Plant invasions alter settlement patterns of breeding grassland birds

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Citation: Andersen, E. M., and R. J. Steidl. 2020. Plant invasions alter settlement patterns of breeding grassland birds. Ecosphere 11(1):e03012. 10.1002/ecs2.3012

Abstract. Animals have evolved strategies to identify areas that provide the resources and environmental conditions they need to survive and reproduce. To explore how invasions by nonnative plants might disrupt this fundamental process, we evaluated settlement patterns of migratory birds that breed in grasslands being invaded by two structurally different congeneric grasses. We established 40, 2.25-ha plots across an area where the composition of each nonnative grass ranged from 0% to nearly 100% of total grass cover, which provided individuals with the full range of alternatives in species composition. We then used the temporal sequence by which birds established territories to infer their habitat preferences. We evaluated responses of the most common species that settled the area, two confamilial sparrows that differed markedly in habitat breadth. The species with narrower habitat breadth, the grasshopper sparrow (Ammodramus savannarum ammolegus), first established territories in areas dominated by native grasses, where grass height and cover were substantially lower than in areas dominated by the nonnative grasses. As the settlement period progressed, they increasingly established territories in areas dominated by the smaller nonnative grass (Eragrostis lehmanniana), but never established territories in areas dominated by the larger grass (E. curvula). In contrast, the species with broader habitat breadth, the Botteri’s sparrow (Pezuca botterii arizonae), established territories without regard to grass composition, likely because both nonnative grasses were within the structural range of native grasses used by this grassland generalist. Our results demonstrate that in areas invaded by nonnative plants, changes in habitat use by animals can reflect the interaction between their habitat breadth and the amount of structural contrast between invading plants and the native plant species that are displaced. This interaction provides a mechanism to explain the variation in responses among species to invasions by nonnative plants, which has consequences for broad-scale changes in the geographic distribution of many species.

Key words: arrival date; exotic species; grasslands; habitat preferences; habitat selection; nonnative grasses.

Received 22 June 2019; revised 1 October 2019; accepted 20 November 2019. Corresponding Editor: W. Alice Boyle.
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INTRODUCTION

Habitat selection by animals involves both innate and learned behaviors that enable individuals to identify areas that provide the resources and environmental conditions they need to survive and reproduce (Block and Brennan 1993, Jones 2001). Selective pressure for these behaviors should be strong because habitat resources can affect fitness (Cody 1985, Komdeur 1992). Consequently, spatial heterogeneity and temporal heterogeneity in resources and environmental conditions play an important role in governing the distribution of animals on the landscape (Hutto 1985, Block and Brennan 1993) and provide the theoretical basis for habitat-selection models that link fitness to habitat quality (Fretwell and Lucas 1969, Johnson 2007).

In seasonal environments, breeding animals often select habitat before all of the resources
they require are available; therefore, they rely on proximate cues that have been linked to key resources over evolutionary time (Storch and Frynta 1999, Battin 2004, Chalfoun and Martin 2007). For example, some migratory birds use foliage density as an indicator of the future abundance of caterpillars, a prey item important to successful breeding (Marshall and Cooper 2004). When an area is invaded by a nonnative plant, plant-based cues that indicate habitat (Smith and Shugart 1987, Orians and Wittenberger 1991) might be eliminated, resulting in the area no longer being recognized as habitat. Alternatively, if nonnative plants are structurally similar to the native species they displace, they might provide similar habitat cues, resulting in the area continuing to be recognized as habitat. If these invaded areas do not provide the same levels of resources as uninvaded areas, however, the cues that animals use to gauge habitat quality might be disconnected from true quality (Robertson and Hutto 2006). For example, reproductive success can differ markedly for birds breeding in areas invaded by nonnative plants relative to uninvaded areas because of differences in predation rates (Remes 2003, Ruehmann et al. 2011) or food availability (Lloyd and Martin 2005, Ortega et al. 2006, Andrew et al. 2013). Although negative effects of nonnative plant invasions on demography of animal populations are well documented (Vilà et al. 2011, Pyšek et al. 2012, Simberloff et al. 2013), examples of positive and neutral effects also are common, suggesting that nonnative plants can sometimes function similarly to the native species they displace (Schlaepfer et al. 2011, Vilà et al. 2011, Nelson et al. 2017).

