INVASION BY A NATIVE GRASS: IMPLICATIONS OF INCREASED DOMINANCE OF

HETEROPOGON CONTORTUS (TANGLEHEAD) FOR GRASSLAND BIRDS

A Thesis

by

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INVASION BY A NATIVE GRASS: IMPLICATIONS OF INCREASED

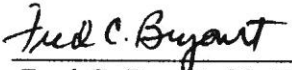DOMINNANCE OF *HETEROPOGON CONTORTUS* (TANGLEHEAD) FOR
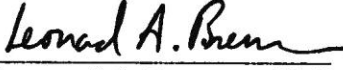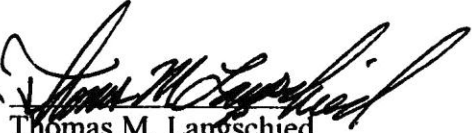
GRASSLAND BIRDS

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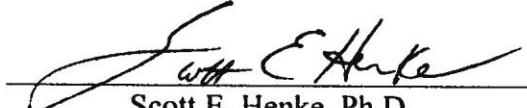
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ABSTRACT

INVASION BY A NATIVE GRASS: IMPLICATIONS OF INCREASED DOMINANCE OF

HETEROPOGON CONTORTUS (TANGLEHEAD) FOR GRASSLAND BIRDS

(May 2013)

Brian J. Bielfelt, B.S., Florida State University

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Heteropogon contortus (tanglehead) is a native grass that has recently spread and become dominant on clay loam soils of southern Texas, leading some land managers to suggest this plant has become invasive. We sought to quantify effects of *H. contortus* dominance on plant and grassland bird communities in summer and winter 2011-2012 and to determine if responses are similar between seasons. Presence and cover of most species of plants decreased with increased dominance of *H. contortus*, but structure was taller, denser, and more homogenous than areas with minimal to no *H. contortus*. Presence and density of Scissor-tailed Flycatcher and presence of Brown-headed Cowbird decreased with *H. contortus*, whereas presence or density of Mourning Dove, Cassin's Sparrow, Lark Sparrow, and Eastern Meadowlark increased in summer. Responses of wintering grassland birds generally were negative, with a few species increasing in presence or density. Based on changes we observed in the plant community, *H. contortus* could be considered an invasive species. Further, we advocate a holistic approach to studying the effects of invasive plants on avifauna because birds have different habitat requirements within each season, resulting in season-specific responses.

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DEDICATION

I dedicate this thesis first and foremost, to my rock and my salvation, Jesus Christ. In the hard times, through the difficult fieldwork, challenging writing, and coursework all I could do is look up for help. I could have not done any of this without His wisdom and guidance. Second, to my wife Melissa, who abandoned stability and comfort in order to support the completion of my thesis. She was always there, encouraging me to press on to the finish line. Finally, to my daughter Autumn 'Iolana, who has replaced the time I spent working on this thesis. She has my heart.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER I: INCREASED DOMINANCE OF A NATIVE GRASS IN GRASSLANDS: DOES BEHAVIOR AND EFFECTS JUSTIFY TERMING HETEROPOGON CONTORTUS AS INVASIVE?

ABSTRACT

Native plants may affect other native species negatively if the dominance of a single native plant species increases beyond previous conditions. *Heteropogon contortus* (tanglehead) is a native grass that recently has increased in dominance in southern Texas. To understand the implications of this increase in dominance on the plant community, we quantified presence and abundance of all herbaceous plant species, compositional and structural characteristics of the vegetation, and soil properties across a gradient of dominance by *H. contortus* (0-80%) in summer and winter of 2010 and 2011. For every 10% increase of *H. contortus* cover, cover of other native grasses decreased 8-10% and forbs decreased 0-2%. Similarly, richness of other native grasses decreased 1.5-2.5 species and richness of forbs decreased 2.0 species across the gradient of dominance. Structural changes with *H. contortus* were most apparent in the canopy cover; vertical density within the grass canopy increased 2.3-3.6 contacts with a Wiens pole and horizontal cover increased 1.0-2.4%. Further, concentration of several soil nutrients, namely cations, differed with *H. contortus* dominance, which may be the result of biological requirements of this grass. Differences in vegetation composition and structure as well as soil chemistry, combined with the rapid spread and increase in dominance, suggest that *H. contortus* has characteristics and effects that are similar to invasive grasses, despite being native, requiring additional research and management actions.

Keywords: cations; grass canopy; native invasive; soil nutrients; winter

INTRODUCTION

Invasions by nonnative species have altered the structure and function of ecosystems worldwide (Vitousek et al. 1996). Although research on invasions often has focused on nonnative species, some ecologists argue that species should be classified as invasive based on

1

ecological traits – life history, behavior of the organism (e.g., rapid spread), or effects on invaded communities – with less emphasis on origin (Botkin 2001; Valéry et al. 2008, 2009; Simberloff 2011). Valéry et al. (2008: 1349) provided a mechanistic definition of invasive species: "A biological invasion consists of a species acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population." Invasion may result from a "change OF the environment", such as moving from one location to another or a "change IN the environment", such as natural processes being altered within an ecosystem (Valéry et al. 2008). By focusing on ecological traits, native species also can be classified as invasive (Alpert et al. 2000). For example, human-related factors, such as forest thinning and overpopulation of *Odocoileus virginianus* (white-tailed deer), facilitated increased dominance of native *Dennstaedtia punctilobula* (hay-scented fern) because this plant has a competitive advantage within its native forest ecosystem (de la Cretaz and Kelty 1999; Horsley et al. 2003; Knight et al. 2009). Similar changes – rapid spread and dominance – have been documented for other native plants within their evolved range and ecosystems, resulting in effects on plant and animal communities that are similar to nonnative invasive plants (Valéry et al. 2004; Pétillon et al. 2005, 2008; Georges et al. 2011; Nielsen et al. 2011; Vallés 2011). Management of native invasive plants may create additional challenges because invasive populations may be located near historic populations (Carey et al. 2012).

Heteropogon contortus (tanglehead) is a perennial bunchgrass native to arid regions throughout the world, including northern Mexico, southern and western Texas, southern Arizona, and southern New Mexico (Reverchon 1886a, 1886b; Tothill 1966; Gould 1978; Hatch et al. 1999). *Heteropogon contortus* has spread rapidly and become dominant in some areas of southern Texas within the past 15 years (F. Bryant, personal communication; Fig. 1.1, pg. 28), leading some land managers and biologists to suggest this grass has become invasive. Under the mechanistic definition of invasive species (Valéry et al. 2008), considering *H. contortus* as a native invasive species would require demonstrating: 1) the disappearance of natural obstacles to proliferation, 2) an acquired competitive advantage over other native plants, and 3) rapid spread and increased dominance into novel areas within recipient ecosystems. To the best of our knowledge, evidence of the rapid spread and increased dominance of *H. contortus* is anecdotal and although several mechanisms have been proposed for increased proliferation and

2

competitive advantages, none have been tested. In Australia, *H. contortus* underwent a similar expansion in the 1950s and 1960s, which may have resulted from changes in land use (Grice and McIntyre 1995; Orr et al. 2004). Land management in much of southern Texas has shifted from an emphasis on cattle ranching to hunting and wildlife management (Smith 2009), often resulting in a change in grazing regimes from overgrazing to undergrazing. Heavy grazing pressure may prevent *H. contortus* from becoming dominant, whereas reduced grazing may allow increased dominance (e.g., Fig. 1.1a, pg. 28). In addition, there may have been concurrent changes to the fire regime with the changing management practices, from no fire with grazing to regular fires. Reports from Australia suggest that increased dominance of *H. contortus* could be related to changes in the timing of annual rainfall, such that *H. contortus* may benefit from later spring and fall rains, or milder winter (Tothill 1966; Grice and McIntyre 1995; Tjelmeland 2011). The increase in *H. contortus* over the last 15 years likely is a result of a combination of these factors.

Changes in vegetation composition and structure are inevitable as a single plant species becomes increasingly dominant, yet the magnitude and direction of the resulting changes may be less predictable. We sought to quantify differences in vegetation composition and structure in native grasslands relative to grasslands with increased *H. contortus*. If increased dominance of *H. contortus* results in ecological effects similar to what has been documented with other invasive grasses, we predicted that richness and abundance of other native grasses and forbs likely would be lower (Bock et al. 1986; D'Antonio and Vitousek 1992) and vegetation structure would change. Although vegetation structure in invaded areas generally differs from more diverse communities, specific structural changes depend on the community type and characteristics of the invasive plant (e.g., Hickman et al. 2006; Davies and Svejar 2008; Sands et al. 2009). Because *H. contortus* is a tall grass with a closed-canopy structure, we predicted vegetation structure in areas dominated by *H. contortus* likely would be taller and denser compared to areas dominated by other native plants.

Although *H. contortus* can create dense, near-monocultures (Fig. 1.1a, pg. 28), this grass also may be patchy where individual bunches are prolific, but do not form a dense canopy (Fig. 1.1c, pg. 28). Relatively few species of native plants grow in sparsely-vegetated locations and those that do are relatively short (e.g., *Bouteloua hirsuta* [hairy grama]). We also sought to determine if characteristics of vegetation or soil differed between thickly- and sparsely-vegetated areas dominated by *H. contortus* and whether these differences were similar to thickly- and

3

sparsely-vegetated areas dominated by native grasses. Sand ridges interspersed throughout these grasslands have very sparse native vegetation, but low-lying areas have very dense mats of native bunchgrasses, including *H. contortus*. Sandier soils could have lower nutrients because they are more porous, such that water could leach nutrients more quickly (Brady and Weil 2008), resulting in poorer growing conditions and lower densities of *H. contortus* and other native plants.

STUDY AREA

We studied areas of relatively open grasslands that represented a gradient of dominance by *H. contortus*, located on the Borregos and Alta Vista ranches (~19 km apart) in Jim Hogg County, Texas, where increases in dominance of *H. contortus* initially were observed (F. Bryant, personal communication). The climate is both semiarid and subtropical, with highly variable rainfall (Fulbright et al. 1990). The growing season in the area lasts for more than 300 days per year (United States Department of Commerce 1970), typically between February and November (F. Smith, personal communication). The study area lies within the Tamaulipan Biotic Province (Dice 1943), at the convergence of Gulf Coastal Grassland and Tamaulipan Thornscrub (Brown et al. 2007), resulting in vegetation characteristics of both plant communities as described in Diamond and Fulbright (1990), Fulbright et al. (1990), and Gould (1975, 1978). Soils are classified as Nueces fine sand (United States Bureau of Soils 1910), which has a texture of sand to loamy sand. Although grasses and areas of brush always have characterized the region (Fulbright et al. 1990), density of woody vegetation currently may be higher than historic conditions (Johnston 1963; Schmidly 2002).

Dominant native grasses in the study area include *H. contortus*, *Trachypogon spicatus* (spiked crinkleawn), *Paspalum plicatulum* (brown-seed paspalum), *Schizachyrium scoparium* var. *littorale* (seacoast bluestem)*,* and *Elionurus tripsacoides* (Pan-American balsam scale). *Schizachyrium scoparium* var. *littorale* hybridizes with *S. scoparium* var. *frequens* (little bluestem), but true varieties of *S. scoparium* var. *frequens* are uncommon in the region; we use *S. scoparium* to refer to both varieties. These semiarid grasslands are interspersed with old dunes and sandy ridges characterized by bare ground, *Aristida oligantha* and *A. purpurea* (threeawn species), and *Monarda punctata* (spotted beebalm). Nonnative *Eragrostis lehmanniana*

(Lehmann lovegrass) is common at Borregos, *Pennisetum ciliare* (buffelgrass) is common within burned mottes and brushy areas, and *Melinis repens* (natal grass) is relatively rare at both ranches; all nonnative grasses are more common within cattle traps. Woody vegetation in our study area is contained mainly in small chaparral thickets and mesquite mottes (stands of trees and brush). Mottes are interspersed within the grasslands and are comprised primarily of *Prosopis glandulosa* (honey mesquite) and the plants dependent on *P. glandulosa* for growth. Common woody plants within mottes include *Celtis pallida* (granjeno), *Opuntia* spp. (prickly pear), *Condalia hookerii* (brasil), and *Diospyros texana* (Texas persimmon). Most woody vegetation occurs within mottes, although some short, woody species, such as *Acacia greggii* (catclaw) and *Colubrina texansis* (Texas hogplum), are interspersed among the grasses.

Mechanical management activities in these open grasslands were similar and minimal; during the study period, activities were limited to disking and mowing along fence lines and occasional mowing of a two-track lane. The stocking rate has been maintained at 1 animal unit/12 ha for the last 15 years, which is lower than the rate maintained 30 years ago (1 animal unit/4 ha, W. Jones, personal communication). Although there are no exact fire records, fires did not occur for at least three years prior to or during our study (W. Jones, personal communication).

Extreme differences in annual rainfall are characteristic of dry grasslands of the region, including in Arizona, New Mexico, and Texas (e.g., Reynolds and Krausman 1998; Bock and Bock 1999). Our study occurred during a period of extreme fluctuations in precipitation. This region experienced a severe drought in 2008 that ended in fall 2009, followed by one of the wettest years in a century, followed by the worst drought ever documented from late 2010 through 2011 (National Weather Service 2010, 2011, 2012). Based on the National Oceanic and Atmospheric Administration (NOAA) weather stations within 60 km of each ranch, rainfall averaged 19.02 cm, 32.89 cm, and 10.49 cm in 2009, 2010, and 2011, respectively (National Climatic Data Center 2011). Therefore, summer sampling periods occurred during a wet (2010) and dry (2011) growing season and winter sampling periods occurred after a dry (2009-2010) and wet (2010-2011) growing season.

METHODS

Plot Selection

We selected study areas that were relatively open grasslands, with minimal woody vegetation. We randomly selected 70 study plots across a range of dominance of *H. contortus*. Using ArcView GIS 10, we generated random points across the study area that were >325 m apart, >150 m from large woody thickets, and >125 m from caliche roads and fences. We located points in the field and selected those with <30% woody vegetation and <20% relative cover of nonnative grasses within a 125-m radius, and that collectively represented the gradient of dominance by *H. contortus*. This study is part of a larger investigation examining how increased dominance by *H. contortus* affects wildlife, which influenced some criteria for plot selection. We marked selected points with a single t-post, which denoted the center of each study plot; all data were collected within 125 m of this central location. Dominance of *H. contortus* ranged from 0 to 80% relative cover (0 to 60% absolute cover) for all sampling periods.

Plant Community Sampling

We sampled vegetation a total of four times, in summer (June) and winter (January/February) of 2010 and 2011. On each of the 70 study plots, we quantified vegetation characteristics along two perpendicular transects. We sampled at 17 locations/plot, each 30 m apart, with eight on each transect and one at the plot center. At each sampling location, we used a 0.5×0.5-m quadrat, elevated 1-m high, to record horizontal cover of bare ground, litter, and each grass and forb species in 5% increments (Daubenmire 1959). If >5% of the quadrat was dominated by woody vegetation, we shifted the sampling location slightly. We estimated the horizontal cover of each species in two vertical strata, ground (<0.4 high) and canopy level (0.4 to1.9-m high), because vegetation cover in the canopy may change independently of cover at the ground level. In addition, we quantified vertical structure of the vegetation within each stratum with a Wiens pole (Wiens and Rotenberry 1981), placed randomly at one corner of each quadrat, by recording the number of times each plant species contacted each 0.1-m increment on the pole.

Plant Sub-communities and Soil Sampling

We observed differences in vegetation structure (e.g., sparse versus thick vegetation cover) that seemed unrelated to dominance by *H. contortus*. As a result, we observed four vegetation "sub-communities": 1) sparsely-vegetated, native grass-dominated, 2) thickly-vegetated, native grass-dominated, 3) sparsely-vegetated, *H. contortus*-dominated, and 4) thickly-vegetated, *H. contortus*-dominated. We sought to determine if soil or vegetation characteristics would distinguish these types. We classified each of the 70 study plots into one of these sub-communities based on vegetation density and dominance, selected a subset of four study plots for each sub-community (*n* = 16, on Borregos Ranch only). On each of the selected plots, we used the same sampling methods previously described to characterize vegetation on three randomly-placed quadrats, except we did not differentiate horizontal cover by height strata. In addition, we also measured litter depth at one corner of the quadrat, recorded height (cm) of the tallest plant, and number of bunchgrasses within each quadrat. After sampling vegetation, we collected soil samples from 5-50 cm below the quadrat and quantified soil pH, nutrients, and texture (Texas AgriLife Extension Service, Soil, Water, and Forage Testing Laboratory, College Station, TX).

ANALYSIS

Plant Community

We assessed changes in the composition and structure of the plant community with *H. contortus* across the dominance gradient. We used relative cover of *H. contortus* (i.e., percent of total vegetation cover represented by *H. contortus*) to characterize the dominance gradient and analyzed data for summer and winter separately to explore seasonal differences. We quantified species richness of other native grasses and forbs per quadrat, based on estimates of cover; we did not include *H. contortus* in calculations of richness of other native grasses. To quantify species-specific changes in vegetation with increased dominance of *H. contortus*, we examined differences in presence and abundance of grasses and forbs. To assess variability in presence across the dominance gradient, a species could not be extremely common or rare. We analyzed

7

variation in presence of a species only if it was detected on 10-60 plots. As a result, some

species of annual grasses and forbs could be analyzed only in a single year because they were

rare during drought periods (i.e., winter 2010 and summer 2011) or ubiquitous during wet

periods (i.e., summer 2010 and winter 2011). Where a plant species was present, we examined

variation in abundance if average relative cover was ≥15% on at least one plot. We grouped

some plant species together for analysis because they were rare, had similar ecological functions,

or because species-specific identification was challenging when plants were desiccated. For

example, *Paspalum setaceum* (thin paspalum) can be difficult to distinguish from *P. plicatulum*

in winter when growing in dense vegetation or during prolonged drought; we grouped these

species together only for winter sampling periods to avoid confusion.

We examined variation in horizontal and vertical structure of ground- and canopy-level

vegetation along the gradient of *H. contortus* dominance. We quantified changes in total cover

(i.e., absolute cover) for all other species of native grasses, all forbs, and all nonnative grasses.

We categorized total cover and total Wiens pole contacts into two height categories: ground level

and canopy level. For most structural variables, we averaged data from all quadrats to compute a

single value for each plot; however, we computed the total number of contacts with the Wiens

pole.

We used a generalized linear mixed model approach for all analyses and selected the

appropriate distribution and link function for each response variable of interest (Littell et al.

2006). When appropriate, we accounted for repeated sampling on the same plots over time (i.e.,

years) by treating plots as subjects and incorporating a compound symmetric covariance

structure (Littell et al. 2006). In addition to examining variation across the gradient of *H.

contortus* dominance, we also included year and a year $\times$ *H. contortus* interaction in models to

explore variation in responses over time and determine if the effects related to *H. contortus*

changed over time. We included site (i.e., ranch) as a blocking factor in all analyses to account

for potential differences in soil characteristics and other factors. For all analyses of

compositional and structural characteristics, we began with a full model that included block,

relative cover of *H. contortus*, year, and a year $\times$ *H. contortus* interaction, but removed the

interaction term if $P > 0.10$ to generate the best estimates of effects. We log-transformed cover

for individual plant species to meet model assumptions. We present slope estimates and 95%

CIs in text and tables that represent multiplicative changes in cover for individual plant species

and linear changes in other compositional and structural characteristics with every 10% increase in *H. contortus* cover. We present details regarding additional covariates in appendices.

Plant Sub-communities and Soils

To detect possible differences in the four vegetation sub-communities, we used stepwise discriminant analysis based on soil (i.e., pH, texture, and nutrients) and vegetation characteristics. We restricted our focus to structural features of the vegetation (e.g., litter, bare ground, height, vertical structure), because we classified vegetation sub-communities based on composition *a priori*. We used a forward variable selection procedure, setting $P \leq 0.05$ to enter the model. We also compared differences in soil characteristics among sub-communities based on analysis of variance (ANOVA). We log-transformed soil variables for analyses, but present raw means and 95% CIs in text and tables.

RESULTS

Species-Specific Results

We observed 84 species of herbaceous plants (Appendix A). With increased *H. contortus*, presence (8 of 13) or abundance (6 of 10) changed for most species of native grasses (Tables 1.1 and 1.2). We detected few changes in presence (2 of 11) or abundance (0 of 1) of native forb species.

Most species that changed with *H. contortus* decreased in either presence or abundance in at least one sampling period. Presence of several species decreased with *H. contortus* in both seasons, including perennial grasses *Elionurus tripsacoides* and *Schizachyrium scoparium*, and perennial, leguminous vines *Galactia canescens*/*Rhynchosia americana* (hoary milkpea/American snoutbean), but the decrease was slight for *E. tripsacoides* in winter (Table 1.1, pg. 24). Abundance of perennial *S. scoparium* and *Aristida* grasses also decreased across the gradient of *H. contortus* dominance in both seasons. Presence of the perennial *Paspalum* grasses decreased with *H. contortus* only in winter. Several species decreased in abundance across the gradient of *H. contortus* dominance in a single season, including *Paspalum plicatulum* in

9

summer and *Paspalum* spp. and *Bouteloua hirsuta* in winter (Table 1.2, pg. 26); the magnitude of change was slight for *Bouteloua hirsuta*.

With increased *H. contortus*, several species increased in presence or abundance, but these species tended to be invasive nonnative grasses or native species associated with disturbance or early succession. The warm-season perennials witchgrasses *Digitaria cognate/Panicum capillarioides* (fall and southern witchgrass) increased in presence with *H. contortus* in both seasons (Table 1.1, pg. 24). Three species increased in presence with *H. contortus* in a single season, including native perennial lovegrasses, *Eragrostis secundiflora* (red lovegrass) and *E. sessilispica* (tumble lovegrass) in summer and nonnative perennial *P. ciliare* in winter. Interestingly, as *H. contortus* increased, no other native plant species increased in abundance across the dominance gradient.

For a few species, the magnitude of the effect of *H. contortus* differed between years (Appendices B, C), which may reflect variability in rainfall. For example, presence of *Trachypogon spicatus* decreased with *H. contortus* in both seasons, but the degree of this change in summer differed between years (Table 1.1, pg. 24). In addition, presence of *Setaria/Urochloa* spp. (signalgrasses) decreased only in summer 2011 (Table 1.1, pg. 24) and abundance of *Cenchrus spinifex* (coastal sandbur) decreased only in winter 2010 (Table 1.2, pg. 26). Although presence of *Monarda punctate* decreased with *H. contortus* in winter of both years, presence decreased in summer 2010, but did not differ in summer 2011. Presence of the perennial forb *Commelina erecta* (dayflower) increased across the dominance gradient in summer 2010, but this species was uncommon during the summer of 2011. Finally, *Eragrostis lehmanniana* increased with *H. contortus* in winter 2011, but not in 2010 (Table 1.2, pg. 26).

