering grounds (Desmond et al. 2005, Macías-Duarte et al. 2009). In the choice trials, Savannah Sparrows mainly consumed natal grass seeds, whereas the other 2 bird species had a more variable diet. This finding might suggest that Savannah Sparrow, sometimes classified as a generalist (Ruth et al. 2014), is better able to rely on a single food source, one that is easily exploitable, whereas the other species require a more diverse array of seeds. Possibly, Savannah Sparrow relies less on native seed sources than the 2 *Ammodramus* spp.; however, both Baird's and Grasshopper sparrows are seemingly able to exploit natal grass seeds in captivity, although field data are lacking. Although natal grass seeds may actually be a preferred food source for winter birds, other habitat characteristics of invaded grasslands might make them unsuitable, such as a lack of plant species diversity or a lack of native plant species, such as suitable near-ground vegetation structure or shrub cover (Flanders et al. 2006, Saalfeld et al. 2016).

Only Grasshopper Sparrows exploited buffelgrass seeds. Buffelgrass seeds were the largest seeds in this study, and they have a husk with large, difficult to manipulate awns. Few grassland passerine species may be able to meet their energy requirements by eating these seeds because of their large size and awns, resulting in a long handling time. By contrast, Lehmann lovegrass seeds are so small that birds consuming these seeds may not be able to meet their energy requirements, at least for the range of bill sizes tested in this study. In this regard, some studies indicate that smaller-billed birds are more efficient at manipulating smaller seeds, whereas larger-billed birds are more efficient at handling larger seeds (Benkman and Pulliam 1988; Díaz 1990, 1994; Soobramoney and Perrin 2007). Our results for Lehmann lovegrass seem to be partly consistent with this hypothesis in that Savannah Sparrow, with the smallest bill, consumed more Lehmann lovegrass than the other 2 sparrows in the choice trials, but this was not true for the nonchoice trials. Chipping Sparrows (*Spizella passerina*) have been found to consume Lehmann lovegrass seeds in the field, although it may not be their preferred seed

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(Pulliam 1986, Méndez-González 2010). Chipping Sparrows have smaller bills and therefore may be able to manipulate small seeds more efficiently than the larger-billed birds in this study.

Thus, the invasion of buffelgrass and Lehmann lovegrass may pose an important threat to granivorous grassland birds because they are probably not able to consume sufficient buffelgrass and Lehmann lovegrass seeds to meet their daily energy requirements. Exotic grasses often form monocultures, replacing native grasses and reducing native food sources, which may be detrimental to wintering grassland birds (Saalfeld et al. 2016). A loss of grass species diversity associated with exotics decreases the range of seed species available to birds, limiting the possibility for seed selection based on handling time and reducing the variability of the diet. Furthermore, the structural vegetation changes associated with buffelgrass and Lehmann lovegrass may also affect birds negatively (Bock et al. 1986). Our results suggest that the carrying capacity of grasslands invaded by buffelgrass and Lehmann lovegrass is reduced for wintering bird populations because they feed almost exclusively on seeds, and therefore highlight the importance of discouraging planting of exotic grasses and actively managing their spread.

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Literature cited

Askins RA, Chavez-Ramirez F, Dale BC, Haas CA, Herkert JR, et al. 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. Ornithological Monographs. 64:1–46.

Bates D, Maechler M, Bolker B, Walker S. 2014. Lme4: linear mixed-effects models using eigen and S4. R package. Version 1.1-7; [accessed 20 Sep 2016]. http://CRAN.R-project.org/package=lme4

Benkman CW, Pulliam HR. 1988. The comparative feeding rates of North American sparrows and finches. Ecology. 69:1195–1199.

Bock CE, Bock JH, Jepson KL, Ortega JC. 1986. Ecological effects of planting African love-grasses in Arizona. National Geographic Research. 2:456–463.

Bock CE, Jones ZF, Bock JH. 2008. The oasis effect: response of birds to exurban development in a southwestern savanna. Ecological Applications. 18:1093–1106.

Brennan LA, Kuvlesky WP. 2005. North American grassland birds: an unfolding conservation crisis? Journal of Wildlife Management. 69:1–13.

Brenner JC. 2010. What drives the conversion of native rangeland to buffelgrass (*Pennisetum ciliare*) pasture in Mexico's Sonoran desert?: the social dimensions of a biological invasion. Human Ecology. 38:495–505.

Camín SR, Cueto VR, Lopez de Casenave J, Marone L. 2015. Exploring food preferences and the limits of feeding flexibility of seed-eating desert birds. Emu. 115:261–269.

Carillo CM, Moreno E, Valera F, Barbosa A. 2007. Seed selection by the trumpeter finch, *Bucanetes githagineus*. What currency does this arid-land species value? Annales Zoologici Fennici. 44:377–386.

Charnov EL. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology. 9:129–136.

Chesson J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology. 64:1297–1304.