Variability in demographic responses to plant invasions might be attributable to differences in how animal species perceive the suitability and quality of areas invaded by nonnative plants, but few studies have sought to understand how invasions influence the process through which animals select habitat. Individuals of territorial species that breed in areas dominated by nonnative plants might select those areas (1) preferentially from all possible alternatives or (2) only after areas dominated by native plants have been occupied by conspecifics that prevent access to preferred sites, a process labeled relegation (Sergio and Newton 2003, Sergio et al. 2007). The mechanism for relegation could be either behavioral dominance (e.g., ideal-despotic model, Fretwell 1972) or earlier arrival on breeding grounds (e.g., ideal-preemptive or site-dependence models, Pulliam and Danielson 1991, Rodenhouse et al. 1997, McPeek et al. 2001). The distinction between preference and relegation can have important implications for population persistence. For example, areas that animals select preferentially but where fitness is low can function as ecological traps and increase the risk of local extinction in small populations (Delibes et al. 2001, Kristan 2003, Hale et al. 2015).

Settlement patterns—the temporal and spatial establishment of territories—express the result of the habitat-selection process by a collection of individuals and provide insight into habitat preferences (Robertson and Hutto 2006). Migratory species are expected to settle areas in a sequence that reflects variation in habitat quality, from highest to lowest (Fretwell and Lucas 1969, Kokko 1999, Johnson 2007), an expectation that has been confirmed repeatedly (Lanyon and Thompson 1986, Marra and Holmes 2001, Smith and Moore 2005, Gunnarsson et al. 2006, Sergio et al. 2007, Injaian et al. 2018). Therefore, the sequence in which breeding animals establish territories along a plant-invasion gradient can provide insight into how they perceive the quality of areas invaded by evolutionarily novel plants (Remes 2003, Lloyd and Martin 2005). Although challenging in natural settings, settlement patterns can demonstrate preferences in plant community composition when invaded and non-invaded areas exist at scales where animals can acquire complete knowledge of their availability (Robertson and Hutto 2006). For example, if animals recognize invaded areas as high-quality habitat, then invaded areas will be preferred and should be settled first; in contrast, if animals recognize invaded areas as low-quality habitat, then invaded areas will be settled later by individuals that were relegated to those areas after preferred areas were occupied by conspecifics.

To evaluate how plant invasions can influence habitat selection by animals, we studied settlement patterns of migratory birds that breed in arid grasslands that are being invaded by nonnative grasses. Grassland birds provide useful models for studying the influence of plant invasions on settlement patterns because resource
heterogeneity in grasslands is high, driven by high spatial and temporal variation in precipitation and disturbances, such as fire and grazing (McClaran 1995, Fuhlendorf et al. 2010). In response to this heterogeneity, many species of grassland birds are locally nomadic and select different breeding sites each year or with each nesting attempt in a breeding season, reducing the influence of site fidelity on settlement patterns (Ahlering et al. 2009, Dornak et al. 2013, Williams and Boyle 2017). We focus on the two most common migratory sparrows (Passerellidae) that nest sympatrically in semiarid grasslands of southeastern Arizona, USA, Botteri’s sparrow (Peucaea botterii arizonae) and grasshopper sparrow (Ammodramus savannarum ammolegus). The grasslands in this region are being invaded by two congeneric, but structurally different, species of perennial grasses, Eragrostis lehmanniana and E. curvula (Kupfer and Miller 2005). Both nonnative grasses grow taller and more densely than native upland grasses, with E. curvula typically growing larger than E. lehmanniana and often forming dense monocultures (Fig. 1; Kupfer and Miller 2005).