Plant Community

Increased dominance by *H. contortus* was associated with decreases in richness of other native plants. For every 10% increase in *H. contortus*, richness of other species of native grasses decreased 0.19 species/0.25 m^2 in summer (95% CI = -0.33 to -0.05) and 0.33 species/0.25 m^2 in winter (-0.47 to -0.19; Fig. 1.2, pg. 29). Forb richness decreased 0.27 species/0.25 m^2 (-0.49 to -0.04) in 2010 with each 10% increase in *H. contortus*, but did not differ in 2011 (Fig. 1.2, pg. 29).

Total cover of bare ground and other species of native grasses and forbs decreased with increased *H. contortus*, whereas litter increased (Fig. 1.3, pg. 30). For every 10% increase in *H. contortus*, cover of other native plants decreased 7.5% (95% CI = -8.8 to -6.2%) in summer 2010 and 10.4% (-11.5 to -9.2%) in 2011 (Fig. 1.3, pg. 30). In winter, total cover of other native grasses decreased 10.1% (-10.9 to -9.3%) for every 10% increase in *H. contortus* (Fig. 1.3, pg. 30). Forb cover decreased -2.1 (-3.2 to -1.1%) with every 10% increase in *H. contortus* in summer 2010, but did not vary in 2011 (0.3%, -0.6 to 1.2%; Fig. 1.3, pg. 30). For every 10% increase in *H. contortus*, cover of bare ground decreased 2.4% (-3.5 to -1.3%) in summer 2010 and 1.1% (-2.1 to -1.7%) in summer 2011; cover of bare ground decreased 1.1% (-1.9 to -0.2) in winter (Fig 1.3, pg. 30). In contrast, cover of litter increased 1.4% (0.3 to 2.4%) in winter 2010, but did not differ in winter 2011 or summer (Fig. 1.3, pg. 30). Total cover of nonnative grasses did not differ with *H. contortus* in either season or year (Fig. 1.3, pg. 30).

In general, vegetation structure in areas dominated by *H. contortus* differed and was characterized by increased cover and density at the canopy level in both seasons, whereas changes at the ground level may be dependent on season or year. Differences in vegetation structure with *H. contortus* were of greater magnitude during the summer with high rainfall (2010). Absolute cover at the ground level increased 3.2% and 1.1% (2.0 to 4.4% and 0.1 to 2.1%) for every 10% increase in *H. contortus* in summer 2010 and 2011, but increased only slightly (1.3%, -0.01 to 2.1%) in winter 2011 (Table 1.3, pg. 27). Absolute cover at the canopy level increased 1.8% (0.4 to 1.5%) in summer, and 2.4% and 1.6% (1.8 to 3.0 and 1.0 to 2.2) in winter 2010 and 2011 with *H. contortus* (Table 1.3, pg. 27). For every 10% increase in *H. contortus*, vertical density of vegetation at ground level increased 11.0 contacts (5.9 to 16.1 contacts/40 cm) in summer 2010, but differed little in the other three sampling periods. In contrast, vertical density of vegetation at canopy level increased in all but one sampling period. Vertical density of vegetation at canopy level increased 3.6% and 2.3% (2.5 to 4.6% and 0.1 to 3.6%) across the gradient in summer 2010 and winter, but did not differ in summer 2011 during low rainfall (Fig. 1.3, pg. 30).

Plant Sub-communities and Soils

The four vegetation sub-communities we defined could be distinguished based on relatively few vegetation and soil characteristics. Bunchgrass density and litter depth distinguished sparsely-vegetated areas from thickly-vegetated areas ($r = 0.83$ and $r = 0.74$ with the first canonical axis), whereas magnesium concentrations distinguished areas dominated by native plants from those dominated by *H. contortus* ($r = 0.87$ with the second canonical axis, Fig. 1.4, pg. 31). The first two canonical axes explained 94% of the variation.

Five of seven soil nutrients and pH differed among the vegetation sub-communities (Fig. 1.5, pg. 32). Areas dominated by *H. contortus* generally had more phosphorus and four cations (potassium, calcium, magnesium, and sodium) than areas dominated by other native plants. Sub-communities dominated by *H. contortus* had higher concentrations of magnesium, calcium, and potassium than native plant-dominated sub-communities, however the sub-community dominated by thick, native vegetation had somewhat similar calcium and potassium concentrations to one or both of the *H. contortus* sub-communities (Fig. 1.5, pg. 32). Concentrations of potassium and sodium within sparse, *H. contortus* and thick, native vegetation were intermediate between the sub-communities with sparse, native and thick *H. contortus*, whereas concentrations of phosphorus were highest within thick *H. contortus* (Fig. 1.5, pg. 32). Soil pH differed between native plant-dominated sub-communities, but were similar in both *H. contortus* sub-communities (Fig. 1.5, pg. 32). We did not detect differences in nitrogen-nitrate, sulfur, and sand content, but sand content was slightly lower in *H. contortus* (Fig. 1.5, pg. 32). Clay comprised less than 8% of the total soil content and demonstrated the opposite pattern of sand content.

DISCUSSION

Similarities between *H. contortus* and Nonnative Invasive Plants

Native invasive plants likely follow a path to invasion similar to nonnative plants, as described in Sakai et al. (2001), but native invasive plants result from changes occurring within the native range instead of introduction or movement from the native to a novel range and

establishment in the novel range (Valéry et al. 2008). Similar to nonnative invasive plants, some native plants also spread rapidly and have ecological and economic impacts on the historic or adjacent ecosystems. For example, increased dominance of *D. punctilobula* within its historic ecosystem has resulted in reduced recruitment of other native plants in the forest because of reduced light availability at the ground level (de la Cretaz and Kelty 1999). Anecdotal evidence suggests that either path to invasion may have occurred for *H. contortus* because the historic ecosystem has experience human-induced changes (Tjelmeland 2011) but nonnative varieties of *H. contortus* may have been introduced into Texas (Burr 1955; Smith 2009).

If traits and effects were used to identify invasive plants (Botkin 2001; Valéry et al. 2008, 2009), then *H. contortus* would have to be considered invasive because it has effects analogous to nonnative plants. Nonnative invasive grasses typically result in decreases in abundance of cover and richness of native plant species (i.e., forbs, grasses) and bare ground (Bock et al. 1986; Belcher and Wilson 1989; Christian and Wilson 1999; Davies 2011). In contrast, litter and total cover tend to increase with nonnative invasive plants, but the direction and magnitude of the effects vary depend upon the invading species and grassland type (Davies and Svejar 2008; Sands et al. 2009). Changes in the plant community with increased *H. contortus* were analogous to nonnative invasive plants because of decreased richness and cover of other native grass and forbs, decreased presence and abundance many native grass species, decreased bare ground, and increased total cover. We acknowledge that similar changes in composition and structures also could be found in native plant communities that naturally are dominated by a few species.

Although we lack data linking the increased dominance of *H. contortus* to a "change OF" or "change IN" the environment (Valery et al. 2009), the observed pattern of spread is what would be expected of a nonnative variety. *Heteropogon contortus* was first reported as being problematic at one ranch location 15 years ago, then other ranches in surrounding area, and now ranches farther north and west (Tjelmeland 2011), a typical pattern observed in many nonnative invasive species (Cox 2004). Further, Tjelmeland (2011) observed two phenotypic varieties of *H. contortus* in the region, of which one was more "leafy" and the other was more "stemmy", which could indicate two different varieties. We lack sufficient genetic evidence to classify the increased dominance of *H. contortus* definitively as a nonnative or native variety. If a native variety were invading, then changes in the environment ought to have resulted in *H. contortus*

spreading from multiple points, which supports hypothesis that it is a nonnative variety; however, the spread may not have been reported in some locations until recently.

Given that changes in land use and climate have occurred within the native range of *H. contortus* (Tjelmeland 2011; W. Jones, personal communication) and increases in dominance results in changes in the vegetation community, this species could be a native invasive plant. Alternatively, a nonnative invasive variety of *H. contortus* may have been introduced sometime between the 1900s and 1950s, when many species of nonnative grasses were introduced in south Texas for cattle (Smith 2009). If the increase in *H. contortus* were due to a native variety, our results could build upon recent research on the characteristics and effects of native invasive plants in North America (de la Cretaz and Kelty 1999) and Europe (Valéry et al. 2004; Pétillon et al. 2005; Georges et al. 2011; Nielsen et al. 2011; Vallés et al. 2011). If it is a nonnative invasive, these results could further research on cryptic invasion, as has been documented with *Phragmites australis* (Saltonstall 2002). Regardless of the source of invasion, the rapid spread, ecological impact, and the potential to effect economic interested (e.g., hunting and ranching) indicate that *H. contortus* is an invasive plant.

Effects of *H. contortus* on the Plant Community

Similar to other invasive plants (nonnative or native), *H. contortus* had mostly negative effects on the native plant community within south Texas grasslands. Differences in vegetation structure with increased *H. contortus* were most apparent at the canopy level, where vegetation was denser vertically and more continuous horizontally. Although some native grasses have culms that are taller than *H. contortus*, most have blades closer to the ground whereas mature *H. contortus* plants can be pillar-like, having blades and culms distributed equally along the entire height of the plant resulting in more biomass higher in the canopy than other native plants (e.g., Fig. 1.1c). Changes in canopy cover and density with *H. contortus* can reduce the amount of surface light, limiting the growth of other plants, such as annuals and shorter species (D'Antonio and Vitousek 1992). Further, the plant community could be affected by *H. contortus* if increased dominance of this species result in changes to nutrients or soil microbes. *Heteropogon contortus* also seems to alter fire regimes and be associated with roads, soil disturbance, and mechanical management, such as disking (Tjelmeland 2011; B. Bielfelt, unpublished data; Fig. 1.1a, pg. 29),

common traits associated with invasive plants (D'Antonio and Vitousek. 1992; Hobbs and Huenneke 1992; Sakai et al. 2001).

Soils

Heteropogon contortus has become extremely dominant in grasslands within sandy soils of the coastal sand sheet (Fulbright et al. 1990; Tjelmeland 2011), but the degree of dominance is much lower closer to the Gulf of Mexico, perhaps because soils are too sandy. Indeed, *H. contortus* appears to be invading more rapidly in open areas of the Tamaulipan thornscrub community (north and west of our study site), but slower within the Gulf Coastal grassland community (east of our study site). Although sand ridges within our study site generally lack *H. contortus*, we found some evidence that sand content could be limiting *H. contortus*; sparsely-vegetated islands of native grasses, in a sea of thickly-vegetated, *H. contortus*-dominated areas. Although we were not able to detect differences in the amount of sand in the soils, small differences may be sufficient to limit growth of *H. contortus*. Further research, such as common garden experiments, investigating *H. contortus* growth across a wider range of sand content values may provide insights. An alternative explanation sand ridges and coastal sites generally lacking *H. contortus* could be that these soils may slow rate of spread, but is not an insurmountable obstacle preventing H. contortus from eventually achieving density similar to the study sites.

Nutrients, namely cations, differentiated areas dominated by *H. contortus* from those dominated by other native plants, especially where *H. contortus* was dense. Plants with high rates of growth, high net primary productivity, or deep roots may increase soil nutrients through increased rates of uptake and turnover (Blank and Young 2002; Jobbágy and Jackson 2004; Chapuis-Lardy et al. 2006), such that *H. contortus* may be altering soil characteristics. However, higher soil nutrients also could result from a low rate of uptake by an individual plant species (Dassonville et al. 2007). For example, soils below invasive *Solidago gigantea* (early goldenrod) have higher concentrations of phosphorus because concentrations in *S. gigantea* plant tissues are low (Vanderhoeven et al. 2005, 2006). High concentrations of cations, especially within soils of thickly-vegetated, *H. contortus*-dominated areas, could result from a low rate of uptake by *H. contortus*. Playne (1970) documented low levels sodium within tissues of *H. contortus*.

Although changes in soil nutrients have been attributed to changes in soil pH created by *Microstegium vimineum* (Japanese stiltgrass), a nonnative invasive plant (McGrath and Binkley 2009), pH would not explain differences with *H. contortus* in grasslands. Invasive plants that modify the soil microbial community also affect soil nutrients indirectly by reducing absorption (Hooper and Vitousek 1998; Ehrenfeld 2003; Davies and Svejar 2008). Regardless of the mechanism, increased *H. contortus* result in differences in concentrations of phosphorus and several cations, potentially facilitating changes in plant, microbial, and arthropod communities (e.g., Kourtev et al. 2003; McGrath and Binkley 2009; Shaben and Myers 2010; Vallés et al. 2011). Although *H. contortus* could be influencing soils, possibly promoting further invasion, soil differences also could be a preexisting condition that limits or facilitates the dominance of *H. contortus*.

Precipitation and *H. contortus*

Compositional and structural changes in grassland vegetation with *H. contortus* were more pronounced with increased precipitation, especially during summer. Vegetation may respond to ecological changes differently under varying rainfall conditions (e.g., Bock and Bock 1999). Although presence or abundance of forbs often decreases with invasion by nonnative plants (Bock et al. 1986; Davies and Svejar 2008; Hickman et al. 2006), we observed decreases in only two species of forbs. Given that forbs were uncommon during the summer drought, forbs may have been affected more by variation in rainfall than by *H. contortus*. Although grouping some forb species may have obscured our ability to detect changes, changes in the total cover of all forb species combined did indicate that the effect of *H. contortus* on forb production was contingent on rainfall. In addition, slower plant growth during drought periods could explain why structural differences were detected only in summer. Alternatively, structural differences may have been consistent between winters because of late-season rains in 2009.

Drought conditions are predicted to become more frequent and severe in the southwestern United States over the next century (Christensen et al. 2007), which could minimize the compositional and structural changes to the plant community associated with *H. contortus* during the growing season, but effects may persist in winter. Understanding potential interactive effects

of rainfall and *H. contortus* on the plant community will be important to predict changes expected under future climatic conditions.

Implications for Wildlife

Changes in the plant community with *H. contortus* likely have implications for animals, both positive and negative. For example, Northern Bobwhite (*Colinus virginianus*) uses this bunchgrass for nesting substrate (Buelow 2009), yet diversity and abundance of several insect groups decrease with *H. contortus* (Cord 2011). Changes in the insect community may translate to effects on other fauna, such as birds and mammals, which rely on insects for food (Flanders et al. 2006; Hickman et al. 2006; Litt and Steidl 2011). Vegetation structural changes with increased *H. contortus*, such as the amount of cover at the ground and canopy levels, can further affect behavior of wildlife by limiting movement or altering responses to predators (e.g., Devereux et al. 2005; Severns 2008). Given the negative effects documented in the plant community and changes to vegetation structure, management of *H. contortus* may be necessary to support biodiversity in these grasslands.

CONCLUSIONS

Although we quantified changes in the grassland plant community with increased dominance of *H. contortus*, many questions remain regarding the cause of invasion, genetics, potential competitive advantages, and soil requirements. Grasslands dominated by *H. contortus* are near-monocultures and thus, differ in vegetation composition and structure from more diverse grasslands, indicating that *H. contortus* may be functioning as an invasive plant. Differences in soil characteristics, such as sand content, may limit the distribution of *H. contortus* and invasion by this species may affect soil nutrients. At a minimum, *H. contortus* merits additional investigation because increases in dominance of this species throughout its range in the southwestern United States could result in widespread, concomitant changes in plant and animal communities.

17

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Table 1.1 Magnitude and direction of changes in presence of other plants with *H. contortus*, after accounting for covariates, including slope estimates that show a multiplicative changes in presence for every 10% increase in dominance of *H. contortus*, 95% confidence intervals, test statistics, and *P*-values, $n = 70$ plots, Jim Hogg County, Texas, 2010-2011.[a]

Species	Effect	SUMMER Estimate	95% CI		t	P	WINTER Estimate	95% CI		t	P
Decreased											
Native Grass											
Elionurus tripsacoides	*H. contortus*	-24	-40	-4	-2.31	0.02	-17	-33	4	-1.67	0.10
Paspalum spp.	*H. contortus*						-37	-56	-11	-2.69	0.009
Schizachyrium scoparium	*H. contortus*	-29	-42	-13	-3.44	0.001	-51	-61	-39	-6.19	<0.0001
Setaria/Urochloa	*H. contortus*				2.05 [b]	0.04	6	-21	41	0.37 [b]	0.71
	2010	39	-24	155							
	2011	-27	-43	-7							
Trachypogon spicatus	*H. contortus*				-2.12 [b]	0.04	-56	-69	-37	-3.51	<0.0001
	2010	-54	-68	-33							
	2011	-39	-54	-20							
Forb											
Galactia/ rhynchosia	*H. contortus*	-30	-44	-14	-3.36	0.001					
Monarda punctata	*H. contortus*				-2.05 [b]	0.04	-56	-76	-17	-2.59 [b]	0.01
	2010	-52	-69	-26							
	2011	-18	-37	6							
Increased											
Native Grass											
Digitaria/Panicum	*H. contortus*	59	24	104	3.72	0.0004	36	11	65	3.06	0.003
Eragrostis secundiflora [c]	*H. contortus*	33	5	68	2.41	0.02				0.99	0.32
	2011only						14	-13	50		
Eragrostis sessilispica	*H. contortus*	25	1	55	2.09	0.04					
Nonnative Grass											
Pennisetum ciliare	*H. contortus*						57	17	111	3.07	0.003
Forb											
Commelina erecta	*H. contortus*				2.23 [b]	0.03					
	2010 only	43	4	97							

Table 1.1 Continued

Species	Effect	SUMMER					WINTER				
		Estimate	95% CI		*t*	*P*	Estimate	95% CI		*t*	*P*
Did not change											
Native Grass											
Aristida spp.	*H. contortus*	-2	-23	24	-0.19	0.85	1	-20	26	0.05	0.96
Bouteloua hirsuta	*H. contortus*	7	-14	31	0.61	0.55	-1	-20	22	0.10	0.92
Cenchrus spinifex	*H. contortus*				-0.09 [b]	0.62				-0.23 [b]	0.82
	2010 only						-3	-25	28		
	2011 only	-6	-28	22							
Paspalum plicatulum	*H. contortus*	-21	-43	7	-1.54	0.13					
Paspalum setaceum	*H. contortus*	-3	-21	19	-0.32	0.75					
Nonnative Grass											
Eragrostis lehmanniana	*H. contortus*	-28	-12	236	1.63	0.11	-7	-12	29	0.67	0.50
Forb											
Acalypha radians	*H. contortus*				1.21 [b]	0.23					
	2010 only	21	-12	65							
Ambrosia psilostachya	*H. contortus*	7	-31	65	0.31	0.76					
Croton spp.	*H. contortus*				-0.73 [b]	0.47					
	2010 only	-9	-29	17							
Evolvulus spp.	*H. contortus*				-1.27 [b]	0.21					
	2011 only	-17	-36	11							
Fabaceae	*H. contortus*	14	-6	39	1.35	0.18					
Phlox spp.	*H. contortus*				-1.35 [b]	0.18					
	2010 only	-26	-52	15							
Physalis spp.	*H. contortus*	10	-13	39	0.79	0.43					

[a] Slope estimates are back-transformed. Additional analysis details are in Appendix B.

[b] *df* = 67. For all other variables, *df* = 68.

[c] Both summers, but winter for 2011 only.

Table 1.2 Magnitude and direction of changes in relative cover of other plants with *H. contortus*, after accounting for covariates, including slope estimates that show a multiplicative changes in presence for every 10% increase in dominance of *H. contortus*, 95% confidence intervals, test statistics, and *P*-values, *n* = 70 plots, Jim Hogg County, Texas, 2010-2011.[a]

Species or Variable	Effect	SUMMER						WINTER					
		Estimate	95% CI		*df*	*t*	*P*	Estimate	95% CI		*df*	*t*	*P*
Decreased													
Native Grass													
Aristida spp.	*H. contortus*	-14	-22	-5	47	-3.05	0.004	-10	-17	-3	42	-2.78	0.01
Bouteloua hirsuta [b]	*H. contortus*							-10	-21	2	30	-1.69	0.10
Cenchrus spinifex	*H. contortus*	-4	-12	5	47	-0.83	0.41				43	2.50	0.02
	2010							-13	-21	-3			
	2011							1	-8	10			
Paspalum plicatulum	*H. contortus*	-19	-36	-2	15	-1.97	0.07						
Paspalum spp.	*H. contortus*							-26	-41	-8	18	-2.85	0.01
Schizachyrium scoparium	*H. contortus*	-22	-30	-13	47	-4.57	< 0.0001				45	-2.14	0.04
	2010							-8	-5	-2			
	2011							-2	-4	-1			
Increased													
Nonnative Grass													
Eragrostis lehmanniana	*H. contortus*	1	-9	11	44	0.16	0.88				43	2.52	0.02
	2010							-2	-12	9			
	2011							14	3	27			
No Change													
Native Grass													
Elionurus tripsacoides	*H. contortus*	-4	-16	9	39	-0.64	0.53	-8	-17	2	41	-1.61	0.12
Paspalum setaceum	*H. contortus*	-10	-24	6	8	-1.97	0.17						
Setaria/Urochloa	*H. contortus*	-5	-14	-5	37	-1.08	0.29	-1	-9	8	42	-0.26	0.80
Trachypogon spicatus	*H. contortus*	-11	-28	10	30	-1.14	0.26	0	-15	17	27	-0.01	0.99
Forb													
Asteraceae	*H. contortus*				63	-1.52	0.13						
	2010 only	-6	-20	3									

[a] All details of analyses are in Appendix C.

[b] Insufficient cover to be analyzed in summer. Only a slight change for this species.

Table 1.3 Magnitude and direction of changes in total cover and density of all vegetation in two height strata with *H. contortus*, after accounting for covariates, including slope estimates that show a multiplicative changes in presence for every 10% increase in dominance of *H. contortus*, 95% confidence intervals, test statistics, and *P*-values, $n = 70$ plots, Jim Hogg County, Texas, 2010-2011.[a]

	Variable	Effect[b]	SUMMER					WINTER				
			Estimate	95% CI		*t*	*P*	Estimate	95% CI		*t*	*P*
Horizontal Structure	Ground cover [b]	*H. contortus*				3.58	0.0006				-2.78	0.007
		2010	3.21	2 04	4.37			-0.61	-1.91	0.69		
		2011	1.07	0.07	2.07			1.30	-0.01	2.61		
	Canopy cover [b]	*H. contortus*	0.95	0.40	1.51	3.44[c]	0.001				2.39	0.02
		2010						2.37	1.76	2.99		
		2011						1.60	0.98	2.21		
Vertical Structure	Density at ground-level	*H. contortus*				3.48	0.0009	2.09	-1.83	6.01	1.06[c]	0.29
		2010	10.99	5.90	16.08							
		2011	1.14	-3.23	5.51							
	Density at canopy-level	*H. contortus*				5.91	<0.0001	2.25	0.10	3.50	3.59[c]	0.0006
		2010	3.57	2.51	4.63							
		2011	0.00	-0.91	0.91							

[a] Estimates represent a linear change. Other details are reported in Appendices D and E.