Cueto VR, Marone L, Lopez de Casenave J. 2001. Seed preferences by birds: effects of the design of feeding-preference experiments. Journal of Avian Biology. 32:275–278.

Cueto VR, Milesi FA, Marone L. 2013. Litter and seed burying alter food availability and foraging efficiency of granivorous birds in the Monte desert. Journal of Avian Biology. 44:339–346.

Curtin CG, Sayre NF, Lane BD. 2002. Transformation of the Chihuahuan borderlands: grazing, fragmentation, and biodiversity conservation in desert grasslands. Environmental Science & Policy. 5:55–68.

Desmond MJ, Méndez-González C, Abbott LB. 2008. Winter diets and seed selection of granivorous birds in southwestern New Mexico. Studies in Avian Biology. 37:101–112.

Desmond MJ, Young KE, Thompson BC, Valez R, Lafón Terrazas A. 2005. Habitat associations and conservation of grassland birds in the Chihuahuan Desert region: two case studies in Chihuahua. In: Cartron JE, Ceballos G, Felger RS, editors. Biodiversity, ecosystems and conservation in Northern Mexico. New York (NY): Oxford University Press; p. 439–451.

Díaz M. 1990. Interspecific patterns of seed selection among granivorous passerines: effects of seed size, seed nutritive value and bird morphology. Ibis. 132:467–476.

Díaz M. 1994. Variability in seed size selection by granivorous passerines: effects of bird size, bird size variability, and ecological plasticity. Oecologia. 99:1–6.

Díaz M. 1996. Food choice by seed-eating birds in relation to seed chemistry. Comparative Biochemistry and Physiology. 113A:239–246.

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Flanders AA, Kuvlesky WP Jr, Ruthven DC III, Zaiglin RE, Bingham RL, et al. 2006. Effects of invasive exotic grasses on south Texas rangeland breeding birds. Auk. 123:171–182.

Fox J, Weisberg S. 2011. An R companion to applied regression. 2nd edition. Thousand Oaks (CA): Sage.

Franklin, KA, Lyons K, Nagler PL, Lampkin D, Glenn EP, et al. 2006. Buffelgrass (*Pennisetum ciliare*) land conversion and productivity in the plains of Sonora, Mexico. Biological Conservation. 127:62–71.

George AD, O'Connell TJ, Hickman KR, Leslie DM Jr. 2013. Food availability in exotic grasslands: a potential mechanism for depauperate breeding assemblages. Wilson Journal of Ornithology. 125:526–533.

Gordon CE. 2000. Movement patterns of wintering grassland sparrows in Arizona. Auk. 117:148–159.

Grzybowski JA. 1983. Sociality of grassland birds during winter. Behavioral Ecology and Sociobiology. 13:211–219.

Hrabar HDK, Perrin MR. 2002. The effect of bill structure on seed selection by granivorous birds. African Zoology. 37:67–80.

Jackson CH. 2011. Multi-state models for panel data: the msm package for R. Journal of Statistical Software. 38:1–29.

Johansen SM, Horn DJ, Wilcoxen TE. 2014. Factors influencing seed species selection by wild birds at feeders. Wilson Journal of Ornithology. 126:374–381.

Keating JF, Robel RJ, Adams AW, Behnke KC, Kemp KE. 1992. Role of handling time in selection of extruded food morsels by two granivorous bird species. Auk. 109:863–868.

Larson JA, Fulbright TE, Brennan LA, Hernández F, Bryant FC. 2012. Selection of seeds of an exotic and three native grasses by Northern Bobwhites (*Colinus virginianus*). Southwestern Naturalist. 57:319–322.

Lyons KG, Maldonado-Leal BG, Owen G. 2013. Community and ecosystem effects of buffelgrass (*Pennisetum ciliare*) and nitrogen deposition in the Sonoran Desert. Invasive Plant Science and Management. 6:65–78.

Macías-Duarte A, Montoya AB, Méndez CG, Rodríguez-Salazar JR, Hunt G, Krannitz P. 2009. Factors influencing habitat use by migratory grassland birds in the State of Chihuahua, Mexico. Auk. 126:896–905.

Macías-Duarte A, Panjabi AO, Pool D, Youngberg E, Levandoski G. 2011. Wintering grassland bird density in Chihuahuan Desert grassland priority conservation areas, 2007–2011. Brighton (CO): Bird Conservancy of the Rockies, Technical Report I-NEOTROP-MXPLAT-10-2.

Melgoza-Castillo A, Balandrán-Valladares, Mata-González R, Pinedo-Álvarez C. 2014. Biology of natal grass *Melinis repens* (Willd.) and implications for its use or control. Review. Revista Mexicana de Ciencias Pecuarias. 5:429–442.

Melgoza-Castillo A, Morales-Nieto C. 2013. Lehmann lovegrass *Eragrostis lehmanniana* Nees. In: Quero Carillo AR, editor. Introduced grasses. Importance and impact in livestock ecosystems. Texcoco (Mexico): Colegio de Posgraduados; p. 53–60.