Botteri’s and grasshopper sparrows establish territories soon after arriving on breeding grounds in late April or May when conditions are dry, grasses are dormant, and abundance of arthropods is low (Whitford et al. 1995). They postpone nesting until the onset of monsoon rains, typically in July, that trigger growth of grasses and increases in abundance of arthropod prey (Capinera and Horton 1989). This unusually long period between territory establishment and reproduction makes the link between proximate cues used to select habitat and future resources especially important (Włodarczyk and Minias 2016). Because the proximate cues animals use to select habitat are often related to plant structure, settlement responses to invasions may be conditional on structural similarities between nonnative and native plants and the habitat preferences of the species selecting habitat (Steidl et al. 2013).

Although these two sparrows are similar ecologically and both are classified as grassland obligates (Vickery et al. 1999), they differ in their habitat preferences and breadth (i.e., the width of the habitat component of a species’ niche). For example, in Arizona, grasshopper sparrows are restricted primarily to upland grasslands with few shrubs and relatively small-statured grasses (Ruth and Skagen 2017, Andersen and Steidl 2019). In contrast, Botteri’s sparrows nest sympatrically with grasshopper sparrows, but also nest in areas where shrub cover reaches 30% and in relatively mesic bottomlands that support tall, robust native grasses (e.g., sacaton, Sporobolus wrightii; Jones and Bock 2005, Andersen and Steidl 2019).

Fig. 1. Relative to native grasslands (left), which support a diverse array of plant species, invasions by Eragrostis lehmanniana (middle), and E. curvula (right) can create dense monocultures characterized by higher grass biomass, height, and cover.
Because the two nonnative grasses invading the area we studied differ structurally from each other and from native upland grasses, we anticipated that differences in the habitat breadth of the two sparrows might manifest as differences in settlement responses to invasions. Specifically, we hypothesized that grass composition would be more likely to influence settlement by grasshopper sparrows, given their narrower habitat requirements, and less likely to influence settlement by Botteri’s sparrows, given that both nonnative grasses are within the structural range of native grasses used by this species. We used the sequence by which sparrows established territories along invasion gradients of each nonnative grass to infer their habitat preferences and to evaluate how variation in habitat breadth and grass structure can influence habitat selection in invaded areas. Additionally, we evaluated whether the settlement was influenced by conspecific attraction (i.e., using territorial behaviors of conspecifics as habitat cues; Muller et al. 1997, Ward and Schlossberg 2004), which could confound the effect of vegetation composition on settlement patterns. Differential effects of plant invasions on the habitat-selection process have the potential to explain broad-scale changes in distributions and demography of animal populations.

**METHODS**

**Study area**

We studied semiarid grasslands of southeastern Arizona, USA (Appleton-Whittell Research Ranch, 31.6° N, 110.5° W), that were dominated by perennial grasses with few forbs or shrubs. We selected a 2-km² study area that was interspersed with homogeneous patches of native grasses, *E. lehmanniana*, or *E. curvula*, all within an area small enough to ensure that breeding birds could acquire knowledge of the area with only modest search costs (Stamps et al. 2005). These grasslands had not been burned or grazed by livestock for at least 10 yr, which eliminated the potential for artifacts of those disturbance processes to influence site fidelity and confound settlement patterns (Wiens et al. 1987). The area is located at an elevation of 1500 m where precipitation averages 430 mm annually, the majority of which occurs during a monsoon period that typically spans July–September (Bock and Bock 2000).

**Sampling design**

We established 40, 2.25-ha plots (150 × 150 m) systematically across the study area to capture the full invasion gradient of each nonnative grass (Fig. 2). Plots were small enough to ensure that grass composition within many plots was homogeneous, but large enough to encompass portions of several sparrow territories, which average 0.7 ha for grasshopper sparrow (Ruth 2017) and 1.4 ha for Botteri’s sparrow (Webb 1985).

We initiated surveys before male sparrows of either species arrived on the breeding grounds (9 April 2016) and ended surveys five weeks later (14 May 2016) when both species reached densities expected for the area (Andersen 2019). We recorded the presence of singing males on each plot twice per week during 10-min surveys that we completed within 2.5 h of sunrise. Because bird activity tended to decrease later in the morning, we reversed our survey route on each visit. For analysis, we grouped surveys by week to ensure that the sequence in which we surveyed plots did not confound settlement patterns. We established the date we first observed territorial behavior (23 April) as the beginning of week 1.