[b] Absolute cover.

[c] $df = 68$. For analyses of all other variables, $df = 67$.
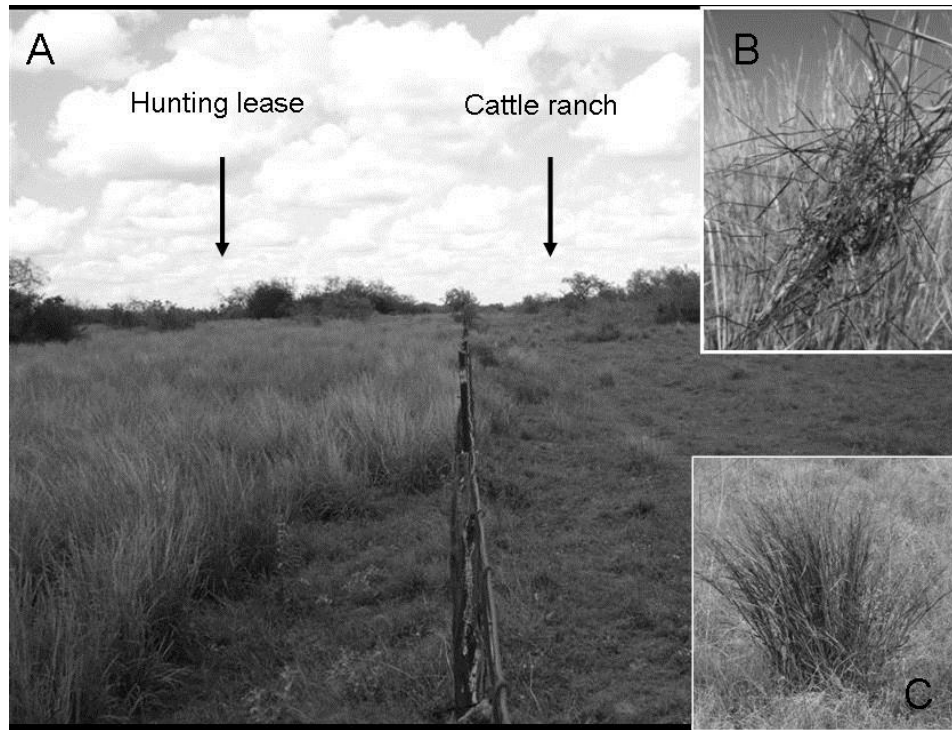
Figure 1.1 A) *Heteropogon contortus* can form almost complete monocultures, as depicted on the left side of the fence. Differences in grazing pressure have been postulated as one cause for the recent change in *H. contortus* dominance. Additionally, the hunting lease (left) has more mechanical management, which also could explain differences in vegetation composition and structure. B) *H. contortus* is known as tanglehead (USA) or black-spearhead grass (Africa and Australia) because of the seed heads. C) *H. contortus* is a tall grass with a closed canopy structure. Most other grasses in the picture are *Aristida* spp. and *E. lehmanniana*, which are structurally very different from *H. contortus*. In locations with *Schizachyrium scoparium*, another tall grass, structural differences are less pronounced.

SUMMER

WINTER
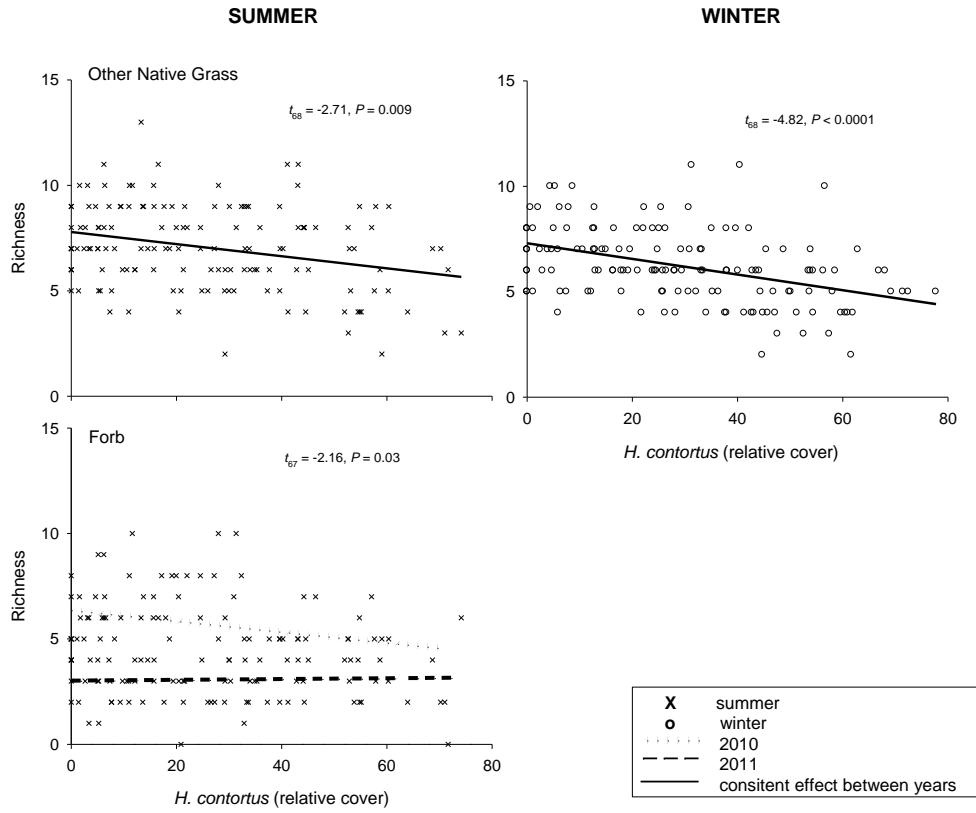
Figure 1.2 Changes in richness of other native grasses and forbs with increased *H. contortus*.

SUMMER

WINTER

Bare Ground $t_{67} = -1.77, P = 0.07$ $t_{68} = -2.38, P = 0.02$

Litter $t_{68} = -0.11, P = 0.9$ $t_{68} = 1.75, P = 0.08$

Other Native Grass $t_{67} = -3.73, P = 0.0004$ $t_{68} = -25.70, P < 0.0001$

Nonnative Grass $t_{68} = 1.00, P = 0.32$ $t_{68} = 1.02, P = 0.31$

Forb $t_{67} = -3.85, P = 0.0003$

H. contortus (relative cover)

X   summer
o   winter
      2010
      2011
      consitent effect between years

H. contortus (relative cover)
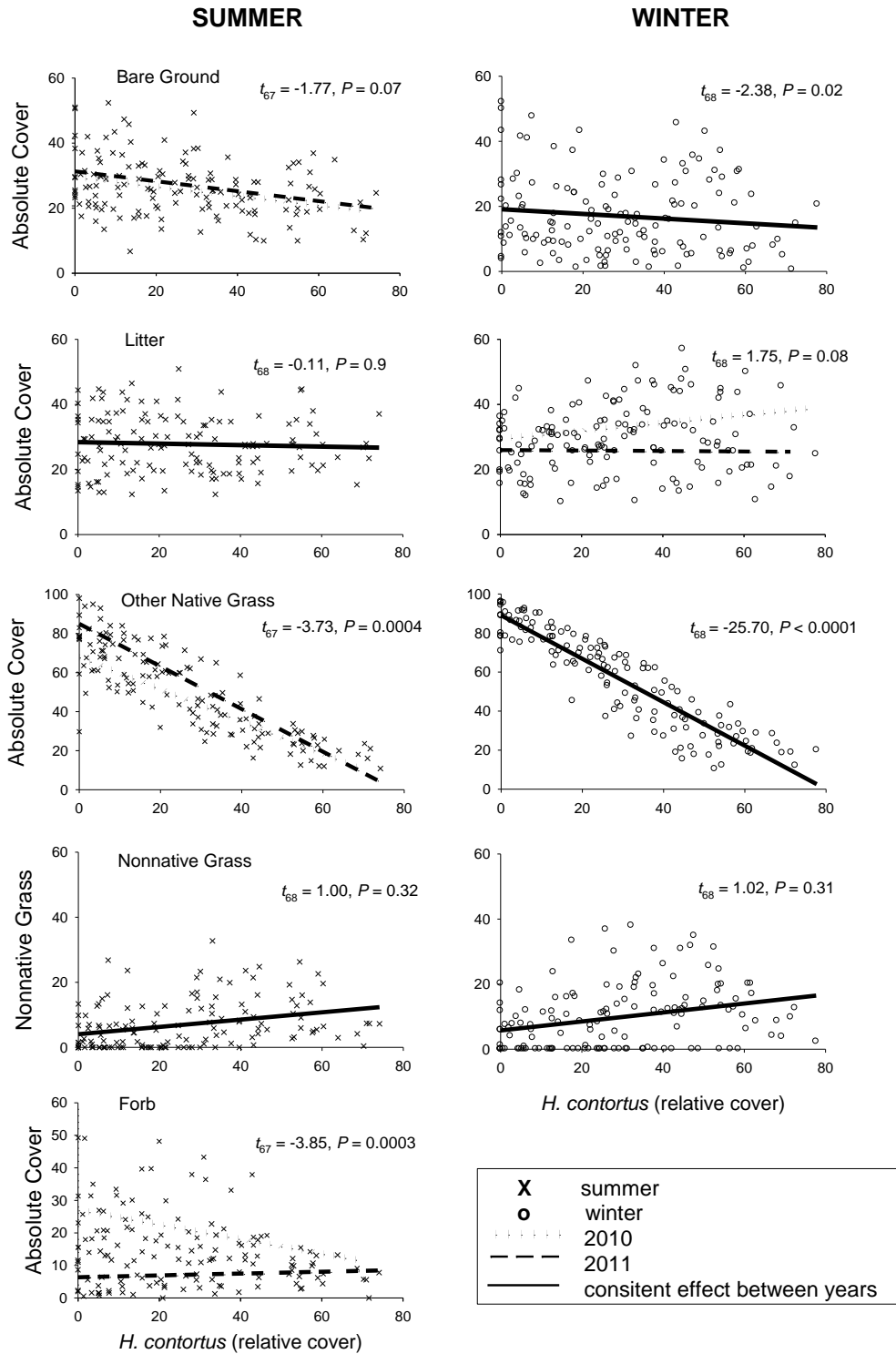
Figure 1.3 Changes in cover (absolute cover) of bare ground, litter, other native grasses, nonnative grasses, and forbs with increased *H. contortus*.
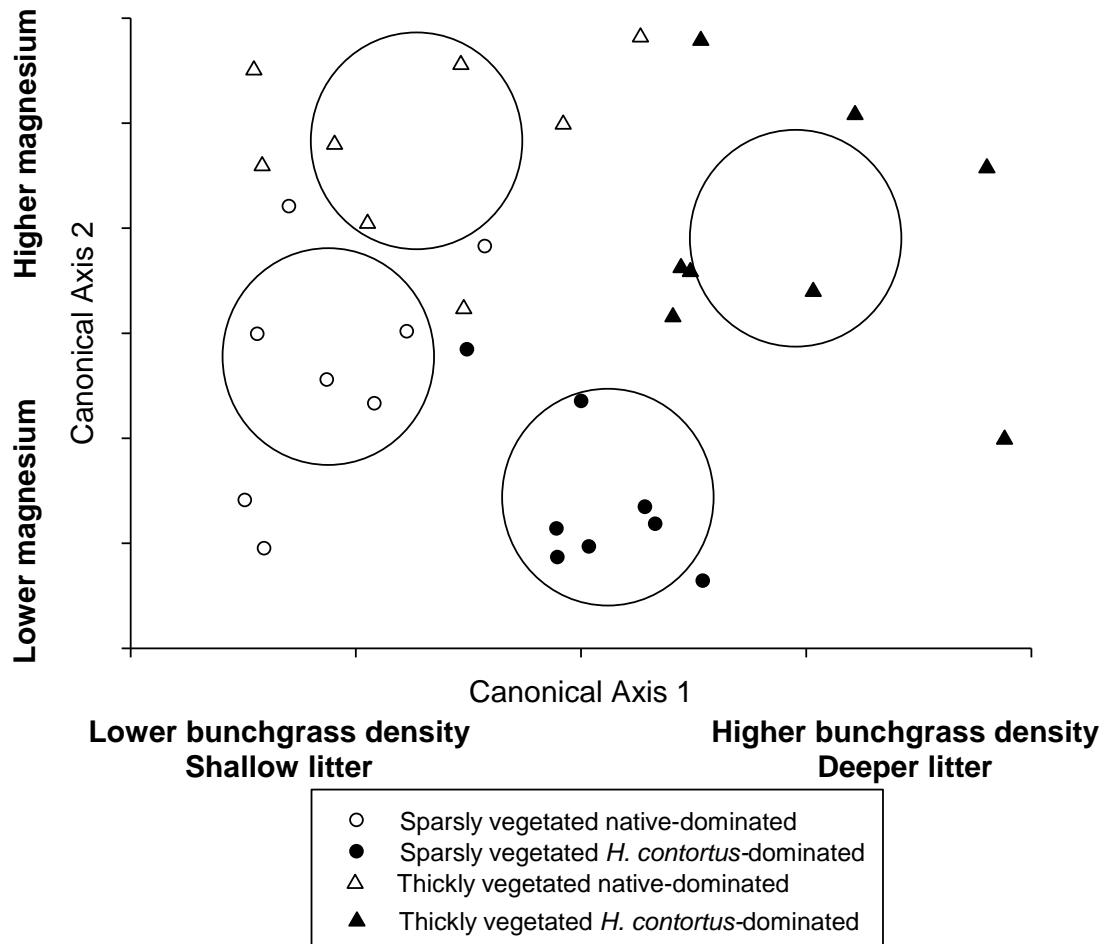
Figure 1.4 Differences among vegetation sub-communities based on vegetation and soil variables most related to canonical axes 1 and 2 from the discriminant function analysis. Large circles represent 95% confidence intervals for the mean.

31
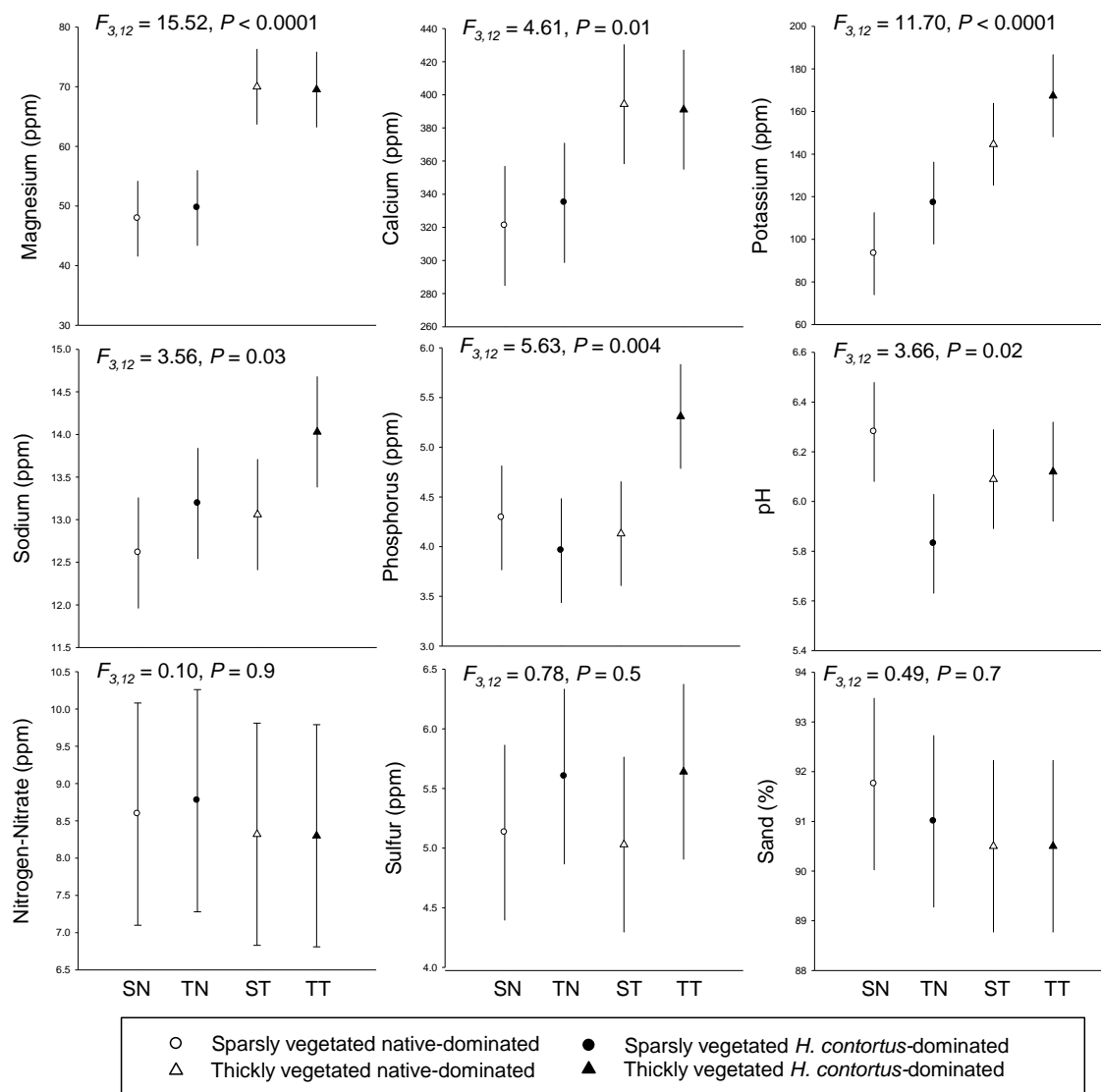
Figure 1.5 Means and 95% confidence intervals for soil characteristics in each vegetation sub-community ($n = 16$), June 2011, Jim Hogg County, Texas. We did not examine differences in silt content because it was a minor and often absent component in samples; silt averaged 1.85% of the soil texture.

CHAPTER II: HOME ON THE RANGE OR HABITAT LOST? RESPONSE OF GRASSLAND BIRDS TO INCREASED DOMINANCE OF HETEROPOGON CONTORTUS

ABSTRACT

As invasive grasses become more dominant, breeding grassland birds may experience a tradeoff between negative effects, such as decreased food resources, and positive effects, such as better nest concealment. I documented changes in the avian community across a gradient of dominance by an invasive-like native grass, *Heteropogon contortus* (tanglehead), and related differences to corresponding changes in vegetation structure and composition. With increased *H. contortus*, vegetation structure was taller, denser, and less diverse, which ought to have an overall negative effect on avifauna. However, presence or density of Mourning Dove (*Zenaida macroura*), Lark Sparrow (*Chondestes grammacus*), Cassin's Sparrow (*Peucaea cassinii*), and Eastern Meadowlark (*Sturnella magna*) increased with *H. contortus*, whereas only Scissor-tailed Flycatcher (*Tyrannus forticatus*) and Brown-headed Cowbird (*Molothrus aeneus*) decreased in presence or density with *H. contortus*. For Scissor-tailed Flycatcher and Cassin's Sparrow, both presence and density changed with *H. contortus*. Presence of Cassin's Sparrow increased by 40% (95% CI = 10 to 77) and density increased by 13% (2 to 26) for every 10% increase in *H. contortus*, whereas presence of Scissor-tailed Flycatcher (*Tyrannus forticatus*) decreased by 19% (-35 to 3) and density decreased by 10% (-18 to -2). Avian responses to *H. contortus* also varied by year, which may be related to differences in vegetation created by varying precipitation. Although increased dominance of *H. contortus* results in similar changes to the vegetation community as a nonnative invasive plant, the avian community did not provide evidence this native plant would have serious implications for grassland birds, as long as precipitation promotes growth of other native plants.

Keywords: nest concealment; community composition; density; native invasive; precipitation; presence; vegetation structure

INTRODUCTION

Declines in populations of grassland birds have been greater and more widespread than birds from any other ecological group (Knopf 1994). Despite much recent conservation focus, populations of more than 50% of grassland bird species in North America continue to decline (North American Bird Conservation Initiative 2011, 2009; Sauer et al. 2011). Decreases in populations of grassland birds have been fueled primarily by habitat loss (Samson and Knopf 1994; Brennan and Kuvlesky 2005). Although habitat loss is slowing in some areas (Bock et al. 1999), continued declines of grassland birds may be spurred by secondary factors associated with habitat loss such as fragmentation, woody encroachment, altered fire regimes and grazing patterns, loss of keystone species, and increased dominance of invasive plants (Peterjohn and Sauer 1999; Scheiman et al. 2003; Brennan and Kuvlesky 2005). Additionally, many anthropogenic effects are interrelated – for example, fragmentation, grazing, and altered fire regimes can promote increased dominance by invasive plants – creating complex challenges for conservation.

Increased dominance of invasive plants can modify plant diversity and vegetation structure (Belcher and Wilson 1989; Davies and Svejcar 2008; Litt and Steidl 2010), which can affect quantity and quality of habitat for breeding grassland birds. Changes in vegetation composition and structure associated with invasive plants may create conditions that no longer meet habitat requirements for some species of grassland birds, but improve habitat conditions for other species. For some birds, changes in vegetation structure may provide better concealment from predators or result in higher nest success (Schmidt et al. 2005; Winter et al. 2005). However, changes in plant composition also can reduce abundance and diversity of arthropod prey (Jonas et al. 2002; Tallamy 2004; Litt and Steidl 2010) and seed resources. Further, changes in vegetation structure can affect arthropod diversity and abundance negatively (Samways and Moore 1991; Kruess and Tscharntke 2002; Litt and Steidl 2010), diminish the ability to detect prey or predators (Devereux et al. 2005; Whittingham and Devereux 2008; Kennedy et al. 2009), and result in reduced nest success (Lloyd and Martin 2005).

Although nonnative invasive plants are a major threat to biodiversity (Wilcove et al. 1998), some native plants also can spread rapidly and become dominant within the ecosystem and geographic range in which they evolved, creating effects on plant communities similar to

34

invasive plants (e.g., de la Cretaz and Kelty 1999; Valéry et al. 2004; Vallés et al. 2011; Georges et al. 2011). The increased dominance, rapid spread, and negative ecological effects of some native plants within their evolved ecosystem have led to the term "native invasive species" (Valéry et al. 2008, 2009; Simberloff 2011). Similar to nonnative invasive plants, native invasive plants can alter soil nutrients, vegetation composition and structure (Vallés et al. 2011), and diversity and abundance of the arthropod community (Pétillon et al. 2005, 2008; Georges et al. 2011), creating a complex management challenge (Carey et al. 2012). Native invasive plants that affect vegetation and arthropods also have the potential to affect vertebrates, such as grassland birds.