Méndez-González CE. 2010. Influence of seed resources on the diet, seed selection, and community dynamics of wintering birds in semi-arid grasslands [dissertation]. Las Cruces: New Mexico State University.

Molokwu MN, Nilsson JA, Olsson O. 2011. Diet selection in birds: trade-off between energetic content and digestibility of seeds. Behavioral Ecology. 22:639–647.

Ortega-S JA, Ibarra-Flores FA, Melgoza A, Gonzalez-Valenzuela EA, Martin-Rivera MH, et al. 2013. Exotic grasses and wildlife in northern Mexico. Wildlife Society Bulletin. 37:537–545.

Panjabi AO, Youngberg E, Levandoski G. 2010. Wintering grassland bird density in Chihuahuan Desert Grassland Priority Conservation Areas, 2007–2010. Brighton (CO): Bird Conservancy of the Rockies, Technical Report I-MXPLAT-08-03.

Pool DB, Panjabi AO, Macías-Duarte A, Soljhem DM. 2014. Rapid expansion of croplands in Chihuahua, Mexico threatens declining North American grassland bird species. Biological Conservation. 170:274–281.

Pulliam HR. 1985. Foraging efficiency, resource partitioning, and the coexistence of sparrow species. Ecology. 66:1829–1836.

Pulliam HR. 1986. Niche expansion and contraction in a variable environment. American Zoologist. 26:71–79.

R Core Team. 2016. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Ríos JM, Mangione A, Marone L. 2012. Effects of nutritional and anti-nutritional properties of seeds on the feeding ecology of seed-eating birds of the Monte Desert, Argentina. Condor. 114:44–55.

Roa R. 1992. Design and analysis of multiple-choice feeding-preference experiments. Oecologia. 89:509–515.

Ruth JM, Stanly TR, Gordon CE. 2014. Associations of wintering birds with habitat in semidesert and plains grasslands in Arizona. Southwestern Naturalist. 59:199–211.

Saalfeld DT, Saalfeld ST, Conway WC, Hartke KM. 2016. Wintering grassland bird responses to vegetation structure, exotic invasive plant composition, and disturbance regime in coastal prairies of Texas. Wilson Journal of Ornithology. 128:290–305.

Sanchez-Muñoz A. 2009. Invasive Lehmann lovegrass (*Eragrostis lehmanniana*) in Chihuahua, Mexico: consequences of invasion [dissertation]. Stillwater: Oklahoma State University.

Sands JP, Brennan LA, Hernández F, Kuvlesky WP Jr, Gallagher JP, et al. 2009. Impacts of buffelgrass (*Pennisetum ciliare*) on a forb community in south Texas. Invasive Plant Science and Management. 2:130–140.

Sauer JR, Hines JE, Fallon JE, Pardieck KL, Ziolkowski DJ Jr, Link WA. 2014. The North American Breeding Bird Survey, results and analysis 1966–2013. Version 01.30.2015. Laurel (MD): USGS, Patuxent Wildlife Research Center; [accessed 8 February 2016]. http://www.mbr-pwrc.usgs.gov/bbs/bbs.html

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Soobramoney S, Perrin MR. 2007. The effect of bill structure on seed selection and handling ability of five species of granivorous birds. Emu. 107:169–176.

Steidl RJ, Litt AR, Matter WJ. 2013. Effects of plant invasions on wildlife in desert grasslands. Wildlife Society Bulletin. 37:527–536.

Thompson DB, Tomback DF, Cunningham MA, Baker MC. 1987. Seed selection by Dark-Eyed Juncos (*Junco hyemalis*): optimal foraging with nutrient constraints? Oecologia. 74:106–111.

Valera F, Wagner RH, Romero-Pujante M, Gutiérrez JE, Rey PJ. 2005. Dietary specialization on high protein seeds by adult and nestling serins. Condor. 107:29–40.

Van der Meij MAA, Griekspoor M, Bout RG. 2004. The effect of seed hardness on husking time in finches. Animal Biology. 54:195–205.

Van Devender TR, Reeder JR, Reeder CG, Reina AL. 2005. Distribution and diversity of grasses in the Yécora region of the Sierra Madre Occidental of eastern Sonora, Mexico. In: Cartron JE, Ceballos G, Felger RS, editors. Biodiversity, ecosystems and conservation in Northern Mexico. New York (NY): Oxford University Press; p. 107–121.

Vickery PD, Herkert JR. 2001. Recent advances in grassland bird research: where do we go from here? Auk. 118:11–15.

Vickery PD, Tubaro PL, Cardoso da Silva JM, Peterjohn BG, Herkert JR, Cavalcanti RB. 1999. Conservation of grassland birds in the western hemisphere. Studies in Avian Biology. 19:2–16.

Willson MF. 1971. Seed selection in some North American finches. Condor. 73:415–429.

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