We characterized vegetation in August after nesting was completed and the presence of grass inflorescences aided identification. The composition of C₄ perennial grasses in the study area is stable during summer months (Geiger 2006), so estimates of composition at the end of the

![Fig. 2. Percent of grass cover comprised of native species, *Eragrostis lehmanniana*, and *E. curvula* on 40 plots in semiarid grasslands of southeastern Arizona, USA.](image-url)
breeding season reflect composition early in the season when birds select breeding sites. Across the center of each plot, we established two parallel, 120-m transects spaced 50 m apart. At points spaced systematically along each transect (mean = 65, range = 50–84; we allocated greater sampling effort to areas where grass diversity was higher), we placed a Weins pole and recorded the presence of bare ground, litter, forbs, grasses, and shrubs to estimate cover, measured grass height, and identified grasses to species (Wiens 1969).

**Statistical analyses**

For each plot, we averaged values from the two vegetation transects, estimated diversity of grasses with the Shannon index, and quantified grass composition as the percentage of total canopy cover of all grasses comprised by each focal species or group (i.e., native or nonnative). We used simple linear regression to describe how cover, height, and diversity of grasses varied with the composition of nonnative grasses.

Although our objective was to evaluate the influence of plant invasions on habitat selection, we first explored whether settlement patterns could be explained by conspecific attraction. To determine whether the locations of plots settled by territorial birds were clustered over time in a pattern indicative of conspecific attraction, we used Moran’s $I$, a measure of global spatial autocorrelation (Moran 1950). Specifically, for each sparrow species, we tested the null hypothesis that the sequence plots were settled was random in space over time. We calculated Moran’s $I$ and the associated Z statistic (Mitchell 2009) with the spatial autocorrelation tool in ArcGIS 10.2.2 (ESRI 2011). Specifically, we used the center of each plot as the spatial feature, the week each plot was first settled as the feature value, established fixed-distance bands as the maximum distance between centers of adjacent plots (155 m), and standardized spatial weights to contend with the irregular plot layout (Perry et al. 2002, Mitchell 2009). Moran’s $I$ values range from $-1$ to $1$, which indicate perfect negative and positive spatial autocorrelation, respectively. Positive values for $I$ would indicate that plots were settled in a clustered pattern indicative of conspecific attraction, whereas values near 0 would indicate that settlement was independent of settlement patterns on nearby plots.

To evaluate the influence of nonnative grass invasions on settlement patterns, we used mixed-effects logistic regression. For each sparrow species, we related the presence of one or more males ($=1$) vs. absence ($=0$) on each plot during each survey to the proportion of grass cover comprised of *E. curvula* and *E. lehmanniana*, week of the settlement period, and the interaction between the composition of each grass species and week, which provided a direct test of whether nonnative grasses influenced settlement patterns. We did not include other vegetation attributes that we characterized on plots because they changed systematically with the composition of nonnative grasses, and we were interested in the overall effect of each invasion, which was captured by the terms for each nonnative grass. We specified plot as a random effect and all other effects as fixed and standardized values of cover and week (mean = 0, SD = 1). Coefficients ($b$s) of the interaction terms allowed us to distinguish among three alternatives that would link the sequence in which territories were established to habitat selection along the invasion gradient. If sparrows select nesting territories without regard to grass composition, then the composition of grasses on plots settled earlier would be similar to those settled later ($b \approx 0$). In contrast, if sparrows select areas dominated by either nonnative grass preferentially, then plots settled earlier would be composed of more nonnative grasses than those settled later ($b < 0$). Alternatively, if sparrows nesting in areas dominated by either nonnative grass were relegated there after being excluded from preferred sites by conspecifics, then grass composition on plots settled early would be dominated by native grasses ($b > 0$). We fit models in R version 3.5.3 (R Core Team 2015) with the function glm from the lme4 package (Bates et al. 2015) and inspected scaled residuals with the DHARMa package (Hartig 2019) to ensure model assumptions were met. Unless indicated otherwise, all estimates are based on $n = 40$ plots and reported $\pm 1$ SE.