Heteropogon contortus (tanglehead) is perennial bunchgrass native to arid regions throughout the world, including Texas, Arizona, and New Mexico (Reverchon 1886a, 1886b; Gould 1978). Historically, *H. contortus* was a minor component of southwestern grasslands, but conditions have changed in areas of southern Texas over the past 15 years that may have allowed *H. contortus* to form dense, near-monocultures. *Heteropogon contortus* may represent a native invasive plant because of its origin, rapid spread and dominance, and effects on the plant community, but the recent increased dominance of *H. contortus* also could be the result of a nonnative variety (Chapter 1). Regardless of origin, changes in vegetation composition and structure (Chapter 1) and insect communities (Cord 2011) associated with increased dominance by *H. contortus* may have concomitant effects on grassland bird communities.

I sought to quantify the effects of increased dominance by *H. contortus* on breeding grassland birds. Changes in vegetation composition and structure resulting from increased *H. contortus* could modify population characteristics and the composition of the avian community because grassland birds rely on characteristics of the plant community to produce food, provide protection from predators, and influence nest site selection. I hypothesized that changes in vegetation characteristics associated with increased dominance by *H. contortus* would alter the avian community, relative to areas dominated by other native plants. I expected that increased dominance of this native plant generally would have negative effects on the avian community, but conditions created could benefit a few species of grassland birds, similar to nonnative invasive plants (Bock et al. 1986; Wilson and Belcher 1989; Scheiman et al. 2003; Hickman et al. 2006; Flanders et al. 2006).

STUDY AREA

I studied areas of relatively open grasslands that represented a gradient of dominance by *H. contortus*, located on the Borregos and Alta Vista ranches (~19 km apart) in Jim Hogg County, Texas, where increases in dominance of *H. contortus* initially were observed (F. Bryant, personal communication). The climate is both semiarid and subtropical, with highly variable rainfall (Fulbright et al. 1990). The growing season in the area lasts for more than 300 days per year (United States Department of Commerce 1970), typically between February and November (F. Smith, personal communication). The study area lies within the Tamaulipan Biotic Province (Dice 1943) and has vegetation characteristics of the coastal sand and southern Texas plains communities as described in Diamond and Fulbright (1990), Fulbright et al. (1990), and Gould (1975, 1978), because the study area occurs at the convergence of both communities. Soils are classified as Nueces fine sand (United States Bureau of Soils 1910), which has a texture of sand to loamy sand. Although grasses and areas of brush always have characterized the region (Fulbright et al. 1990), density of woody vegetation currently may be higher than historic conditions (Johnston 1963; Schmidly 2002).

Dominant native grasses in the study area include *H. contortus*, *Trachypogon spicatus* (spiked crinkleawn), *Paspalum plicatulum* (brown-seed paspalum), *Schizachyrium scoparium* var. *littorale* (seacoast bluestem)*,* and *Elionurus tripsacoides* (Pan-American balsam scale). These grasslands are interspersed with old dunes and sandy ridges characterized by bare ground, *Aristida oligantha* and *A. purpurea* (threeawn species), and *Monarda punctata* (spotted beebalm), where *H. contortus* is nearly absent (Chapter 1). Nonnative *Eragrostis lehmanniana* (Lehmann lovegrass) is common at Borregos, *Pennisetum ciliare* (buffelgrass) is common within burned-out mottes and brushy areas, and *Melinis repens* (natal grass) is relatively rare at both ranches; all nonnative grasses are more common within cattle traps. Woody vegetation is contained mainly in small chaparral thickets and mesquite mottes (stands of trees and brush). Mottes are interspersed within the grasslands and are comprised primarily of *Prosopis glandulosa* (honey mesquite) and the plants dependent on *P. glandulosa* for growth. Common woody plants within mottes include *Celtis pallida* (granjeno), *Opuntia* spp. (prickly pear), *Condalia hookerii* (brasil), and *Diospyros texana* (Texas persimmon). Most woody vegetation

occurs within mottes, although some shorter woody species, such as *Acacia greggii* (catclaw) and *Colubrina texansis* (Texas hogplum), are interspersed among the grasses.

Mechanical management activities in these grasslands were similar and minimal; during the study period, activities were limited to disking and mowing along fence lines and occasional mowing of a two-track lane. The stocking rate has been maintained at 1 animal unit/12 ha for the last 15 years, which is lower than the rate maintained 30 years ago (1 animal unit/4 ha; W. Jones, personal communication). Although there are no exact fire records, fires did not occur for at least three years prior to or during our study (W. Jones, personal communication).

Extreme differences in annual rainfall are characteristic of grasslands in Arizona, New Mexico, and Texas (e.g., Reynolds and Krausman 1998; Bock and Bock 1999). Our study occurred during a period of extreme fluctuations in precipitation. This region experienced a severe drought between 2008 and fall 2009, followed by one of the wettest years in a century in 2010, followed by the worst drought ever documented, which began in late 2010 and extended through 2011 (National Weather Service 2010, 2011, 2012). Based on National Oceanic and Atmospheric Administration (NOAA) weather stations within 60 km of each ranches, rainfall averaged 19.02, 32.89, and 10.49 cm in 2009, 2010, and 2011, respectively (National Climatic Data Center 2011). Therefore, summer sampling periods occurred during a wet (2010) and dry (2011) growing season.

METHODS

Plot Selection

I randomly selected 70 study plots based on a series of criteria. Using ArcView GIS 10, I generated random points across the study area that were >325 m apart, >150 m from large woody thickets, and >125 m from caliche roads and fences. I located points in the field and selected those with <30% woody vegetation and <20% relative cover of nonnative grasses within a 125-m radius, and collectively represented the gradient of dominance by *H. contortus*. I marked selected points with a single t-post, which denoted the center of each study plot. Dominance of *H. contortus* ranged from 0 to 80% relative cover (0 to 60% absolute cover) during the two years of this study.

Vegetation Sampling

On each plot, I quantified vegetation characteristics in June 2010 and 2011 along two, perpendicular, 250-m transects passing through the plot center. I sampled at 17 locations/plot, each 30 m apart, with eight locations on each transect and one at the plot center. At each sampling location, I used a 0.5 x 0.5-m quadrat, elevated 1-m high, to record horizontal cover of bare ground, litter, and each plant species in 5% increments (Daubenmire 1959). If >5% of the quadrat was dominated by woody vegetation, I shifted the sampling location slightly. I quantified horizontal cover and vertical density of the herbaceous vegetation in two height strata (<0.4 and ≥0.4 m tall) because birds may be able to move below the grass canopy if the cover remains unchanged at the ground level. I quantified vertical density of the vegetation with a Wiens pole (Wiens and Rotenberry 1981), placed randomly at one corner of each quadrat; I recorded the number of times each plant species contacted each 0.1-m increment on the pole. I also measured litter depth at one corner of the quadrat and recorded the number of bunchgrasses and maximum height (cm) within each quadrat.

Motte Sampling

Because density of woody vegetation could affect community or population characteristics of breeding birds, I quantified characteristics of mesquite mottes, which are the most prominent woody vegetation on this landscape. I defined mesquite mottes as stands of brush with at least three plants ≥2 m tall, with at least two *P. glandulosa* and nursery plants that depend upon *P. glandulosa* for shade. I quantified motte characteristics by mapping all potential mottes within a 125-m radius of each plot center with ArcView 10 and ground-truthing maps to determine which mottes met our definition. For all confirmed mesquite mottes, I estimated maximum height to the nearest 0.5 m and computed the average motte height for each plot in 2010 and 2011. In 2010, I also used GIS to compute total motte area for each plot.

Avian Sampling

I surveyed breeding birds with point counts from the center of each plot and used a rangefinder to record precise distances to each individual detected aurally or visually, by species (Buckland et al. 2001). A single observer surveyed for 10 minutes, after a 1-2 minute settling period (Ralph et al. 1993, 1995), between 0.5 hours before and 3.5 hours after sunrise. I surveyed birds on each plot five times/year from April 8-June 3, 2010 and April 4-June 10, 2011, to coincide with the timing of breeding behavior, and completed each set of surveys within 11 days. To minimize any potential biases in detection related to time and weather, I rotated the order plots were surveyed and did not survey points when precipitation exceeded a light mist or when average wind speeds were $\geq$19 kph (Martin et al. 1997). Survey time and weather variables were not correlated with *H. contortus* dominance ($|r| < 0.32$ for all variables).

ANALYSIS

I examined differences in vegetation composition and structure and community- and population-level characteristics of breeding birds along the gradient of *H. contortus* dominance. I used percent of total vegetation cover represented by *H. contortus* (i.e., relative cover) to characterize the dominance gradient. I quantified species richness of other native grasses and forbs per quadrat, based on estimates of cover; I did not include *H. contortus* in calculations of richness. I examined variation in horizontal and vertical structure of ground- and canopy-level vegetation along the gradient of *H. contortus* dominance. I quantified changes in total cover (i.e., absolute cover of all non-woody vegetation), as well as relative cover of individual plant groups (i.e., other native grasses, forbs, and nonnative grasses). I categorized total cover and total Wiens pole contacts into two height categories: ground level (<0.4 m tall) and canopy level ($\geq$0.4 m). Finally, I converted the number of bunchgrasses within each quadrat to density/m^2 by multiplying by four. For most structural variables, I averaged data from all quadrats to compute a single value for each plot; however I computed the total number of contacts with the Wiens pole.

I restricted our focus to grassland birds, as I predicted this group would be most affected by changes created with increased dominance by *H. contortus* because the majority of their life

cycle occurs within grasslands. Although I documented all birds during surveys, those detected >162 m from the point (½ the distance to the next closest possible point) and flyovers were excluded from analyses to reduce the potential for double-counting. I used Vickery et al. (1999) to distinguish between obligate and facultative grassland and non-grassland birds, and classified species further based on migration status (Appendix F). I consider both Grasshopper Sparrow (*Ammodramus savannarum*) and Ash-throated Flycatcher (*Myiarchus cinerascens*) as permanent residents because Grasshopper Sparrow will breed in the region after extremely wet winters (T. Langschied, personal communication) and Ash-throated Flycatcher will winter in the region, but the abundance varies annually.

At the community-level, I assessed changes in avian species richness, or the total number of breeding species/plot. I excluded Grasshopper Sparrow from richness computations in summer 2011, as this species was present as a migrant earlier in the season but did not breed. At the population-level, I examined changes in presence and density of avian species. I used presence as an indication that an area provided habitat and density as a measure of habitat quality, although I acknowledge that density alone may not provide a complete understanding of habitat quality (Van Horne 1983). To assess variability in presence across the dominance gradient, a species could not be extremely common or rare, meaning a species had to be present on 10-90% of plots (i.e., 7-63 plots). I defined presence as detecting at least one individual of a species on a plot during at least one survey. Based on this criterion, I examined changes in presence for nine species in both years; two additional species could be analyzed only in 2010 or 2011 (Appendices F and G).

I generated estimates of density (individuals/ha) to account for variation in detection probability with distance and among avian species (Buckland et al. 2001). I estimated density for species with ≥40 total detections using program DISTANCE 6.0 (Thomas et al. 2009). Birds were considered a group if ≥3 individuals were detected within 10 m of each other. I truncated data to improve fit of the detection function, but included birds detected within 125 m of the transect (Buckland et al. 2001). I considered uniform and hazard key functions with cosine or simple polynomial expansion terms and the half-normal key function with cosine or hermite polynomial expansion terms. I used density estimates from the model with the smallest Akaike's information criterion adjusted for small sample bias (AICc; Buckland et al. 2001) and analyzed

40

density only for plots where the species occurred. Based on these criteria, I assessed changes in density for seven species.

I used a generalized linear mixed model approach for all analyses and selected the appropriate distribution and link function for each response variable of interest (Littell et al. 2006). I accounted for repeated sampling on the same plots over time (i.e., years) by treating plots as subjects and incorporating a compound symmetric covariance structure (Littell et al. 2006). In addition to examining variation across the gradient of *H. contortus* dominance, I also included year and a year $\times$ *H. contortus* interaction in models to explore variation in responses over time and to determine if the effects related to *H. contortus* changed over time. I included site (i.e., ranch) as a blocking factor in all analyses to account for potential differences. For all analyses, I began with a full model that included block, relative cover of *H. contortus*, year, and a year $\times$ *H. contortus* interaction, but removed the interaction term if $P > 0.10$ to generate the best estimates of effects. Average motte height and area also were included as covariates in models for avian variables because woody vegetation could affect the species and abundance of grassland birds. I log-transformed density for individual bird species to meet model assumptions. I present slope estimates and 95% CIs in text and tables that represent multiplicative changes in cover for individual plant species and linear changes in other compositional and structural characteristics with every 10% increase in *H. contortus* cover. *Heteropogon contortus*-related effects are presented in the text and tables; details regarding additional covariates are presented in appendices.

In January 2011, several lanes (~2-2.5 m wide) were mowed on the Borregos Ranch, affecting 11 of our study plots. Although these lanes did not affect how I sampled or vegetation characteristics in sampled locations, reduced vegetation cover may have altered avian activity or facilitated predator movement. I detected little correlation between the size of the mowed area and dominance by *H. contortus* on the affected plots ($r = -0.26$). However, because two lanes were mowed on each of three plots, the total mowed area on each of these plots (range = 768-1161 m^2) greatly exceeded that observed on the other nine plots (range = 370-572 m^2). I excluded the data from these three plots from analyses of avian characteristics in 2011 as a precaution.

RESULTS

Vegetation

In general, with increased dominance of *H. contortus*, total vegetation cover increased, whereas bare ground and plant richness decreased (Table 2.1, pg. 59). Total cover at the canopy level increased 1.0% (95% CI = 0.4 to 1.5) with each 10% increase of *H. contortus*. Although total cover at the ground level increased 3.2% (2.0 to 4.4) in 2010 and 1.1% (0.7 to 2.1) in 2011 with each 10% increase of *H. contortus*, cover of other native grasses and forbs decreased such that the increase in total cover was predominately due to *H. contortus* (Table 2.1, pg. 59). Cover of other native grasses decreased 7.5% (-8.8 to -6.2) in 2010 and 10.4% (-11.5 to -9.2) in 2011 with each 10% increase of *H. contortus*. Cover of forbs decreased 2.1% (-3.2 to -1.1) with each 10% increase of *H. contortus* in 2010 and did not differ in 2011. Cover of nonnative grasses and litter did not differ over the gradient of *H. contortus*, but cover of bare ground decreased 2.4% (-3.5 to -1.3) in 2010 and 1.1% (-2.1 to -1.7) in 2011 with each 10% increase of *H. contortus* (Table 2.1, pg. 59). Richness of other native grasses decreased 0.19 species/0.25 m^2 (-0.33 to -0.05) for every 10% increase in *H. contortus* (t_{68} = -2.7, P = 0.009). Forb richness decreased 0.27 species/0.25 m^2 (-0.49 to -0.04) in 2010 with each 10% increase in *H. contortus*, but did not differ in 2011 (t_{67} = -2.2, P = 0.03).

Vertical density of vegetation increased with *H. contortus*, but the differences were detected only in 2010 (Table 2.1, pg. 59). Vertical density of vegetation at the ground level increased by 11.0 contacts (95% CI = 5.9 to 16.1) and vertical density at the canopy level increased by 3.6 contacts (2.5 to 4.6) with each 10% increase of *H. contortus* in 2010, but neither differed in 2011. Over the gradient of *H. contortus*, bunchgrass density increased and vegetation height changed, but the direction of the effect differed by year (Table 2.1, pg. 59). Bunchgrass density increased 0.8 plants/m^2 (0.7 to 1.0) in 2010 and 0.1 plants/m^2 (0.00 to 0.3) in 2011 with each 10% increase of *H contortus*. Average vegetation height increased 3.1 cm (1.8 to 4.4) in 2010, but slightly decreased -0.1 cm (-1.2 to 0.1) in 2011 with each 10% increase of *H contortus*. Litter depth increased 0.07 cm (0.02 to 0.13) with each 10% increase of *H contortus* in 2011, but did not differ in 2010.

Avian Community

I detected 96 species of birds in summer, including 30 species of migrants and 51 breeding species; fifteen of these species breed locally, but not within the study area (Appendix F). I detected 19 species of grassland birds breeding on plots (16 each in 2010 and 2011) and 13 of these were detected breeding in both years, but I were able to analyze presence or density for 11 species. I detected differences in presence or density for 55% (6 of 11) of breeding grassland birds across the gradient of *H. contortus* (Table 2.2, pg. 60). For five species, changes in presence or abundance in response to *H. contortus* differed between years (Figs. 2.1, pg. 61 and 2.2, pg. 62). In addition, richness of breeding grassland birds increased 0.2 species (95% CI = 0.0 to 0.3) for every 10% increase of *H. contortus*, or approximately two species across the entire dominance gradient (t_{65} = 2.19, P = 0.03).

I analyzed data for three species of obligate grassland birds, all were permanent residents, and two increased in presence or density with *H. contortus*. For every 10% increase in *H. contortus*, presence of breeding Cassin's Sparrow (*Peucaea cassinii*) increased 40% (95% CI = 10 to 77) and density increased 13% (2 to 26%) in 2010, but I did not detect changes of density in 2011 (Figs. 2.1, pg. 61 and 2.2, pg. 62). Presence of breeding Eastern Meadowlark (*Sturnella magna*) increased 45% (7 to 98) with every 10% increase in *H. contortus* in 2010; presence in 2011 and density did not differ (Fig. 2.1, pg. 61). I did not detect differences in presence or density of Grasshopper Sparrow or density of Eastern Meadowlark (Table 2.2, pg. 60).

Four of eight species of facultative grassland birds differed in presence or density with *H. contortus* (Table 2.2, pg. 60), but Scissor-tailed Flycatcher (*Tyrannus forticatus*) and Western Kingbird (*Tyrannus verticalis*) were the only two species that were not permanent residents. Density of Mourning Dove (*Zenaida macroura*) increased 10% (95% CI = 1 to 21) with every 10% increase in *H. contortus* during 2010 (Fig. 2.2, pg. 62), but I did not detect differences in density in 2011 or presence in either year (Table 2.2, pg. 60). For every 10% increase in *H. contortus*, presence of breeding Lark Sparrow (*Chondestes grammacus*) increased 27% (-4 to 69). Presence of Brown-headed Cowbird (*Molothrus aeneus*) decreased 34% (4 to 54) with every 10% increase in *H. contortus* in 2011, but did not differ in 2010. Presence of Scissor-tailed Flycatcher decreased 19% (-35 to 3, Fig. 2.1, pg. 61) and density decreased 10% (-18 to -2) with every 10% increase in *H. contortus* in 2011, but did not differ in 2010 (Fig. 2.2, pg. 62).

I did not detect differences in presence or density of Northern Bobwhite (*Colinus virginianus*), Common-ground Dove (*Columbina passerina*), Ash-throated Flycatcher, and Western Kingbird with *H. contortus* (Table 2.2, pg. 60).

DISCUSSION

Invasions by nonnative plants generally result in decreases in plant diversity and changes in vegetation structure, which can reduce the quantity or quality of habitat for breeding grassland birds. Changes in vegetation structure may mean that invaded areas no longer function or are recognized as habitat for some bird species. For example, Savannah Sparrow requires some bare ground and moderate grass height for foraging (Weins 1969; Wheelwright and Rising 2008) and this species generally is less abundant when nonnative plants alter these features (Scheiman et al. 2003; Bakker and Higgins 2009). Even if an invaded area can still provide habitat for nesting or foraging, invasive plants may alter habitat quality. Nonnative plant invasions can result in reduced abundance or diversity of arthropods (Samways and Moore 1991; Jonas et al. 2002; Tallamy 2004; Litt and Steidl 2010) or seeds (Gan et al. 2010), which contributes to lower avian abundance (Flanders et al. 2006; Hickman et al. 2006). If food resources are not affected, then dense vegetation cover often associated with nonnative invasive plants may reduce the ability of birds to find available food resources (e.g., ground-dwelling Coleoptera [Kennedy et al. 2009]) or interfere with predator detection (Devereux et al. 2005). Further, dense cover around the nest may result in the incubating adult being less able to detect and escape predators (Götmark et al. 1995; Devereux et al. 2005). All of these changes may lead to regional decreases in avian populations because nonnative invasive plants often result in lower nest success (Borgmann and Rodewald 2004; Lloyd and Martin 2005; Rodewald et al. 2010).

Although changes in vegetation with plant invasions may result in areas no longer meeting habitat requirements for some species of grassland birds, habitat conditions may be improved for other species (e.g., Schmidt et al. 2005; Grant et al. 2006; Kennedy et al. 2009). For example, although increased dominance of nonnative *E. lehmanniana* creates conditions that do not meet the habitat requirements for many breeding grassland birds, increased cover benefits breeding activities for Botteri's Sparrow (*Aimophila botterii*; Bock et al. 1986; Jones and Bock 2005). Changes in vegetation characteristics associated with nonnative invasive plants also may

benefit some grassland bird species by increasing abundance of some arthropod groups (e.g., Bock et al. 1986; Jonas et al. 2002; Pétillon et al. 2008; Litt and Steidl 2010). However, the most abundant foods may not provide all nutrients required for reproduction or other life stages, such that increases in abundance of arthropods may not translate to benefits for birds (Robel et al. 1995). In addition, dense vertical and horizontal structure associated with some nonnative invasive plants can benefit birds if individuals are better concealed from predators during foraging (Jones and Bock 2005; Whittingham and Devereux 2008) or may better conceal nests from predators and result in higher nest success or fledgling survival (Scheiman et al. 2003; Schmidt et al. 2005; Winter et al. 2005). All of these changes could lead to regional population increases for a few species because higher nest success often means birds will use the site in subsequent years (Haas 1998; Hoover 2003; Ortega et al. 2006).

Despite *H. contortus* being a native grass, increased dominance of this species could result in similar effects on grassland birds as nonnative invasive plants. Changes in vegetation composition and structure associated with increased dominance of *H. contortus*, such as increased height and decreased bare ground (Table 2.1, pg. 59), may be detrimental for some species, but beneficial for others. Increased bunchgrass density associated with *H. contortus* could create more available nest sites by providing a nesting substrate for many grassland birds. For example, Northern Bobwhite prefers dense, tall cover of bunchgrasses around the nest (Townsend et al. 2001; Lusk et al. 2006) and this species is equally likely to nest within *H. contortus* as other native grasses (Buelow 2009). With increased dominance of *H. contortus*, grassland birds may encounter fewer food resources, such as insects and seeds, given reductions in richness and cover of native grasses and forbs. Some food resources may still be available with *H. contortus* (Cord 2011; Chapter 1), but increased canopy cover and density with *H. contortus* could hinder detection of prey. A change in insects or the ability to detect prey with increased *H. contortus* is supported by decreased presence and density of Scissor-tailed Flycatcher (Table 2.2, pg. 60) because flycatchers generally use grassland for food resources, nest in trees rather than grasses, and a perch hunters that would be affected by changes to visibility (Regosin 1998); an additional flycatcher species, Eastern Phoebe (*Sayornis phoebe*), seemly also is affected negatively by decreased insects and visibility within *H. contortus* in winter (unpublished data). In contrast, dense canopy structure associated with *H. contortus*

could benefit ground-foraging species by providing better protection from aerial predators, such as accipiters, or better conceal nests.

Avian responses to *H. contortus* generally did not match what I would have predicted based on life history characteristics or previous research on nonnative invasive species. For example, I would have predicted decreases in presence or abundance of Northern Bobwhite, Mourning Dove, and Cassin's Sparrow with *H. contortus* because changes in vegetation would not seem beneficial given their habitat requirements. In addition, I would have predicted an increase or no change in occurrence of Brown-headed Cowbird with *H. contortus* because this species is a nest parasite that typically forages in human-altered ecosystems. Based on habitat requirements, I expected Lark Sparrow would have occurred less often within dense *H. contortus* because these areas had taller vegetation with little bare ground (Bock and Webb 1984; Martin and Parrish 2000). Similarly, Eastern Meadowlark requires shorter, sparser grasses for foraging, but selects dense cover of bunchgrasses for nesting (Wiens 1969; Bock and Webb 1984; Lanyon 1995).

Given that presence or density increased for four species of birds and richness increased in response to *H. contortus*, perhaps *H. contortus* benefits these species, whereas other invasive plants may be detrimental. Lark Sparrow may be using *H. contortus* for activities associated with breeding, conditional on proximity to adjacent roadways that have structure suitable for foraging because this species was only detected on plots with adjacent roadways; *H. contortus* is densest along caliche roads with disked shoulders, whereas most areas dominated by other native plants were farther from these disturbed areas (unpublished data). Although increases in presence of Eastern Meadowlark with *H. contortus* indicates increased dominance of this grass creates more nesting habitat, this insectivorous species likely would be faced with a tradeoff between selecting areas with abundant, diverse food resources (Cord 2011) and areas with quality nest sites. A similar tradeoff may exist for Mourning Dove, which requires shorter, sparse grasses and bare ground for foraging (Leopold 1972; Otis et al. 2008), although this species is less territorial and could fly to foraging sites that are farther from the nest site. Lark Sparrow, Eastern Meadowlark, and Mourning Dove may be able to benefit from *H. contortus* if individuals are able to select territories close to foraging habitat or if they find enough food such that they can benefit from increased nest concealment. Avian species may be able to persist despite changes in vegetation associated with invasive plants if they can capitalize on the most

readily available food. For example, reduced cover of bare ground by a nonnative grass better concealed ground beetles such that grassland birds consume fewer ground-dwelling beetles and more grasshoppers that are gleaned from the vegetation (Kennedy et al. 2009). Although our results tend to support that avifauna are able to benefit or persist within *H. contortus*, presence or abundance may not reflect nest success accurately (e.g., Remes 2003) and *H. contortus* could be an ecological trap (Schlaepfer et al. 2002).

Alternatively, the current invasion by *H. contortus* may not have reached a level that is detrimental to grassland birds, a possibility that may be exemplified by congeneric species, Cassin's Sparrow and Botteri's Sparrow. Cassin's Sparrow requires grasslands with moderate grass cover and height (Bock and Webb 1984; Bock and Bock 1992; Dunning et al. 1999), whereas Botteri's Sparrow utilizes grasslands with taller and denser vegetation (Webb and Bock 1990, 1999; Jones and Bock 2005). As grass density increases with invasive grasses, I would expect that available habitat for Cassin's Sparrow would decrease (Bock et al. 1986; Flanders et al. 2006) and habitat for Botteri's Sparrow would increase (Jones and Bock 2005). However, I found that presence and density of Cassin's Sparrow increased with *H. contortus*. I observed a single Botteri's Sparrow – a territorial male – on the plot where *H. contortus* was most dominant (74% relative cover). Although the vegetation structure matches documented habitat requirements, this observation is surprising because Botteri's Sparrow should not be present within 70 km of the study area, given that it breeds within *Spartina* grasses closer to the Texas coast (Marshall and Clapp 1985). Results from Jones and Bock (2005) indicate that dense cover of invasive grasses may result in more available habitat for Botteri's Sparrow, allowing this species to expand their range from the historic, native plant communities into novel areas. Based on the habitat requirements for these two birds, perhaps the current degree of *H. contortus* invasion more closely matches habitat requirements of Cassin's Sparrow and other grassland birds but if *H. contortus* were to become denser throughout its range then there could be a similar shift in avian composition.

I assumed that changes in plant and arthropod communities created by increased dominance of *H. contortus* would have the same effects on grassland birds as invasion by a nonnative plant. However, *H. contortus* evolved within this region and, as a result, may benefit grassland birds in ways that a nonnative invasive plant does not. For example, increased abundance of *H. contortus* seeds could be beneficial to grasslands birds, if birds consume these

seeds. Increased dominance by a native plant may not affect abundance of insects that depend upon that plant negatively; abundance of Orthoptera is similar between *H. contortus* and other native grasses (Cord 2011). In contrast, encroachment of woody vegetation, another group of native invasive plants (Simberloff 2011; Carey et al. 2012), has effects comparable to nonnative plants and result in generally negative effects on birds (Coppedge et al. 2001; Grant et al. 2004; Klaus and Keyes 2007). However, this type of invasion greatly changes the dominant vegetation type from grassland to forest or shrublands, whereas the grassland ecosystem still is maintained despite increased dominance by *H. contortus*. Therefore, comparing our results to native woody plants that are invasive may not adequately explain why I found that a majority of bird species increased in presence or abundance with *H. contortus*. Additional research on native plants that are becoming invasive within their evolved ecosystem is required to better understand mechanisms for observed changes.

Precipitation and *H. contortus*

Avian responses to plant invasions can be altered by variability in climatic conditions, such as rainfall events or drought (e.g., Igl and Johnson 1997; Reynolds and Krausman 1998; Bock and Bock 1999). Changes in vegetation characteristics with *H. contortus* were greatest during the wet summer, which also was when I observed increases in Mourning Dove and Eastern Meadowlark; I observed decreases in Scissor-tailed Flycatcher and Brown-headed Cowbird with *H. contortus* during the drier summer. Therefore, plant invasions and precipitation may create interactive effects for birds that stem from changes in plant growth, vegetation structure, abundance of forbs and seeds (Chapter 1), and arthropod responses (Frampton et al. 2000; Cord 2011). I observed that the density of Scissor-tailed Flycatcher decreased with *H. contortus* only during the drought year, which could indicate that food resources were sufficient across the gradient of *H. contortus* during the wet year. Conversely, many of the birds that seemed to benefit from *H. contortus* during the wet year did not show similar responses during the drought, such that the additional stress of drought could alter the effects of *H. contortus*. Therefore, a more productive plant community during wet periods may offset any negative effects of *H. contortus* on grassland birds.

CONCLUSIONS

   When a plant increases in dominance, changes in vegetation composition and structure may have concomitant effects on birds. Grasslands dominated by *H. contortus* differ from grasslands with a diversity of native plants, resulting in changes in vegetation composition and structure (Chapter 1), diversity and abundance of arthropods (Cord 2011), and presence and abundance of grassland birds (Figs. 2.1, pg. 61 and 2.2, pg. 62). Native invasive plants may not have the same effects on grassland birds as the invasion by a novel, nonnative plant. Alternatively, changes in vegetation characteristics and other ecosystem components with *H. contortus* could create an ecological trap, which might not be detected based on presence or abundance. Regardless, avifauna likely face a tradeoff when selecting breeding sites given that *H. contortus* may increase the quantity or quality of nesting sites, whereas food abundance and foraging success may decrease. Increased dominance by *H. contortus* may benefit the overall avian community, but could pose a threat to conservation of grassland birds in combination with drought. Predictions from climate change models suggest that the climate in the southwestern United States will become drier (Christensen et al. 2007), which may mean the effects of the continued spread of *H. contortus* may result in mostly negative effects on grassland birds, similar to what I observed in the dry summer. Additional research on demographic changes and the mechanisms driving avian responses are needed to inform management and conservation.

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Table 2.1 Multiplicative changes in the composition and structure of vegetation in two height strata for every 10% increase in dominance of *H. contortus*, as well as 95% confidence intervals, test statistics, and *P*-values, after accounting for covariates, $n = 70$ plots, Jim Hogg County, Texas, 2010-2011.[a] Where I detected interactions, I provide estimates for the effect of *H. contortus* in each year.

	Variable	Effect [b]	Estimate	95% CI		*t*	*P*
Composition (Absolute Cover)							
Ground-level	Litter	*H. contortus*	-0.04	-0.75	0.67	-0.11	0.92
	Bare ground	*H. contortus*				-1.88[b]	0.07
		2010	-2.42	-3.54	-1.30		
		2011	-1.13	-2.09	-1.72		
	Total veg cover [c]	*H. contortus*				3.58[b]	0.0006
		2010	3.21	2.04	4.37		
		2011	1.07	0.07	2.07		
	Native Grass	*H. contortus*				3.73[b]	0.0004
		2010	-7.48	-8.80	-6.16		
		2011	-10.38	-11.51	-9.24		
	Nonnative Grass	*H. contortus*	0.31	-0.31	0.93	1.00	0.32
	Forb	*H. contortus*				-3.85[b]	0.0003
		2010	-2.13	-3.20	-1.06		
		2011	0.31	-0.61	1.23		
Canopy-level	Total cover [e]	*H. contortus*	0.95	0.40	1.51	3.44	0.001
Structure							
Ground-level	Litter depth (cm)	*H. contortus*				-2.62[b]	0.01
		2010	-0.01	-0.08	0.05		
		2011	0.07	0.02	0.13		
	Vertical density	*H. contortus*				3.48[b]	0.0009
	<0.4 m	2010	10.99	5.90	16.08		
		2011	1.14	-3.23	5.51		
	Bunchgrass	*H. contortus*				8.86[b]	<0.0001
	Density (m^2)	2010	0.81	0.66	0.97		
		2011	0.13	-0.00	0.26		
Canopy-level	Average height	*H. contortus*				4.55[b]	<0.0001
	(cm)	2010	3.07	1.76	4.38		
		2011	-0.09	-1.21	0.10		
	Vertical density	*H. contortus*				5.91[b]	<0.0001
	≥0.4 m	2010	3.57	2.51	4.63		
		2011	0.00	-0.91	0.91		

[a] Other details are reported in Appendix D.

[b] *df* = 67. All other variables, *df* = 68.

[c] Total cover (absolute cover) = combined cover of *H. contortus,* other native and nonnative grasses, and forbs. Relative cover is presented for other native and nonnative grasses and forbs.

Table 2.2 Avian species that did not change with *H. contortus*. I present multiplicative changes in presence or abundance for every 10% increase in dominance of *H. contortus*, 95% confidence intervals, degrees of freedom, test statistics, and *P*-values, after accounting for covariates, $n = 70$ plots, Jim Hogg County, Texas, 2010-2011.[a] Where I detected interactions, I provide slope estimates for the effect of *H. contortus* in each year.

Grassland status and species	Variable		Estimate	95% CI		df	t	P
Obligate Grassland Species								
Grasshopper Sparrow [b]	Presence	2010	-6	-56	40	65	-0.29	0.78
	Density	2010	0	-27	37	23	0.03	0.98
Eastern Meadowlark [c]	Density		1	-7	11	31	0.32	0.75
Facultative Grassland Species								
Northern Bobwhite	Presence		-9	-29	17	65	-0.76	0.45
	Density		1	-6	8	39	-0.36	0.80
Mourning Dove [d]	Presence		2	-23	38	65	0.20	0.84
Common Ground-dove	Presence		-6	-23	14	65	-0.65	0.52
Ash-throated Flycatcher	Presence		4	-14	27	65	0.45	0.65
	Density		2	-8	4	10	-0.91	0.38
Western Kingbird [b]	Presence	2011	33	-18	116	65	1.20	0.23

[a] Slope estimates and confidence intervals have been back-transformed to show a multiplicative change (%) in presence or density for every 10% increase of *H. contortus*. Additional details are in Appendix H.

[b] Analyzed only in one year.

[c] Presence changed with *H. contortus* (Fig. 2.1, pg. 61), but density did not.

[d] Density changed with *H. contortus* (Fig. 2.2, pg. 62), but presence did not.
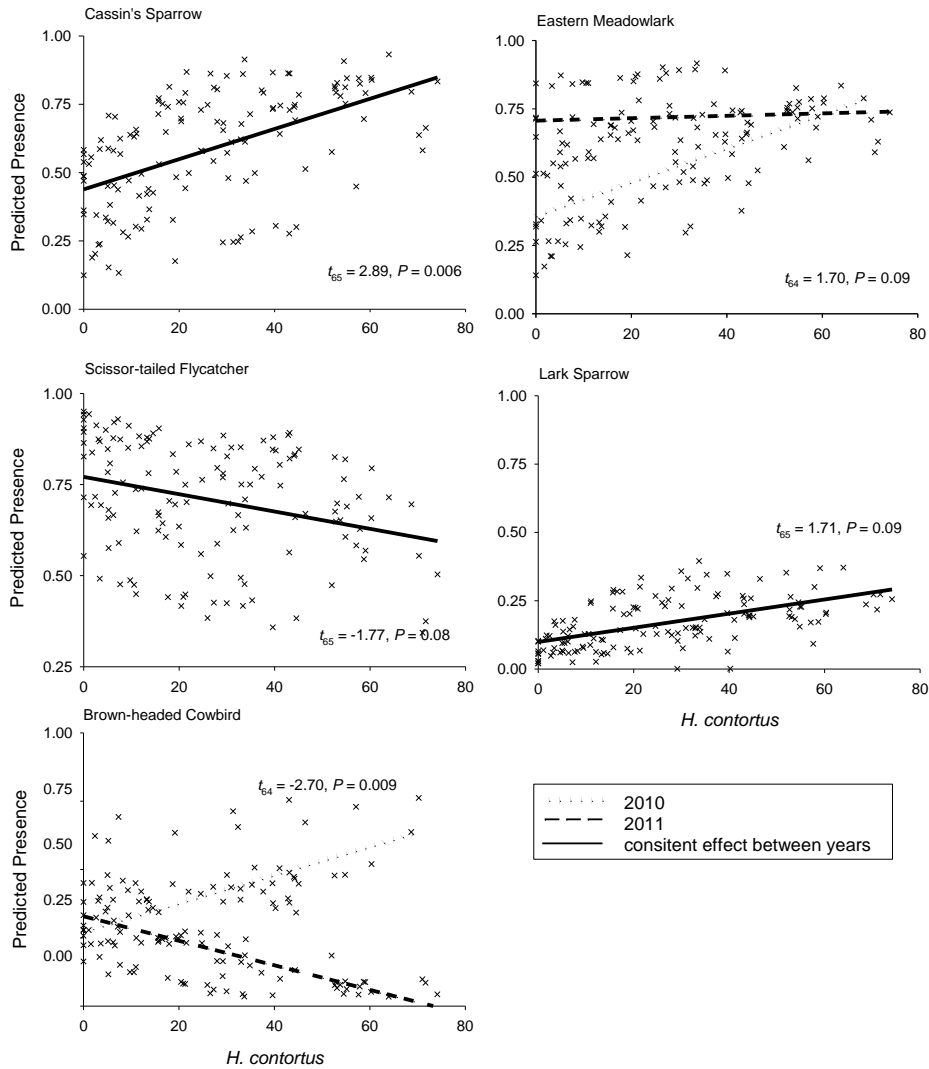
Figure 2.1 Changes in the probability of presence for species of obligate (Cassin's Sparrow and Eastern Meadowlark) and facultative grassland birds (Scissor-tailed Flycatcher, Lark Sparrow, and Brown-headed Cowbird) with increased *H. contortus*, based on predicted values from generalized linear models.
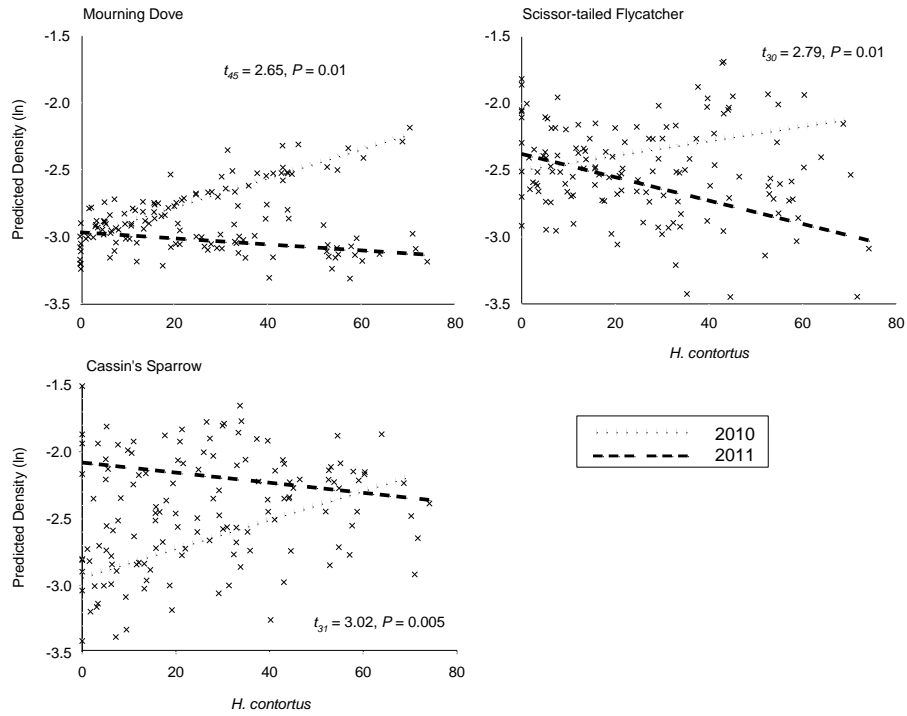
Figure 2.2 Multiplicative changes in density of obligate (Cassin's Sparrow) and facultative grassland birds (Mourning Dove and Scissor-tailed Flycatcher) with increased *H. contortus*, based on predicted values from generalized linear models. Data points were generated from predicted density.

CHAPTER III: A HOLISTIC APPROACH TO EVALUATING GRASSLAND BIRD RESPONSES TO INVASIVE PLANTS: ARE WE MISSING SOMETHING BY FOCUSING ON BREEDING BIRDS?

ABSTRACT

Invasive plants present a major conservation challenge for grassland birds, but avian responses to invasive plants may differ seasonally because habitat requirements for nesting likely differ from what is needed to survive winter and prepare for the next breeding season. I quantified the effects of *Heteropogon contortus*, a native grass with characteristics of an invasive plant, on breeding and wintering birds. Several bird species responded to increased *H. contortus*, but responses were inconsistent between seasons. For example, presence of Eastern Meadowlark (*Sturnella magna*) increased 45% (95% CI = 7 to 98) with every 10% increase in *H. contortus* during the breeding season, but decreased 30% (-52 to 1) during winter. Similarly, presence and density of wintering Grasshopper Sparrow (*Ammodramus savannarum*) decreased 40% (13 to 59) and 19% (10 to 27) for every 10% increase in *H. contortus*, but I did not detect differences for breeding birds. This trend was not detected for all species; presence of Cassin's Sparrow increased with *H. contortus* during both the breeding and wintering seasons. Breeding birds may benefit from changes in cover and structure of vegetation with *H. contortus* because nests would be better concealed, but wintering birds may avoid areas dominated by *H. contortus* because the need for nesting sites with dense cover is no longer applicable. Further research on the effects of invasive plants during multiple seasons is warranted because declines in bird populations may be further exacerbated by the negative effects of invasive plants on wintering grounds.

Keywords: density; grassland birds; *Heteropogon contortus*; native invasive; presence; wintering birds

INTRODUCTION

Grasslands are among the most endangered ecosystems in North America. More than 80% of all grasslands have been lost since European settlement, largely due to development associated with agriculture (Samson and Knopf 1994; Brennan and Kuvlesky 2005). Although the rate has slowed since the beginning of the 20th century, loss of grasslands is still occurring (Bock et al. 1999; Scheiman et al. 2003) and only 2% of all grasslands in the United States are publicly-owned and fully protected (North American Bird Conservation Initiative 2011). A number of factors have resulted in degradation of remaining grasslands, including fragmentation, increased dominance of invasive plants, and altered fire or grazing regimes. The overall reduction and lack of fully protected grasslands highlight the importance of conserving and restoring grasslands to benefit plants and wildlife.

Changes in quality and abundance of grasslands affect the wildlife dependent on this plant community. More than 50% of grassland bird species in North America are declining in abundance (Peterjohn and Sauer 1999; North American Bird Conservation Initiative 2009; Sauer et al. 2011); other taxa may show similar declines, resulting in an overall loss of ecosystem function. Declines of grassland bird populations have been greater and more widespread than birds from any other ecological group (Knopf 1994). Much attention has been placed on grassland birds because of these declines and the resulting increase in research and conservation of breeding and wintering habitat primarily within the United States ought to diminish population declines because most grassland birds are short-distance migrants.

Invasive plants are a major threat to biodiversity because they can alter plant communities and ecosystem function, with concomitant effects on animal communities (Bock et al. 1986; Wilcove et al. 1998; Christian and Wilson 1999; Davies and Svejar 2008; Litt and Steidl 2010, 2011). However, some native plants also can spread rapidly and become dominant within the ecosystem and geographic range in which they evolved, creating effects on plant communities similar to nonnative invasive plants (de la Cretaz and Kelty 1999; Valéry et al. 2004; Vallés et al. 2011; Chapter 1). With the exception of changes in insect communities (e.g., Pétillon et al. 2005; Nielsen et al. 2008; Cord 2011), responses of animals to native invasive plants rarely have been studied. Responses of larger vertebrates have been examined primarily in the context of invasions by nonnative plants and encroachment by woody species, both of

which involve invasion into novel or adjacent ecosystems. Studies quantifying responses to nonnative plants and woody encroachment have shown that, in general, avian communities are affected negatively (Bock et al. 1986; Wilson and Belcher 1989; Coppedge et al. 2001; Klaus and Keyes 2007), so I assume that native invasive plants also would negatively affect grassland birds.