**Results**

We surveyed areas that spanned the full invasion gradient for both nonnative grasses, with the composition of *E. lehmanniana* ranging from 0% to 95% and *E. curvula* ranging from 0% to...
100% across all plots (Fig. 2). Areas dominated by native grasses and each nonnative species were available to birds in similar proportions. Specifically, total grass cover on plots averaged 82% (SE = 1.1, range = 66–98%), of which native species comprised 38% (4.5%), *E. lehmanniana* 36% (4.4%), and *E. curvula* 26% (5.6%). As non-native grasses increased in dominance, cover and height of grasses increased and cover of bare ground, forbs, and species diversity of grasses decreased, which simplified composition and altered the structure of the plant community markedly (Table 1, Fig. 3).

Grasshopper sparrows began to exhibit territorial behavior one week earlier than Botteri’s sparrows and established territories on 58% of plots (23 of 40) within four weeks; during the same period, Botteri’s sparrows established territories on 100% of plots (Fig. 4). Conspecific attraction did not exert a strong influence on settlement patterns for either grasshopper (Moran’s *I* = 0.29, *Z* = 1.30, *P* = 0.19) or Botteri’s sparrows (Moran’s *I* = 0.20, *Z* = 1.34, *P* = 0.18).

Settlement patterns indicated that the two sparrows responded differently to nonnative grasses when selecting breeding habitat (Table 2, Fig. 5). During the first two weeks of the settlement period, grasshopper sparrows established territories on plots dominated by native grasses (mean composition = 60.1%, SE = 5.18, *n* = 9 plots). As the settlement period progressed and native-dominated areas were occupied by territorial conspecifics, grasshopper sparrows were more likely to establish territories on plots that were dominated increasingly by *E. lehmanniana* (Fig. 5, Table 2, week × *E. lehmanniana* interaction). Conversely, grasshopper sparrows did not establish territories on plots where *E. curvula* exceeded 21% of grass cover and the probability of territory establishment did not change across the settlement period (Table 2, week × *E. curvula* interaction).

In contrast to grasshopper sparrows, Botteri’s sparrows did not distinguish between native and nonnative grasses when selecting breeding habitat. Specifically, the composition of nonnative grasses had no effect on the sequence with which Botteri’s sparrows settled plots (Fig. 5, Table 2, interaction terms) or whether plots were ultimately settled (Table 2, main effects).

**DISCUSSION**

The breadth of resources that are suitable for a species can vary widely, even across members of the same ecological guild; responses of vertebrates to plant invasions likely reflect that breadth. For species whose habitat breadth is narrow, for example, nonnative plants are less likely to provide the proximate cues that indicate habitat than for species whose habitat breadth is broad. Because the cues that animals use to identify habitat often are associated with structural characteristics of vegetation (Cody 1981, Smith and Shugart 1987, Fisher and Davis 2010), structural similarities between novel, nonnative plants and the native species they displace could be especially important in determining whether invaded areas are perceived as habitat (Steidl et al. 2013). The difference in settlement patterns of grasshopper and Botteri’s sparrows in

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**Table 1.** Mean, standard error, minimum and maximum values of vegetation categories across plots, and the average change (β) for each category for every 10% increase in dominance of nonnative grasses as estimated from simple linear regressions (*n* = 40 plots).

| Measure     | Category   | Mean | SE  | Min | Max | Estimate | SE  | t     | P    |
|-------------|------------|------|-----|-----|-----|----------|-----|-------|------|
| Cover (%)   | Forbs      | 3.1  | 0.50| 0.0 | 13.0| 0.01     | 0.18| 0.07  | 0.95 |
|             | Litter     | 3.6  | 0.48| 0.0 | 11.3| 0.12     | 0.175| 0.49  |      |
|             | Shrubs     | 12.4 | 0.88| 0.0 | 27.6| 0.85     | 0.290| 2.98  | 0.005|
|             | Bare ground| 82.3 | 0.01| 65.8| 98.3| 1.20     | 0.300| 3.46  | 0.001|
| Height (cm) | Grasses    | 55.9 | 1.12| 43.2| 69.5| 2.10     | 0.200| 10.17 | <0.001|
| Diversity (H’)| Grasses   | 1.2  | 0.11| 0.0 | 2.2 | 0.20     | 0.015| 14.29 | <0.001|
response to invasions by two structurally different grasses demonstrates how habitat preferences and structural characteristics of novel plants interact to influence habitat use, and ultimately species’ distributions.