Although breeding drives population increases (Latta and Baltz 1997; Clark and Martin 2007), wintering grounds also are important for avian conservation (Rappole and McDonald 1994; Marra et al. 1998; Rappole et al. 2003), but ecological studies generally are lacking on how ecological changes affect wintering grassland birds (Knopf 1994; Vickery et al. 1999; Vickery and Herkert 2001). Given that some birds, including grassland species, can be territorial in winter (e.g., Holmes et al. 1989; Plentovich et al. 1998; Latta and Faaborg 2002), they could be affected by ecological changes related to plant invasions occurring on wintering grounds. Adequately addressing declines in grassland bird populations likely requires a holistic approach to determine if invasive plants have the same effects on breeding and wintering populations. For example, invasive plants may provide excellent cover to reduce predation at nest sites, but could create low-quality habitat during post-breeding periods (Buelow 2009) because of decreased diversity and abundance of insects (Litt and Steidl 2010; Cord 2011) and other food resources. Considerable research has focused on the effects of invasive plants on breeding birds (e.g., Lloyd and Martin 2005; Hickman et al. 2006; Kennedy et al. 2009), but fewer studies have quantified the effects on wintering birds in grasslands (but see Bock et al. 1986; Woodin et al. 2010). Based on the few studies in grasslands and other ecosystems, I would expect responses of wintering birds to invasive plants to be negative (Bock et al. 1986; Gan et al. 2010; Woodin et al. 2010; but see Wilcox and Beck 2007; McCusker et al. 2010).

Grasslands in southern North America have ample populations of breeding, wintering, and resident birds, and thus provide an opportunity to examine variation in the effects of invasive plants on breeding and wintering grassland birds and consider the potential advantages of a holistic approach to conservation. Grasslands in south Texas provide an excellent study system because many grassland birds are permanent residents, there are more species of wintering than breeding grassland birds, and several species of invasive plants, including *Heteropogon contortus*, are prevalent in the region. *Heteropogon contortus* (tanglehead) is a perennial bunchgrass native to arid regions throughout the world, including Texas, Arizona, and New

Mexico (Reverchon 1886a, 1886b; Hatch et al. 1999), but also is invasive in portions of its range (Chapter 1). Historically, *H. contortus* was a minor component of southwestern grasslands, but conditions have changed in areas of southern Texas over the past 15 years that have allowed *H. contortus* to form dense, near-monocultures, resulting mostly negative effects on vegetation composition and structure (Chapter 1), insect communities (Cord 2011), and some breeding birds (Chapter 2).

I sought to quantify the effects of increased dominance by *H. contortus* on both breeding and wintering grassland birds. Specifically, I were interested in determining if the effects of increased *H. contortus* on birds were consistent in both seasons, despite seasonal variation in habitat requirements. I examined richness of the avian community, as well as presence and density of individual species across a gradient of dominance by *H. contortus*, which allowed us to draw inferences about thresholds where responses may change in direction and magnitude. I compared responses by season for several species that are residents or have breeding and wintering populations in the region.

STUDY AREA

I studied areas of relatively open grasslands that represented a gradient of dominance by *H. contortus*, located on the Borregos and Alta Vista ranches (~19 km apart) in Jim Hogg County, Texas, where increases in dominance of *H. contortus* initially were observed (F. Bryant, personal communication). The climate is both semiarid and subtropical, with highly variable rainfall (Fulbright et al. 1990). The growing season in the area lasts for more than 300 days per year (United States Department of Commerce 1970), typically between February and November (F. Smith, personal communication). The study area lies within the Tamaulipan Biotic Province (Dice 1943) and has vegetation characteristics of the coastal sand and southern Texas plains communities as described in Diamond and Fulbright (1990), Fulbright et al. (1990), and Gould (1975, 1978), because the study area occurs at the convergence of both communities. Soils are classified as Nueces fine sand (United States Bureau of Soils 1910), which has a texture of sand to loamy sand. Although grasses and areas of brush always have characterized the region (Fulbright et al. 1990), density of woody vegetation currently may be higher than historic conditions (Johnston 1963; Schmidly 2002).

Dominant native grasses in the study area include *H. contortus*, *Trachypogon spicatus* (spiked crinkleawn), *Paspalum plicatulum* (brown-seed paspalum), *Schizachyrium scoparium* var. *littorale* (seacoast bluestem)*,* and *Elionurus tripsacoides* (Pan-American balsam scale). These semiarid grasslands are interspersed with old dunes and sandy ridges characterized by bare ground, *Aristida oligantha* and *A. purpurea* (threeawn species), and *Monarda punctata* (spotted beebalm). Nonnative *Eragrostis lehmanniana* (Lehmann lovegrass) is common at Borregos, *Pennisetum ciliare* (buffelgrass) is common within burned-out mottes and brushy areas, and *Melinis repens* (natal grass) is relatively rare at both ranches; all nonnative grasses are more common within cattle traps. Woody vegetation in our study area is contained mainly in small chaparral thickets and mesquite mottes (stands of trees and brush). Mottes are interspersed within the grasslands and are comprised primarily of *Prosopis glandulosa* (honey mesquite) and the plants dependent on *P. glandulosa* for growth. Common woody plants within mottes include *Celtis pallida* (granjeno), *Opuntia* spp. (prickly pear), *Condalia hookerii* (brasil), and *Diospyros texana* (Texas persimmon). Most woody vegetation occurs within mottes, although some short, woody species, such as *Acacia greggii* (catclaw) and *Colubrina texansis* (Texas hogplum), are interspersed among the grasses.

Mechanical management activities in these grasslands were similar and minimal; during the study period, activities were limited to disking and mowing along fence lines and occasional mowing of a two-track lane. The stocking rate has been maintained at 1 animal unit/12 ha for the last 15 years, which is lower than the rate maintained 30 years ago (1 animal unit/4 ha, W. Jones, personal communication). Although there are no exact fire records, fires did not occur for at least three years prior to or during our study (W. Jones, personal communication).

Extreme differences in annual rainfall are characteristic of dry grasslands of the region, including Arizona, New Mexico, and Texas (e.g., Reynolds and Krausman 1998; Bock and Bock 1999). This region experienced a severe drought between 2008 and fall 2009, followed by one of the wettest years in a century in 2010, followed by the worst drought ever documented, which began in late 2010 and extended through 2011 (National Weather Service 2010, 2011, 2012). Based on the National Oceanic and Atmospheric Administration (NOAA) weather stations within 60 km of each ranch, rainfall averaged 19.02 cm, 32.89 cm, and 10.49 cm in 2009, 2010, and 2011, respectively (*n* = 5; National Climatic Data Center 2011). Therefore, summer

sampling periods occurred during a wet (2010) and dry (2011) growing season and winter sampling periods occurred after a dry (2009-2010) and wet (2010-2011) growing season.

METHODS

Plot Selection

I randomly selected 70 study plots in relatively open grasslands based on a series of criteria. Using ArcView GIS 10, I generated random points across the study area that were >325 m apart, >150 m from large woody thickets, and >125 m from caliche roads and fences. I located points in the field and selected those with <30% woody vegetation and <20% relative cover of nonnative grasses within a 125-m radius, that collectively represented the gradient of dominance by *H. contortus*. I marked selected points with a single t-post, which denoted the center of each study plot. Dominance of *H. contortus* ranged from 0 to 80% relative cover (0 to 60% absolute cover) during all sampling periods.

Motte Sampling

Because density of woody vegetation could affect community or population characteristics of breeding and wintering birds, I quantified characteristics of mesquite mottes, which are the most prominent woody vegetation on this landscape. I defined mesquite mottes as stands of brush with at least three plants ≥2-m tall, with at least two *Prosopis glandulosa* and nursery plants that depend upon *P. glandulosa* for shade. I quantified motte characteristics by mapping all potential mottes within a 125-m radius of each plot center with ArcView 10 and ground-truthing maps to determine which mottes met our definition. For all confirmed mesquite mottes, I estimated maximum height to the nearest 0.5 m and computed the average motte height for each plot in 2010 and 2011. I also used GIS to compute total motte area on each plot in 2010.

Summer Avian Sampling

I surveyed breeding birds with point counts from the center of each plot and used a rangefinder to record precise distances to each individual detected aurally or visually, by species (Buckland et al. 2001). Point counts are more appropriate for surveying breeding birds because most species sing, call, display, or otherwise engage in conspicuous activities that would increase detectability (Fletcher et al. 2000; Roberts and Schnell 2006, and citations within). I conducted surveys using a single observer for 10 minutes, after a 1-2 minute settling period (Ralph et al. 1993, 1995), between 0.5 hours before and 3.5 hours after sunrise. I surveyed birds on each plot five times/year from April 8-June 3, 2010 and April 4-June 10, 2011, to coincide with the timing of breeding behavior, and completed each set of surveys within 11 days. To minimize any potential biases in detection related to time and weather, I rotated the order plots were surveyed and did not survey points when precipitation exceeded a light mist or when average wind speeds were ≥19 kph (Martin et al. 1997). Survey time and weather variables were not correlated with dominance of *H. contortus* ($|r| < 0.32$ for all variables).

Winter Avian Sampling

I used a single observer to survey wintering birds along a 250-m line-transect (Emlen 1971, 1977), which bisected the center of each plot (i.e., the point count location). Line transects were more appropriate for surveying wintering birds because individuals are flushed while walking transects, few individuals are detected at distance, and most sightings were visual (e.g., Reynolds et al. 1980). We acknowledge that each method has different pitfalls with regards to estimating detection but the purpose of differing methods was to use the methods most appropriate for each season to generate enough detections to be able to draw comparisons between seasons; neither method would have been ideal for both season. Point counts are not appropriate for surveying wintering birds because few species sing, call, display, or otherwise engage in conspicuous activities that would increase detectability (Fletcher et al. 2000; Roberts and Schnell 2006, and citations within). Line transects are more useful in the winter than the summer because individuals are flushed while walking the transects.

I used a rangefinder to record precise perpendicular distances to each individual detected by species (Buckland et al. 2001). The observer walked slowly along each transect (12-20 minutes), after a 1-minute settling period (Ralph et al. 1993). Surveys began 0.25 hours before sunrise, light permitting, and ended 3.5 hours after sunrise. Surveys in winter began later in the morning because most detections were visual, requiring better light conditions. I surveyed birds on each plot three times/year from January 19-March 3, 2010 and January 17-February 25, 2011, after all migrants settled into the area. I completed a single round of surveys within 14 days. To minimize any potential biases in detection related to time and weather, I rotated the order plots were surveyed and did not survey points when precipitation exceeded a light mist, average wind speeds were ≥ 19 kph, or the temperature was $\leq 0°C$. Survey time and weather variables were not correlated with dominance of *H. contortus* ($|r| < 0.20$ for all variables).

ANALYSIS

I restricted our focus to grassland birds, as I predicted this group would be most affected by changes resulting from increased dominance by *H. contortus* because most of their life cycle occurs within grasslands. Although I documented all birds during surveys, those detected >162 m from the point (½ the distance to the next closest possible point) and flyovers were excluded from analyses to reduce the potential for double-counting. I used Vickery et al. (1999) to distinguish between obligate and facultative grassland and non-grassland birds and classified species further based on migration status (Appendices F and G). I considered Grasshopper Sparrow (*Ammodramus savannarum*) as a permanent resident, given that it will breed in the region after extremely wet winters (T. Langschied, personal communication) Likewise, I considered Ash-throated Flycatcher (*Myiarchus cinerascens*) as a permanent resident because it will winter in the region. I considered Loggerhead Shrike (*Lanius ludovicianus*) to be a permanent resident because it breeds in southern Texas, although this species may be localized within Jim Hogg County in summer.

At the community level, I assessed changes in avian species richness, which I computed as the total number of breeding or wintering species/plot. I excluded Grasshopper Sparrow from species richness computations in summer 2011, as this species was present as a migrant, but did not breed. At the population-level, I examined changes in presence and density of avian species. I used presence as an indication that an area provided habitat and density as a measure of habitat

70

quality, although I acknowledge that density alone may not provide a complete understanding of habitat quality (Van Horne 1983). I defined presence as detecting at least one individual of a species on a plot during at least one survey. To assess variability in presence across the dominance gradient, a species could not be extremely common or rare, meaning a species had to be present on 10-90% of plots (i.e., 7-63 plots). Based on this criterion, I examined changes in presence for nine species in summer and 11 species in winter in both years; two additional species could be analyzed only in summer and winter 2010 and two additional species in winter 2011 (Appendices H and I). Although our survey methods are not ideal for raptors, I included observations for a few raptor species that were hunting or perched during surveys, such as Northern Harrier (*Circus cyaneus*), to provide some information regarding raptor response.

I generated estimates of density (individuals/ha) to account for variation in detection probability with distance and among avian species (Buckland et al. 2001). I estimated density for species with ≥40 total detections using program DISTANCE 6.0 (Thomas et al. 2009). Birds were considered a group if ≥3 individuals were detected within 10 m of each other. I truncated data to improve fit of the detection function, but included birds detected within 125 m of the transect (Buckland et al. 2001); most detections of wintering birds were close to the transect. I considered uniform and hazard key functions with cosine or simple polynomial expansion terms and the half-normal key function with cosine or hermite polynomial expansion terms. I used density estimates from the model with the smallest Akaike's information criterion adjusted for small sample bias (AICc; Buckland et al. 2001) and analyzed density only for plots where the species occurred. Based on these criteria, I assessed changes in density for seven species in summer and seven species in winter. I did not have sufficient detections to examine changes in density of Northern Bobwhite (*Colinus virginianus*) and Mourning Dove (*Zenaida macroura*) in both seasons because these species form flocks in winter.

I examined differences in community- and population-level characteristics of breeding and wintering birds along the gradient of *H. contortus* dominance. I used a generalized linear mixed model approach for all analyses and selected the appropriate distribution and link function for each response variable of interest (Littell et al. 2006). I accounted for repeated sampling on the same plots over time (i.e., years) by treating plots as subjects and incorporating a compound symmetric covariance structure (Littell et al. 2006). I used relative cover of *H. contortus* to characterize the dominance gradient (i.e., percent of total vegetation cover represented by *H.*

contortus); absolute cover did not quantify the degree of dominance adequately where vegetation was sparse and *H. contortus* was the only plant growing and providing structure. I considered hypothesis tests related to increased dominance of *H. contortus* and also included year and year ×️ *H. contortus* interaction terms in models to explore variation in responses over time and to determine if the effect of *H. contortus* differed by year. For all analyses, I began with a full model that included *H. contortus*, year, and the year ×️ *H. contortus* interaction, but removed the interaction term if $P > 0.10$, to generate the best estimates of effects. I included ranch as a blocking factor in all analyses to account for potential differences between the two study areas and included average motte height and motte area when modeling avian response variables, to account for the potential influence of woody vegetation on birds. I log-transformed density of avian species to meet model assumptions.

I present slope estimates and 95% confidence intervals in text and tables to express changes in avian characteristics with increased *H. contortus*. Changes in richness are expressed as linear changes and changes in presence and density are expressed as multiplicative changes for every 10% increase in *H. contortus* cover. Details of all avian analyses are provided in Appendices G and H.

In January 2011, several lanes (~2-2.5-m wide) were mowed on the Borregos Ranch, affecting 11 of our study plots. Although these lanes did not affect how I sampled, the reduced vegetation cover may have altered avian activity or facilitated predator movement. I detected little correlation between the size of the mowed area and dominance by *H. contortus* on the affected plots ($r = -0.26$). However, because two lanes were mowed on each of three plots, the total mowed area on each of these plots (range = 768-1161 m^2) greatly exceeded that observed on the other nine plots (range = 370-572 m^2). I excluded the data from these three plots in 2011 from analyses of avian characteristics as a precaution.

RESULTS

I detected 96 species of birds in summer, but only 51 species were breeding; 15 species breed in the region but were not breeding on either study area and 30 species were migrants (Appendix F). Nineteen species of grassland birds were breeding on plots (16 each in 2010 and 2011) and 13 of these species were detected in both years. I detected 68 bird species in winter;

24 of these species were grassland birds and 16 of these species were detected in both years (Appendix I).

Avian richness increased with *H. contortus* in summer, whereas the effects in winter differed by year. Richness of breeding grassland birds increased 0.2 species (95% CI = 0.0 to 0.3) for every 10% increase of *H. contortus*, or approximately one species across the entire dominance gradient (t_{65} = 2.19, *P* = 0.03). With every 10% increase in *H. contortus*, richness of wintering grassland birds increased by 0.2 species (0.0 to 0.4) in 2010 and decreased slightly by 0.2 species (-0.4 to 0.0) in 2011 (t_{67} = 2.58, *P* = 0.01).

I detected differences in presence or density for 55% of breeding (6 of 11) and 38% of wintering (5 of 13) species of grassland birds with *H. contortus* (Tables 3.1 and 3.2). Of the breeding grassland birds that changed, presence or density increased for 67% of species (4 of 6) and decreased for 33% of species (2 of 6) with *H. contortus*. For wintering grassland birds, presence or density increased for 40% of species (2 of 5) and decreased for 60% of species (3 of 5) with *H. contortus*.

Permanent Residents

Of the six permanent residents that changed in presence or density with *H. contortus*, four could be examined in both breeding and wintering seasons: Mourning Dove, Grasshopper Sparrow, Cassin's Sparrow (*Peucaea cassinii*), and Eastern Meadowlark (*Sturnella magna*). Only Cassin's Sparrow had consistent results between seasons (Table 3.1, pg. 87). For every 10% increase in *H. contortus*, presence of Cassin's Sparrow increased 40% (95% CI = 10 to 77) during the breeding season and 27% (1 to 59) during the winter. Density of breeding Cassin's Sparrow increased 13% (2 to 26) with every 10% increase in *H. contortus* in 2010, but I did not detect changes in 2011. Presence of Mourning Dove did not differ with *H. contortus* in either season, but density increased 10% (1 to 21) with every 10% increase in *H. contortus* during the breeding season of 2010, did not differ in 2011, and could not be examined in winter. For wintering Grasshopper Sparrow, presence decreased 40% (13 to 59) for every 10% increase in *H. contortus* in 2011 and differed little in 2010; density decreased 19% (10 to 27) for every 10% increase in *H. contortus* in winter 2011. I did not detect differences in presence or density with *H. contortus* for Grasshopper Sparrow in summer 2010. Presence of breeding Eastern Meadowlark (*Sturnella magna*) increased 45% (7 to 98) with every 10% increase in *H. contortus*

73

in 2010, but did not differ in 2011; presence in winter decreased 30% (-52 to 1) with *H. contortus* in 2011, but did not differ in 2010. Density of Eastern Meadowlark did not differ with *H. contortus* in either season (Table 3.1, pg. 87). For every 10% increase in *H. contortus*, presence of breeding Lark Sparrow (*Chondestes grammacus*) increased 27% (-4 to 69) and could not be examined in winter. Presence of Brown-headed Cowbird (*Molothrus aeneus*) decreased 34% (4 to 54) with every 10% increase in *H. contortus* in 2011, did not differ in 2010, and could not be examined in winter. I did not detect differences in presence or density of Northern Bobwhite, Common-ground Dove (*Columbina passerina*), Ash-throated Flycatcher, and Loggerhead Shrike with *H. contortus* (Table 3.2, pg. 88).

<u>Single-season Residents</u>

Presence or density of one summer and two winter migrants changed with *H. contortus*. With every 10% increase of *H. contortus*, presence of breeding Scissor-tailed Flycatcher (*Tyrannus forticatus*) decreased 19% (95% CI = -35 to 3) and density decreased 10% (2 to 18) in summer 2011, but did not differ in 2010. Presence of Northern Harrier increased 44% (6 to 94) for every 10% increase in *H. contortus* during winter. Density of Savannah Sparrow (*Passerculus sandwichensis*) decreased 18% (8 to 27) for every 10% increase of *H. contortus* in winter 2011, but did not differ in 2010. I did not detect differences in presence or abundance of other summer or winter residents with *H. contortus* (Table 3.2, pg. 88).

DISCUSSION

Addressing conservation challenges facing grassland birds requires a holistic approach because ecological changes occurring in North American grasslands can affect breeding and wintering birds differently. If our study had examined only breeding birds, I would have concluded that overall richness and presence or density for a majority of bird species increased with *H. contortus*. In contrast, a study of only wintering birds would have yielded conclusions that overall richness and presence or density for a majority of bird species decreased with *H. contortus* in at least one year. Studies occurring within CRP lands suggest that avian responses to planting of nonnative seed mixes do not differ by season (McCoy et al. 2001; Thompson et al. 2009). However, Block and Morrison (2010) found that grassland birds that are permanent

residents shifted their spatial use between seasons and Fischer et al. (2012) detected avian responses to invasive woody plants within riparian areas were season-specific. Besides these four studies, the general paucity of multi-season studies within native grasslands limits our ability to make further generalizations regarding avian use among seasons.

I would expect birds to seek a certain set of vegetation characteristics that best supports the behaviors exhibited within each season, such as breeding success, migration, and overwinter survival. Because habitat quality varies over the landscape and can affect winter survival and future breeding (Latta and Faaborg 2002; Marra 2000), wintering birds likely select habitat conditions, such as abundant food and suitable foraging or roosting sites, that maximize survival and preparing for breeding the next year (Sherry et al. 2005; Studds and Marra 2005; Reudink et al. 2009). If foraging sites and available food were the only important habitat characteristics for grassland birds, then I might expect decreased presence or density in both seasons, rather than in just one season. In contrast, breeding birds also must consider vegetation characteristics that support finding a mate and fledging young successfully, in addition to selecting conditions conducive for survival. These additional requirements may necessitate tradeoffs in habitat selection during the breeding season, especially when conditions that support nest concealment do not provide the best foraging sites. For example, Eastern Meadowlark prefers to nest in dense bunchgrasses, but require shorter, sparser grass for foraging (Wiens 1969; Bock and Webb 1984; Lanyon 1995; Rohrbaugh et al. 1999). Changes in vegetation created with increased *H. contortus* may better conceal nests, but these vegetation changes and concomitant changes in insect communities likely reduce quality of foraging sites (Chapter 1; Cord 2011). Given that nest predation is very high for ground-nesting birds, vegetation characteristics that create quality nest sites may take priority when selecting territories in the breeding season (Martin 1993; Davis 2005), whereas vegetation characteristics that create quality foraging sites may take priority in winter.

Differences in annual life cycle between breeding and wintering birds influence what vegetation characteristics are required, but how a site is selected also may depend on season. When making choices about where to settle, breeding birds have to rely on cues, such as foliage or vegetation features, that indicate future food resources and cover because vegetation changes over the course of the summer (Badyaev 1995; Marshall and Cooper 2004; Winter et al. 2005; McGrath et al. 2009). Conversely, wintering birds can select territories based upon current

resources, given that cover and food resources only decrease as winter progresses (Pulliam and Brand 1975; Dunning and Brown 1982; Pulliam and Dunning 1987; Gordon 2000). Therefore, wintering birds may be able to assess differences between sites directly when choosing where to settle and determine *a priori* that *H. contortus* is not suitable, whereas breeding birds may not realize the negative implications of their chosen territory until it is too late to make a change. The ability of grassland birds to determine the adequacy of a site is complicated further if invasive plants provide unreliable cues about the future conditions; here again, wintering birds would have the advantage of selecting habitat based on current conditions.

Diet also may vary seasonally for some avian species. For example, Grasshopper Sparrow and Eastern Meadowlark shift from being mostly insectivorous in summer to granivorous in winter (Lanyon 1995; Vickery 1996). Plant invasions often result in reduced abundance or diversity of arthropods (Bock et al. 1986; Tallamy 2004; Hickman et al. 2006; Litt and Steidl 2010), which are an important food source for breeding birds. Richness and overall abundance of arthropods are lower in areas dominated by *H. contortus*, but abundance of Orthoptera remained unchanged (Cord 2011). Seeds are important food resources for wintering grassland birds (Pulliam and Brand 1975; Woodin et al. 2010) and abundance and diversity of these foods also may decrease with invasive plants (Best et al. 1998; Gan et al. 2010). I detected decreases in richness and abundance of grasses and forbs with increased dominance by *H. contortus* (Chapter 1), which could lead to lower diversity and abundance of seeds. Some breeding birds may be able to use *H. contorus* for nesting and foraging on insects and then shift into more native plant communities with better seed production post-breeding in order to captilalize on the best available resources across the landscape (Beulow 2009).

Breeding birds may be willing to tolerate invaded areas, even in the face of fewer foraging sites or less food items, if they benefit from better nest cover or because the cues used for habitat selection no longer are reliable. Vegetation conditions associated with *H. contortus*, such as increased vegetation height, bunchgrass density, and canopy structure (Chapter 1), create favorable nesting sites for some species, which may explain why I detected increases in presence and density for many breeding species (Chapter 2). If breeding birds are not able to determine future arthropod resources reliably because of false cues, then although presence or density might increase with *H. contortus*, these increases may not be correlated with nest success (Van Horne 1983; Schlaepfer et al. 2002). In the absence of breeding activities, vegetation conditions

associated with *H. contortus* may be less desirable, as the quality of foraging locations becomes more important for habitat selection. Wintering birds likely rely on cues less than breeding birds because habitat can be selected habitat based on current food resources and their body condition after migrating, which may explain why presence or density might be lower in *H. contortus*. Therefore, the differences in responses between seasons I observed may be the result of breeding birds receiving some benefit from *H. contortus*, but *H. contortus* also could be an ecological trap.

I acknowledge that I did not detect season-specific responses for all species and that the different methods used or populations observed also could influence our results. The lack of responses by several species may be because other vegetation features had a greater influence, I had insufficient detections to observe changes, or birds are less affected by the changes in vegetation associated with *H. contortus* because they evolved with this native grass. Our results also could be affected by the presence of different populations because "permanent resident" often describes a species that is present in an area throughout the year, and not necessarily the presence of distinct breeding and wintering populations. However, I expect criteria for habitat selection should be consistent among populations. Instead, I believe the differences detected between seasons are the result of different responses by the birds themselves because changes in the plant community with *H. contortus* were consistent between seasons (Chapter 1).

Our results support the need to conserve wintering habitat for grassland birds because the negative effects of *H. contortus* were more pronounced during this season. Low-quality, wintering habitat may result in Neotropic forest birds having a lower annual return rate, poorer body condition, and later return dates to breeding grounds (Marra et al. 1998; Marra and Holmes 2001; Studds and Marra 2005; Reudink et al. 2009). This recent research on the importance of wintering grounds to forest birds necessitate the need to better understand the role of wintering grounds on grassland birds, especially because invasive species may degrade habitat for grassland birds and could have negative effects during migration and subsequent seasons. Arid and semi-arid grasslands of the southwestern United States and northern Mexico are critical for grassland birds because these areas have a high diversity and abundance of wintering species, but fewer migratory species during the breeding season (Blancher 2003). Invasive plants that affect plant communities in desert grasslands negatively could reduce the quantity or quality of available habitat. Wintering in low-quality grasslands could alter spring arrival dates and territory selection of breeding birds, which could facilitate continued population declines despite

intense conservation efforts on breeding grounds. Further, studying the role of wintering grounds on grassland birds may help to explain why populations continue to decline despite intense management.

CONCLUSIONS

Conserving and managing grassland birds require understanding the effects of ecological changes occurring on both the breeding and wintering grounds. Based on our results, if *H. contortus* increased in dominance throughout the southwestern United States, this grass could pose another conservation challenge for grassland birds, especially during the winter. The variability in responses between seasons may be related to differences in habitat requirements and selection behaviors between breeding and non-breeding periods. Conservation of grassland birds requires consideration of the entire life cycle to understand the multitude of factors contributing to documented declines.

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Table 3.1 Multiplicative changes in the presence or density of birds for every 10% increase in dominance of *H. contortus*, as well as 95% confidence intervals, test statistics, and *P*-values, after accounting for covariates, $n = 70$ plots, Jim Hogg County, Texas, summer and winter 2010-2011.[a] Where I detected interactions, I provide estimates for the effect of *H. contortus* in each year.

Migration status and species		Variable	Summer Est.	95% CI		df	t	P	Winter Est.	95% CI		df	t	P
Permanent Residents														
Mourning Dove [b]		Presence	2	-23	38	65	0.20	0.84	-8	-37	36	65	0.16	0.88
	2010	Density	10	1	21	45	2.65	0.01						
	2011		-3	-11	5									
Cassin's Sparrow		Presence	40	10	77	65	2.84	0.006	27	1	59	65	2.09	0.04
	2010	Density	13	2	26	31	3.02	0.005						
	2011		-2	-12	8									
Lark Sparrow [d]		Presence	27	-4	69	65	1.71	0.09						
Grasshopper Sparrow [c]	2010	Presence	-6	-56	40	65	-0.29	0.78	8	-19	44	64	2.52	0.01
	2011								-40	-59	-13			
	2010	Density	0	-27	37	23	0.03	0.98						
	2011								-19	-27	-10	46	-4.04	0.0002
Eastern Meadowlark	2010	Presence	45	7	98	64	1.70	0.09	22	-6	56	64	2.35	0.02
	2011		9	-17	44				-30	-52	1			
		Density	1	-7	11	31	0.32	0.75	4	-6	14	8	0.88	0.40
Brown-headed Cowbird [d]	2010	Presence	27	-9	76	64	2.70	0.009						
	2011		-34	-54	-4									
Summer Residents														
Scissor-tailed Flycatcher		Presence	-19	-35	3	65	-1.77	0.08						
	2010	Density	4	-5	15	30	2.79	0.01						
	2011		-10	-18	-2									
Winter Residents														
Northern Harrier		Presence							44	6	94	65	2.40	0.02
Savannah Sparrow		Presence							-9	-25	11	65	-0.94	0.35
	2010	Density							3	-8	14	24	3.22	0.004
	2011								-18	-27	-8			

[a] Additional details are in Appendix G and H.

[b] For winter, I analyzed presence only in 2010.

[c] For summer, I analyzed presence and density only in 2010. For winter, I analyzed presence in both years and density only in 2011.

[d] Lark Sparrow and Brown-headed Cowbird are resident species, but I did not have enough detections in winter.

Table 3.2 Multiplicative changes in the presence or density for species that did not change with *H. contortus*, as well as 95% confidence intervals, test statistics, and *P*-values, after accounting for covariates, *n* = 70 plots, Jim Hogg County, Texas, summer and winter 2010-2011.[a] Where I detected interactions, I provide estimates for the effect of *H. contortus* in each year.

Migration status and species	Variable	Summer						Winter					
		Est.	95% CI		df	t	P	Est.	95% CI		df	t	P
Permanent Residents [b]													
Northern Bobwhite	Presence	-9	-29	17	65	-0.76	0.45	-1	-23	26	65	-0.11	0.92
	Density	1	-6	8	39	-0.36	0.80						
Common Ground-dove	Presence	-6	-23	14	65	-0.65	0.52						
Ash-throated Flycatcher	Presence	4	-14	27	65	0.45	0.65						
	Density	2	-8	4	10	-0.91	0.38						
Loggerhead Shrike	Presence							5	-15	29	65	0.43	0.67
	Density							4	-1	9	23	1.54	0.14
Summer Residents													
Western Kingbird [c]	Presence	33	-18	116	65	1.20	0.23						
Winter Residents													
American Kestrel	Presence							-7	-28	20	65	-0.59	0.56
Sedge Wren [c]	Presence							-10	-40	35	62	-0.52	0.61
Sprague's Pipit [d]	Presence							22	-14	72	65	1.15	0.26
Lark Bunting [c]	Presence							3	-32	57	62	0.16	0.87
Western Meadowlark	Presence							11	-10	37	65	0.99	0.33
	Density							3	-8	15	33	0.47	0.64

[a] Additional details are in Appendix G and H.

[b] Common Ground-dove and Ash-throated Flycatcher are resident species, but I did not have enough detections in winter. Loggerhead Shrike breeds in southern Texas but is localized or sporadic in Jim Hogg County. I list this species as a permanent resident, but it could be considered a winter resident within the study area.

[c] Analyzed only in 2011.

[d] Analyzed only in 2010.

Appendix A All species of herbaceous plants detected. Not all individual species were included in analyses because they were less common or abundant or were grouped with other species.

Family	Scientific Name	Common Name	Family	Scientific Name	Common Name
Commelinaceae			Lamiaceae		
	Commelina erecta	narrowleaf dayflower		*Monarda punctata*	spotted beebalm
Cyperaceae				*Scutelleria drummondii*	Drummond's skullcap
	Carex spp.	sedge	Verbenaceae		
Poaceae				*Glandularia bipinnatifida*	prairie purple verbena
	Aristida oligantha	prairie threeawn		*Verbena halei*	Texas vervain
	Aristida purpurea	purple threeawn	Acanthaceae		
*	*Axonopus* spp.	carpetgrass		*Ruellia nudiflora*	wild petunia
	Bothriochloa barbinodis	cane bluestem	Convolvulaceae		
	Bothriochloa laguroides var. *torreyna* & *B. longianiculata*	silver bluestem		*Evolvulus* spp.	
			Polemoniaceae		
	Bouteloua hirsuta	hairy grama		*Phlox drummondii*	phlox
	Cenchrus spinifex	coastal sandbur	Solanaceae		
	Chloris cucullata	hooded windmill		*Physalis* spp.	ground cherry
	Digitaria cognate	fall witchgrass		*Solanum elaeagnifolium*	silverleaf nightshade
	Elionurus tripsacoides	balsam scale	Amaranthaceae		
*	*Eragrostis lehmanniana*	Lehmann lovegrass		*Froelichia drummondii*	snakecotton
	Eragrostis secundiflora	red lovegrass	Brassicaceae		
	Eragrostis sessilispica	tumble lovegrass	*	*Brassica* spp.	mustard
	Heteropogon contortus	tanglehead		*Lesquerella* spp.	bladderpod
*	*Melinis repens*	rose Natal Grass	Malvaceae		
	Panicum capillarioides	witchgrass		*Callirhoe involucrate*	winecup
	Paspalum plicatulum	brownseed paspalum		*Sphaeralcea lindheimeri*	globe mallow
	Paspalum setaceum	thin paspalum	Papaveraceae		
*	*Pennisetum ciliare*	buffelgrass		*Argemone albiflora*	white pricklypoppy
	Schizachyrium scoparium var. *frequens*	seacoast bluestem		*Argemone sanguine*	pink pricklypoppy
	S. scoparium var. *frequens* & *littorale*	hybrid little bluestem	Ranunculaceae		
				Clematis drummondii	old-man's beard
	Setaria leucopila & *vulpiseta*	bristlegrass	Apiaceae		
	Setaria reverchoni ssp. *formula*	knot grass		*Daucus pusillus*	wild carrot
	Sporobolus cryptandrus	sand dropseed	Euphorbiaceae		
	Trachypogon spicatus	crinkleawn		*Acalypha radians*	cardinal feather
	Trichloris crinite	false rhodesgrass		*Chamaesyce albomarginata*	rattlesnake weed
	Trichoneura elegans	Silveus' grass		*Cnidoscolus texanus*	Texas bullnettle
				Croton capitatus	woolly croton

Family	Scientific Name	Common Name	Family	Scientific Name	Common Name
	Tridens eragrostioides	lovegrass tridens		*Croton glandulosus*	northern croton
	Urochloa spp.	signal grass		*Croton texensis*	Texas croton
	Vaseyochloa multinervosa	Texasgrass	Fabaceae		
Iridaceae				*Chamaecrista fasciculata*	partridge pea
	Alophia drummondii	prairie iris		*Chamaecrista flexuosa*	Texas senna
Liliaceae				*Dalea aurea*	golden prairie clover
	Nothoscordum bivalve	crow-poison		*Galactia canescens*	hoary milkpea
Asteraceae				*Hoffmanseggia drepanocarpa*	sicklepod rushpea
	Ambrosia psilostachya	western ragweed		*Lupinus texensis*	Texas bluebonnet
	Aphanostephus skirrhobasis	lazydaisy		*Polanisia erosa*	large clammyweed
	var. *heterophylla*			*Rhynchosia americana*	American snoutbean
	Cirsium texanum	Texas thistle		*Tephrosia lindheimeri*	Lindheimer's hoarypea
	Conoclinium coelestinum	mistflower		*Vicia ludoviciana*	deer pea vetch
	Coreopsis spp.	coreopsis	Oxalidaceae		
	Engelmannia peristenia	Engelmann daisy		*Oxalis dillenii*	yellow wood sorrel
	Erigeron modestus	prairie fleabane	Linaceae		
	Gaillardia pulchella	Indian blanket		*Linum rigidum*	flax
	Helianthus debilis ssp. *runyonii*	sand sunflower	Onagraceae		
	Pyrrhopappus pauciflorus	Texas false dandelion		*Gaura drummondii*	Drummond's beeblossom
	Ratibida columnifera	Mexican hat			
	Solidago spp.	goldenrod			
	Tetragonotheca texana	squarebud daisy			
	Verbesina encelioides	cowpen daisy			

[*] Nonnative

Appendix B   Multiplicative changes in the presence of grasses and forbs with *H. contortus*, as well as 95% confidence intervals, test statistics, and *P*-values, after accounting for covariates, *n* = 70 plots, Jim Hogg County, Texas, summer and winter 2010-2011. Where I detected interactions, I provide estimates for the effect of *H. contortus* in each year. Least squared means provided for year responses are the percent of plots occupied by a given species; means presented when there was not an interaction between year and *H. contortus*. [a]

Response Species	Season	Effect	Estimate	95% CI		*t*	*P*
Decreased							
Native Grass							
Elionurus	summer	*H. contortus*	-24	-40	-4	-2.31	0.02
tripsacoides		2010	64%	50%	77%	-0.37	0.71
		2011	66%	52%	78%		
		site				0.65	0.52
		H. contortus	-17	-33	4	-1.67	0.10
	winter	2010	75%	62%	85%	0.94	0.35
		2011	71%	56%	82%		
		site				-0.96	0.34
Paspalum spp.	winter	*H. contortus*	-37	-56	-11	-2.69	0.009
		2010	36%	21%	54%	-0.54	0.59
		2011	40%	23%	60%		
		site				-3.61	0.001
Schizachyrium	summer	*H. contortus*	-29	-42	-13	-3.44	0.001
scoparium		2010	83%	64%	93%	-3.34	0.001
		2011	89%	74%	96%		
		site				-1.88	0.06
	winter	*H. contortus*	-51	-61	-39	-6.19	< 0.0001
		2010	84%	72%	91%	-1.64	0.11
		2011	87%	76%	93%		
		site				-2.25	0.03
Setaria/	summer	year×*H.contortus*				2.05 [b]	0.04
Urochloa spp.		2010	39	-24	155		
		2011	-27	-43	-7		
		year				0.73 [b]	0.47
		site				2.91	0.005
	winter [c]	*H. contortus*	6	-21	41	0.37 [b]	0.71
		site				3.33 [b]	0.001
Trachypogon	summer	year×*H.contortus*				-2.12 [b]	0.04
spicatus		2010	-54	-68	-33		
		2011	-39	-54	-20		
		year				1.79 [b]	0.08
		site				-3.57	0.0007
	winter	*H. contortus*	-56	-69	-37	-3.51	< 0.0001
		2010	68%	46%	84%	0.29	0.77
		2011	64%	41%	82%		
		site				-4.57	0.001
Galactia/	summer	*H. contortus*	-30	-44	-14	-3.36	0.001
Rhynchosia		2010	66%	51%	78%	0.87	0.39
(legumous vines)		2011	57%	42%	70%		
		site				3.55	0.0007

Response Species	Season	Effect	Estimate	95% CI		t	P
Monarda	summer	year×*H.contortus*				-2.05 [b]	0.04
punctata		2010	-52	-69	-26		
		2011	-18	-37	6		
		year				1.18 [b]	0.24
		site				3.30	0.002
	winter [d]	*H. contortus*	-56	-76	-17	-2.59 [b]	0.01
		site				1.88 [b]	0.06
Increased							
Native Grass							
Digitaria/	summer	*H. contortus*	59	24	104	3.72	0.0004
Panicum spp.		2010	65%	52%	77%	5.50	< 0.0001
		2011	11%	6%	22%		
		site				-2.61	0.01
	winter	*H. contortus*	36	11	65	3.06	0.003
		2010	57%	43%	69%	2.05	0.04
		2011	39%	27%	52%		
		site				1.48	0.14
Eragrostis	summer	*H. contortus*	33	5	68	2.41	0.02
secundiflora		2010	30%	19%	44%	-1.36	0.18
		2011	39%	27%	53%		
		site				-1.67	0.10
	winter [d]	*H. contortus*	14	-13	50	0.99 [b]	0.32
		site				-0.75 [b]	0.46
Eragrostis	summer	*H. contortus*	25	1	55	2.09	0.04
sessilispica		2010	39%	26%	54%	4.16	< 0.0001
		2011	9%	4%	19%		
		site				1.84	0.07
Nonnative Grass							
Pennisetum	winter	*H. contortus*	57	17	111	3.07	0.003
ciliare		2010	11%	5%	21%	-0.11	0.91
		2011	11%	5%	22%		
Forb							
Commelina	summer [c]	*H. contortus*	43	4	97	2.23 [b]	0.03
erecta		site				2.08 [b]	0. 04
Did Not Change							
Native Grass							
Aristida spp.	summer	*H. contortus*	-2	-23	24	-0.19	0.85
		2010	84%	71%	92%	-0.93	0.36
		2011	89%	78%	95%		
		site				-1.42	0.16
	winter	*H. contortus*	1	-20	26	0.05	0.96
		2010	86%	74%	93%	1.69	0.10
		2011	75%	62%	85%		
		site				-0.77	0.44
Bouteloua	summer	*H. contortus*	7	-14	31	0.61	0.55
hirsuta		2010	38%	26%	52%	-1.82	0.07
		2011	50%	37%	64%		
		site				1.14	0.26
	winter	*H. contortus*	-1	-20	22	0.10	0.92
		2010	50%	37%	63%	1.28	0.20
		2011	57%	43%	70%		
		site				1.01	0.32

Response	Species	Season	Effect	Estimate	95% CI		T	P
	Cenchrus spinifex	summer [d]	*H. contortus*	-6	-28	22	-0.09 [b]	0.62
			site				-0.50 [b]	0.93
		winter [c]	*H. contortus*	-3	-25	28	-0.23 [b]	0.82
			site				2.06 [b]	0.04
	Paspalum plicatulum	summer	*H. contortus*	-21	-43	7	-1.54	0.13
			2010	43%	27%	60%	1.09	0.28
			2011	34%	21%	51%		
			site				-4.17	< 0.0001
	Paspalum setaceum	summer	*H. contortus*	-3	-21	19	-0.32	0.75
			2010	72%	59%	82%	5.58	< 0.0001
			2011	18%	10%	30%		
			site				1.74	0.09
Nonnative Grass								
	Eragrostis lehmanniana	summer	*H. contortus*	72	-22	236	1.63	0.11
			2010	70%	34%	91%	0.24	0.81
			2011	65%	33%	88%		
			site				5.20	< 0.0001
		winter [e]	*H. contortus*	7	-12	29	0.67	0.50
			2010	70%	58%	80%	0.90	0.37
			2011	68%	56%	78%		
Forb								
	Acalypha radians	summer [c]	*H. contortus*	21	-12	65	1.21 [b]	0.23
			site				1.59 [b]	0.12
	Ambrosia psilostachya	summer	*H. contortus*	7	-31	65	0.31	0.76
			2010	16%	7%	33%	0.32	0.75
			2011	14%	6%	29%		
			site				-4.75	< 0.0001
	Croton spp.	summer [c]	*H. contortus*	-9	-29	17	-0.73 [b]	0.47
			site				-2.62 [b]	0.01
	Evolvulus spp.	summer [d]	*H. contortus*	-17	-36	11	-1.27 [b]	0.21
			site				3.08 [b]	0.003
	Fabaceae	summer	*H. contortus*	14	-6	39	1.35	0.18
			2010	66%	53%	77%	0.89	0.37
			2011	59%	45%	71%		
			site				-0.33	0.74
	Phlox spp.	summer [c]	*H. contortus*	-26	-52	15	-1.35 [b]	0.18
			site				-0.93 [b]	0.36
	Physalis spp.	summer	*H. contortus*	10	-13	39	0.79	0.43
			2010	27%	17%	41%	0.64	0.53
			2011	23%	14%	37%		
			site				0.17	0.87

[a] Reported year and site estimates come from a full model that also included *H. contortus* (see Table 1.1, pg. 24).

Estimates are back-transformed and show a multiplicative change in species presence with every 10% increase in *H. contortus* and a difference between years or sites.

[b] $df = 67$. For analyses of all other variables, $df = 68$.

[c] Anaylzed 2010 only.

[d] Anaylzed 2011 only.

[e] present at Borregos only.