Grasshopper sparrows, which have declined markedly across their range (Sauer et al. 2017), demonstrated a strong preference for areas dominated by native plants, which tended to be shorter and less dense but more structurally heterogeneous and floristically diverse than areas dominated by either nonnative species (Fig. 3). As the settlement period progressed and native-dominated areas became occupied by conspecifics, grasshopper sparrows increasingly established territories in areas dominated by \textit{E. lehmanniana}, which is more structurally similar to native grasses than \textit{E. curvula} (Kupfer and Miller 2005). This pattern demonstrates that grasshopper sparrows perceived areas dominated by \textit{E. lehmanniana} as habitat, but less preferred relative to areas dominated by native plants. Consequently, individuals that established territories in areas dominated by \textit{E. lehmanniana} likely were relegated there by conspecifics that settled preferred native areas, either by earlier arrival on the breeding grounds or through behavioral dominance. Conversely, grasshopper sparrows did not establish territories in areas dominated by the largest and most dense grass in this system, \textit{E. curvula}, suggesting that they did not

![Fig. 3](a). Invasions by nonnative grasses altered mean cover (a), height (b), and diversity (c; Shannon index) of grasses in semiarid grasslands of southeastern Arizona, USA. Statistics for regression lines are provided in Table 1.

![Fig. 4](b). Percentage of plots (\(n = 40\)) with territories of Botteri’s sparrow (BOSP) or grasshopper sparrow (GRSP) throughout the settlement period in semiarid grasslands of southeastern Arizona, USA.
perceive these areas as breeding habitat. These findings suggest that structural differences between nonnative plants and the native plants they displace can alter the quantity of habitat available to animals, especially species with narrow habitat breadths. This can have important implications for the conservation of grassland specialists, as the degree of habitat specialism has been linked negatively to population trends (Correll et al. 2019) and to increased vulnerability to environmental change (Clavel et al. 2011, Correll et al. 2016).

In contrast, for species whose habitat breadth is broad, nonnative plants are more likely to function similarly to the native plants they displace, including whether they trigger a settlement response (Sogge et al. 2008, Litt and Steidl 2011). In native grasslands, Botteri’s sparrows are habitat generalists that breed in areas dominated by an array of different grasses (Webb 1985). These grasses range from upland species, which are relatively short-statured (e.g., Bouteloua gracilis), to floodplain species, which are taller and denser than the nonnative grasses we studied (e.g., Sporobolus wrightii; Jones and Bock 2005). Consequently, nonnative grasses that have invaded Arizona grasslands are within the structural range of native grasses typical of areas inhabited by Botteri’s sparrow. Accordingly, this species established territories in areas dominated by native and nonnative plants simultaneously, suggesting they recognized each type as offering similar habitat quality.

When animals rely on structural cues to select habitat before key resources are present and nonnative plants are structurally similar to the native species they displace, invasions may not influence the distribution of those animals substantially because the cues that trigger settlement remain. The resources that were linked evolutionarily to the cues used by animals to identify habitat in native grasslands, however, may no longer be present or as abundant in invaded grasslands. For example, many insect taxa important to birds as prey during the nesting period are less abundant in areas dominated by E. lehmanniana compared with native-dominated areas (Bock et al. 1986, Andersen et al. 2019). Further, increases in vegetation biomass in invaded areas could make prey more difficult to find and capture (Reed et al. 2006). This potential decoupling of proximate cues from ultimate resources could have important effects on demography if animals are attracted to invaded areas where fitness is reduced (Schlaepfer et al. 2002). If animals lack the behavioral plasticity to accommodate these rapid disassociations, habitat selection may become maladaptive (Nordby et al. 2008, Hale and Swearer 2016).

Although settlement patterns can provide insight into how migratory animals perceive the quality of invaded areas, other exogenous and endogenous factors might confound the relationship between settlement patterns and plant composition. For example, if animals rely strongly on territorial behaviors of conspecifics as cues to identify habitat (i.e., conspecific attraction; Mul- ler et al. 1997, Ward and Schlossberg 2004), individuals that arrive early could attract later arrivals to settle nearby locations regardless of vegetation composition. In our study, however, plots were not settled in a pattern that suggested

| Grass | Grasshopper sparrow | Botteri’s sparrow |
|-------|---------------------|------------------|
|       | Estimate | SE   | Z   | P   | Estimate | SE   | Z   | P   |
| Intercept | −2.11 | 0.62 | −3.42 | 0.001 | −0.17 | 0.19 | −0.88 | 0.378 |
| Week | 0.97 | 0.52 | 1.87 | 0.062 | 1.36 | 0.23 | 5.95 | <0.001 |
| E. curvula | −2.28 | 0.97 | −2.35 | 0.019 | 0.04 | 0.24 | 0.16 | 0.877 |
| E. lehmanniana | −0.21 | 0.31 | −0.68 | 0.494 | 0.31 | 0.26 | 1.22 | 0.224 |
| Week × E. curvula | 0.36 | 0.83 | 0.43 | 0.665 | −0.03 | 0.26 | −0.10 | 0.922 |
| Week × E. lehmanniana | 0.59 | 0.30 | 1.97 | 0.049 | 0.38 | 0.31 | 1.24 | 0.213 |

Note: Interaction terms evaluate whether the composition of nonnative grasses in areas settled by sparrows changed over time; main effects evaluate whether the composition of each nonnative grass affected settlement systematically across the settlement period.
conspecific attraction. Similarly, fidelity to natal or previous breeding sites could reduce the importance of vegetation-based cues in governing settlement, especially if patches of native and nonnative vegetation are distributed at scales that are large relative to the areas searched by animals (Greenwood 1980, Haas 2012). Studies of return rates of marked grasshopper and Botteri’s sparrows in grasslands of southeastern Arizona demonstrated that some individuals of both species returned to grasslands where they bred previously (Jones and Bock 2005, Ruth 2017). However, return rates were quantified at scales larger than the territory of individual birds (i.e., pasture or study area). Consequently, by establishing a small study area where sparrows could acquire knowledge of all compositional alternatives at modest search costs, we believe that the settlement patterns we observed reflected local features and were not confounded by site fidelity (Orians and Wittenberger 1991). Lastly, it seems unlikely that interspecific competition or displacement influenced settlement patterns. Agonistic behavior is rarely observed between the two species we studied and their territories overlap regularly (Webb 1985), suggesting that the degree of resource partitioning between the two sparrows is adequate to promote coexistence on plots and was unlikely to have affected settlement patterns.

Our results demonstrate that the effects of plant invasions on habitat selection can be species-specific, reflecting both the characteristics of the invading plant species and the habitat requirements of the animal. This interplay between plant characteristics and habitat selection provides a potential mechanism to explain species-level variation in responses to plant invasions. In general, responses will depend on structural contrasts between native and invading plants, the habitat breadth of the animals settling an area, and the degree to which nonnative plants dominate the plant community. Differential responses to plant invasions by closely related species in the same ecological guild reveal the importance of considering the role of habitat-selection behavior in explaining broad-scale changes in the distribution and demography of animals that express at population and community scales.

ACKNOWLEDGMENTS

Our work was supported by the U.S. Bureau of Land Management, the Arizona Game and Fish Department’s Heritage Program, and an Audubon Apacheria Fellowship. We thank Linda Kennedy, Roger Cogan, Karen Simms, and Joann Wang for field and logistical support. Steven Archer, A. Elizabeth Arnold, Judie Bronstein, and R. William Mannan...
offered constructive feedback on an earlier draft of the manuscript. The authors do not have any conflicts of interest with regard to this work.

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