Appendix C Multiplicative changes in the relative cover of each grass and forb species with *H. contortus*, as well as 95% confidence intervals, test statistics, and *P*-values, after accounting for covariates, *n* = 70 plots, Jim Hogg County, Texas, summer and winter 2010-2011. Where I detected interactions, I provide estimates for the effect of *H. contortus* in each year. Least squared means provided for year responses is the average cover within a given year; means presented when there was not an interaction between year and *H. contortus*. [a]

Species	Season	Effect	Estimate	95% CI		df	t	P
Decreased Native Grass								
Aristida spp.	summer	*H. contortus*	-14	-22	-5	47	-3.05	0.004
		2010	3.2%	2.4%	4.1%	47	-3.34	0.002
		2011	5.2%	4.0%	6.7%			
		site				65	1.61	0.11
	winter	*H. contortus*	-10	-17	-3	42	-2.78	0.01
		2010	6.9%	5.6%	8.6%	42	3.28	0.02
		2011	4.7%	3.7	5.9%			
		site				42	3.28	0.02
Bouteloua hirsuta	winter	*H. contortus*	-10	-21	2	30	-1.69	0.10
		2010	2.68	1.86	3.86	30	-2.11	0.04
		2011	3.76	2.66	5.30			
		site				30	-2.11	0.04
Cenchrus spinifex	summer	*H. contortus*	-4	-12	5	47	-0.83	0.41
		2010	5.2%	4.1%	6.6%	47	2.69	0.01
		2011	3.4%	2.6%	4.5%			
		site				68	2.88	0.005
	winter	year×*H.contortus*				43	2.50	0.02
		2010	-13	-21	-3			
		2011	1	-8	10			
		year				43	-0.42	0.68
		site				67	2.68	0.01
Paspalum plicatulum	summer	*H. contortus*	-19	-36	2	15	-1.97	0.07
		2010	2.3%	1.8%	2.7%	15	-0.96	0.35
		2011	2.4%	1.9%	2.9%			
		site				24	-1.88	0.07
Paspalum spp.	winter	*H. contortus*	-26	-41	-8	18	-2.85	0.01
		2010	10.3%	6.5%	16.2%	18	-0.93	0.36
		2011	12.1%	7.8%	18.8%			
		site				18	-1.68	0.11

Appendix C Continued

Species	Season	Effect	Estimate	95% CI		df	t	P
Schizachyrium	summer	*H. contortus*	-22	-30	-13	47	-4.57	< 0.0001
scoparium		2010	9.2%	7.2%	11.7%	47	-4.75	< 0.0001
		2011	17.3%	13.7%	21.8%			
		site				50	-0.41	0.68
	winter	year×*H.contortus*				45	-2.14	0.04
		2010	-8	-5	-2			
		2011	-2	-4	-1			
		year				45	0.99	0.33
		site				49	-1.99	0.05
Increased Nonnative Grass								
Eragrostis	summer	*H. contortus*	1	-9	11	44	0.16	0.88
lehmanniana [c]		2010	2.6%	1.6%	4.3%	44	-4.44	< 0.0001
		2011	4.7%	3.0%	7.6%			
		site				54	2.53	0.01
	winter [d]	year×*H.contortus*				43	2.52	0.02
		2010	-2	-12	9			
		2011	14	3	27			
		year				43	4.19	0.0001
No Change Native Grass								
Elionurus	summer	*H. contortus*	-4	-16	9	39	-0.64	0.53
tripsacoides		2010	4.7%	3.4%	6.6%	39	-1.08	0.29
		2011	5.8%	4.2%	8.1%			
		site				50	1.12	0.27
	winter	*H. contortus*	-8	-17	2	41	-1.61	0.12
		2010	7.1%	5.5%	9.1%	41	0.94	0.35
		2011	6.3%	4.9%	8.2%			
		site				52	1.46	0.15
Paspalum	summer	*H. contortus*	-10	-24	6	8	-1.97	0.17
setaceum		2010	2.0%	0.4%	2.9%	8	-0.53	0.61
		2011	2.3%	1.4%	4.4%			
		site				56	-0.55	0.58
Setaria/	summer	*H. contortus*	-5	-14	5	37	-1.08	0.29
Urochloa spp.		2010	2.46	1.88	6.55	37	2.06	0.05
		2011	1.78	1.28	2.37			
		site				63	3.54	0.001
	winter	*H. contortus*	-1	-9	8	42	-0.26	0.80
		2010	3.6%	2.6%	5.1%	42	1.91	0.06
		2011	2.6%	2.0%	3.4%			
		site				63	0.03	0.97

Species	Season	Effect	Estimate	95% CI		df	t	P
Trachypogon	summer	*H. contortus*	-11	-28	10	30	-1.14	0.26
spicatus		2010	8.5%	6.3%	11.4%	30	-0.46	0.65
		2011	9.3%	6.8%	12.7%			
		site				35	1.46	0.15
	winter	*H. contortus*	0	-15	17	27	-0.01	0.99
		2010	7.4%	5.5%	10.0%	27	-1.68	0.11
		2011	9.6%	7.2%	12.8%			
		site				39	-0.15	0.88
Forb								
Asteraceae [c]	summer	*H. contortus*	-6	-20	3	63	-1.52	0.13
		site				63	-2.49	0.02

[a] Reported year and site estimates come from a full model that also included *H. contortus* (see Table 1.2, pg. 26).

Estimates are back-transformed and show a multiplicative change in species abundance with every 10% increase in

H. contortus and a difference between years or sites.

[b] Site could not be analyzed in winter because I did not detect *E. lehmanniana* at Alta Vista.

[c] Analyzed in summer 2010 only.

[d] Only detected at Borregos during this sampling period.

Appendix D Linear changes in vegetation composition and structure with *H. contortus*, as well as 95% confidence intervals, test statistics, and *P*-values, after accounting for covariates, *n* = 70 plots, Jim Hogg County, Texas, summer 2010-2011. Where I detected interactions, I provide estimates for the effect of *H. contortus* in each year. Least squared means provided for year responses is the average of each metric within a given year; means presented when there was not an interaction between year and *H. contortus*. [a]

Variable	Effect	Estimate	95% CI		*t*	*P*
Richness						
Native grasses	*H. contortus*	-0.19	-0.33	-0.05	-2.71	0.009
	2010	8.3	7.9	8.7	9.20	< 0.0001
	2011	5.9	5.5	6.3		
	site				-0.93	0.35
Forbs	year×*H. contortus*				-2.16 [c]	0.03
	2010	-0.27	-0.49	-0.04		
	2011	0.02	-0.17	0.22		
	year				7.85 [c]	< 0.0001
	site				0.35	0.73
Total Richness	*H. contortus*	-0.17	-0.39	0.04	-1.63	0.11
	2010	15.6	15.0	16.2	15.02	< 0.0001
	2011	10.6	10.0	11.1		
	site				1.28	0.20
Horizontal Structure [b]						
Total ground cover	year×*H. contortus*				3.58 [c]	0.0006
	2010	3.21%	2 04%	4.37%		
	2011	1.07%	0.07%	2.07%		
	year				0.19 [c]	0.85
	site				-0.79	0.43
Native Grass	year×*H.contortus*				3.73 [c]	0.0004
	2010	-7.48%	-8.80%	-6.16%		
	2011	-10.38%	-11.51%	-9.24%		
	year				-6.93 [c]	< 0.0001
	site				-3.87	0.002
Nonnative Grass	*H. contortus*	0.31%	-0.31%	0.93%	1.00	0.32
	2010	3.41%	1.77%	5.07%	-3.72	0.0004
	2011	6.38%	4.77%	7.99%		
	site				5.71	< 0.0001
Forb	year×*H.contortus*					
	2010	-2.13%	-3.20%	-1.06%	-3.85 [c]	0.0003
	2011	0.31%	-0.61%	1.23%		
	year				10.07 [c]	< 0.0001
	site				-0.95	0.34
Litter	*H. contortus*	-0.04%	-0.75%	0.67%	-0.11	0.92
	2010	28.40%	26.15%	30.66%	-0.10	0.92
	2011	28.57%	26.35%	30.79%		
	site				-1.80	0.08

Appendix D Continued

Variable	Effect	Estimate	95% CI		t	P
Bare ground	year×*H. contortus*				-1.88 [c]	0.07
	2010	-2.42%	-3.54%	-1.30%		
	2011	-1.13%	-2.09%	-1.72%		
	year				0.99 [c]	0.32
	site				1.82	0.07
Canopy cover	*H. contortus*	0.95%	0.40%	1.51%	3.44	0.001
	2010	9.44%	7.72%	11.16%	4.77	< 0.0001
	2011	3.64%	1.94%	5.33%		
	site				-3.72	0.0004
Bunchgrasses/m^2	year×*H. contortus*				8.86 [c]	< 0.0001
	2010	0.81	0.66	0.97		
	2011	0.13	-0.00	0.26		
	year				-4.98 [c]	< 0.0001
	site				-0.95	0.34
Vertical Structure						
Average height (cm)	year×*H. contortus*				4.55 [c]	< 0.0001
	2010	3.07	1.76	4.38		
	2011	-0.09	-1.21	0.10		
	year				0.23 [c]	0.82
	site				-0.67	0.50
Vertical density <0.4 m	year×*H. contortus*				3.48 [c]	0.0009
	2010	10.99	5.90	16.08		
	2011	1.14	-3.23	5.51		
	year				-0.68 [c]	0.50
	site				1.31	0.20
Vertical density >0.4 m	year×*H. contortus*				5.91 [c]	< 0.0001
	2010	3.57	2.51	4.63		
	2011	0.00	-0.91	0.91		
	year				0.23 [c]	0.82
	site				1.32	0.19
Litter depth (cm)	year×*H. contortus*				-2.62 [c]	0.01
	2010	-0.01	-0.08	0.05		
	2011	0.07	0.02	0.13		
	year				2.34 [c]	0.02
	site				-4.58	< 0.0001

[a] Estimates represent a linear change. Slope estimates and 95% CI for tanglehead are a linear change for every 10% increase of *H. contortus*. Estimates and CI for year are least squares means. Also see Tables 1.3 and 2.1.

[b] Absolute cover, except for bunchgrass density.

[c] $df = 67$. For analyses of all other variables, $df = 68$.

Appendix E Linear changes in vegetation composition and structure with *H. contortus*, as well as 95% confidence intervals, test statistics, and *P*-values, after accounting for covariates, $n = 70$ plots, Jim Hogg County, Texas, winter 2010-2011. Where I detected interactions, I provide estimates for the effect of *H. contortus* in each year. Least squared means provided for year responses is the average of each metric within a given year; means presented when there was not an interaction between year and *H. contortus*. [a]

Variables	Effect	Estimate	95% CI		*t*	*P*
Richness						
Native grasses	*H. contortus*	-0.33	-0.47	-0.19	-4.82	< 0.0001
	2010	5.62	5.25	5.99	-7.84	< 0.0001
	2011	7.09	6.71	7.46		
	site				-1.73	0.09
Total richness	*H. contortus*	-0.30	-0.43	-0.16	-4.42	< 0.0001
	2010	7.18	6.81	7.55	-6.77	< 0.0001
	2011	8.56	8.19	8.94		
	site				1.82	0.07
Horizontal Structure [b]						
Total cover	year×*H. contortus*				-2.78 [c]	0.007
	2010	-0.61%	-1.91%	0.69%		
	2011	1.30%	-0.01%	2.61%		
	year				-6.89 [c]	< 0.0001
	site				0.84	0.40
Native Grass						
	H. contortus	-10.10%	-10.88%	-9.31%	-25.70	< 0.0001
	2010	56.32%	54.21%	58.43%	-6.53	< 0.0001
	2011	62.93%	60.81%	65.05%		
	site				-6.75	< 0.0001
Nonnative Grass	*H. contortus*	0.38%	-0.36%	1.12%	1.02	0.31
	2010	8.35%	6.37%	10.33%	3.92	0.0002
	2011	5.00%	3.01%	7.00%		
	site				6.97	<0.0001
Litter	year×*H. contortus*				1.75 [c]	0.08
	2010	1.36%	0.29%	2.43%		
	2011	1.02%	-0.74%	1.42%		
	year				2.09 [c]	0.04
	site				-2.98	0.004
Bare ground	*H. contortus*	-1.05%	-1.94%	-0.17%	-2.38	0.02
	2010	23.71%	21.33%	26.10%	13.19	< 0.0001
	2011	8.27%	5.88%	10.66%		
	site				1.98	0.05
Canopy cover	year×*H. contortus*				2.39 [c]	0.02
	2010	2.37%	1.76%	2.99%		
	2011	1.60%	0.98%	2.21%		
	year				-2.11 [c]	0.04
	site				3.26	0.002
Bunchgrasses/m^2	year×*H. contortus*				6.21 [c]	< 0.0001
	2010	0.69	0.54	0.84		
	2011	0.14	-0.01	0.29		
	year				-6.43 [c]	< 0.0001
	site				0.88	0.38

Appendix E Continued

Variable	Effect	Estimate	95% CI		*t*	*P*
Vertical Structure						
Average height (cm)	year×*H. contortus*				5.58 [c]	< 0.0001
	2010	1.75	0.52	2.97		
	2011	-1.53	-2.76	-0.30		
	year				-13.77 [c]	< 0.0001
	site				0.34	0.73
Vertical density <0.4 m	*H. contortus*	2.09	-1.83	6.01	1.06	0.29
	2010	87.47	76.51	98.43	-9.69	< 0.0001
	2011	148.22	137.21	159.23		
	site				0.74	0.46
Vertical density >0.4 m	*H. contortus*	2.25	0.10	3.50	3.59	0.0006
	2010	10.73	7.17	14.28	-9.49	< 0.0001
	2011	30.90	27.33	34.47		
	site				0.46	0.64
Litter depth (cm)	*H. contortus*	0.03	-0.03	0.09	1.04	0.30
	2010	1.66	1.51	1.81	6.54	< 0.0001
	2011	1.17	1.02	1.32		
	site				-3.87	0.0002

[a] Estimates represent a linear change. Slope estimates and 95% CI for tanglehead are a linear change for every 10% increase of *H. contortus*. Also see Table 1.3, pg. 27.

[b] Absolute cover, except for bunchgrass density.

[c] *df* = 67. For analyses of all other variables, *df* = 68.

Appendix F. Bird species detected in summer; raw data used to determine which species to include in analyses, $n = 70$ plots, Jim Hogg County, Texas. Species only detected beyond 162 m or as flyovers are denoted with an $\times$.

	2010		2011	
Grassland status and species	% Plots	No. Detections	% Plots	No. Detections
Obligate Grassland Birds				
Permanent Resident				
Cassin's Sparrow (*Peucaea cassinii*)	56	188	69	112
Botteri's Sparrow (*Peucaea botterii*) [a]			1	2
Grasshopper Sparrow (*Ammodramus savannarum*) [b]	36	110	7	7
Eastern Meadowlark (*Sturnella magna*)	50	120	71	152
Migrant/Winter Resident				
Northern Harrier (*Circus cyaneus*)		$\times$	1	1
Upland Sandpiper (*Bartramia longicauda*)	1	1		$\times$
Sedge Wren (*Cistothorus platensis*)	1	1	6	4
American Pipit (*Anthus rubescens*)	3	2		
Savannah Sparrow (*Passerculus sandwichensis*)	18	25	4	3
Dickcissel (*Spiza americana*)	1	1	3	2
Facultative Grassland Birds				
Permanent Resident				
Northern Bobwhite (*Colinus virginianus*)	97	332	61	112
Cattle Egret (*Bubulcus ibis*)		$\times$	1	1
Black Vulture (*Coragyps atratus*)		$\times$		
Turkey Vulture (*Cathartes aura*)		$\times$		$\times$
White-tailed Hawk (*Buteo albicaudatus*)		$\times$	1	1
Crested Caracara (*Caracara cheriway*)	1	1	1	1
Mourning Dove (*Zenaida macroura*)	89	220	79	125
Common Ground-Dove (*Columbina asserine*)	39	36	36	33
Ash-throated Flycatcher (*Myiarchus cinerascens*)	43	47	39	42
Clay-colored Sparrow (*Spizella asser*)	3	7	6	8
Lark Sparrow (*Chondestes grammacus*)	16	17	17	15
Brown-headed Cowbird (*Molothrus ater*)	27	30	30	28
Summer Resident				
Groove-billed Ani (*Crotophaga sulcirostris*)	1	1		
Common Nighthawk (*Chordeiles minor*)		$\times$		
Lesser Nighthawk (*Chordeiles acutipennis*)	1	1	1	1
Western Kingbird (*Tyrannus verticalis*)	10	9	7	5
Scissor-tailed Flycatcher (*Tyrannus forticatus*)	79	204	7	115

Appendix F Continued

Grassland status and species	2010		2011	
	% Plots	No. Detections	% Plots	No. Detections
Chihuahuan Raven (*Corvus cryptoleucus*)	1	1		×
Bronzed Cowbird (*Molothrus aeneus*)	1	1		×
Local Breeder [c]				
Loggerhead Shrike (*Lanius ludovicianus*)	33	39	14	15
Migrant/Winter Resident				
Blue-winged Teal (*Anas discors*)		×		
American Kestrel (*Falco sparverius*)		×		×
Merlin (*Falco columbarius*)	1	1		
Non-Grassland Species				
Permanent Resident				
Wild Turkey (*Meleagris gallopavo*)		×		
Red-tailed Hawk (*Buteo jamaicensis*)		×		×
Cooper's Hawk (*Accipiter cooperii*)	1	1	1	1
Eurasian Collared-Dove (*Streptopelia decaocto*)		×	1	1
Greater Roadrunner (*Geococcyx californianus*)	13	9	16	20
Common Pauraque (*Nyctidromus albicollis*)	3	3		×
Golden-fronted Woodpecker (*Melanerpes aurifrons*)	76	122	60	94
Ladder-backed Woodpecker (*Picoides scalaris*)	23	16	20	18
Vermilion Flycatcher (*Pyrocephalus rubinus*)	7	10	1	1
Couch's Kingbird (*Tyrannus couchii*)			1	1
Green Jay (*Cyanocorax yncas*)		×	7	5
Black-crested Titmouse (*Baeolohus atricristatus*)	1	1	1	2
Verdin (*Auriparus flaviceps*)	36	36	24	29
Cactus Wren (*Campylorhynchus brunneicappillus*)	1	1	1	2
Bewick's Wren (*Thryomanes bewickii*)	49	64	47	72
Blue-gray Gnatcatcher (*Polioptila caerulea*)	10	7	11	8
Northern Mockingbird (*Mimus polyglottos*)	86	280	69	112
Long-billed Thrasher (*Toxostoma longirostre*)			1	1
Curve-billed Thrasher (*Toxostoma curvirostre*)	20	30	24	20
Olive Sparrow (*Arremonops rufivirgatus*)	1	1		×
Northern Cardinal (*Cardinalis cardinalis*)	60	73	61	90
Pyrrhuloxia (*Cardinalis sinuatus*)	100	461	100	375
Audubon's Oriole (*Icterus graduacauda*)	1	1	1	1
Local Breeder [c]				
Great Blue Heron (*Ardea herodias*)		×		
Swainson's Hawk (*Buteo swainsoni*)		×		×
White-winged Dove (*Zenaida asiatica*)		×		×

Grassland status and species	2010		2011	
	% Plots	No. Detections	% Plots	No. Detections
Inca Dove (*Columbina inca*)				×
Great Horned Owl (*Bubo virginianus*)		×		×
Chimney Swift (*Chaetura 104asseri*)		×		×
White-eyed Vireo (*Vireo griseus*)		×		×
Cave Swallow (*Petrochelidon fulva*)				×
Barn Swallow (*Hirundo rustica*)		×		×
Black-throated Sparrow (*Amphispiza billineata*)				×
Summer Tanager (*Piranga rubra*)		×		
Great-tailed Grackle (*Quiscalus mexicanus*)		×		×
Orchard Oriole (*Icterus spurious*)				×
Summer Resident				
Yellow-billed Cuckoo (*Coccyzus americanus*)	27	21	11	9
Brown-crested Flycatcher (*Myiarchus tyrannulus*)	1	4	10	6
Blue Grosbeak (*Passerina caerulea*)	13	11	7	6
Painted Bunting (*Passerina ciris*)	99	241	90	168
Hooded Oriole (*Icterus cucullatus*)			1	1
Bullock's Oriole (*Icterus bullockii*)	44	57	29	26
Migrant/Winter Resident				
Osprey (*Pandion haliaetus*)		×		
Mississippi Kite (*Ictinia mississippiensis*)		×		×
Sharp-shinned Hawk (*Accipiter striatus*)		×		
Broad-winged Hawk (*Buteo platypterus*)		×		×
Black-necked Stilt (*Himantopus mexicanus*)		×		
Greater Yellowlegs (*Tringa melanoleuca*)		×		
Chuck-will's-widow (*Caprimulgus carolinensis*)				×
Willow Flycatcher (*Empidonax traillii*)			1	1
Purple Martin (*Progne subis*)		×		×
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)		×		×
Bank Swallow (*Riparia riparia*)		×		×
Cliff Swallow (*Petrochelidon pyrrhonota*)		×		×
House Wren (*Troglodytes aedon*)	11	8	24	25
Ruby-crowned Kinglet (*Regulus calendula*)			1	1
Cedar Waxwing (*Bombycilla cedrorum*)			1	1
Orange-crowned Warbler (*Oreothlypis celata*)	1	1		
Yellow Warbler (*Setophaga petechia*)	1	1		
Chipping Sparrow (*Spizella 104asserine*)	1	7		
Lincoln Sparrow (*Melospiza lincolnii*)			1	1

Appendix F Continued

Grassland status and species	2010		2011	
	% Plots	No. Detections	% Plots	No. Detections
Field Sparrow (*Spizella pusilla*)		×	3	2
Red-winged Blackbird (*Agelaius phoeniceus*)		×		

[a] Possibly a 1st county record; typically breeds closer to the coast in *Spartina* grasses.

[b] Only breeds in wet years, detections from 2011 are migrants only.

[c] Local breeders may breed within the county or on adjacent ranches, but did not breed on or near the study plots.

Appendix G. Multiplicative in presence and density of breeding birds with *H. contortus*, as well as 95% confidence intervals, test statistics, and *P*-values, after accounting for covariates, *n* = 70 plots, Jim Hogg County, Texas, summer 2010-2011. Where I detected interactions, I provide estimates for the effect of *H. contortus* in each year. Least squared means provided for year responses are the percent of plots occupied for presence or the estimated density per ha. Means are not provided for year×*H. contortus* interactions. [a]

Grassland status, species, and variable	Effect	Estimate	95% CI		df	t	P
Obligate Grassland Species							
Cassin's Sparrow							
Presence	*H.contortus*	40	10	77	65	2.84	0.006
	2010	62%	47%	75%	65	-0.20	0.85
	2011	64%	48%	77%			
	site				66	-0.87	0.39
	motte area				66	-2.27	0.03
	motte height				66	-1.37	0.18
Density	year×*H.contortus*				31	3.02	0.005
	2010	13	2	26			
	2011	-2	-12	8			
	year				31	-4.89	< 0.0001
	site				53	-0.41	0.68
	motte area				53	-1.82	0.07
	motte height				53	-1.97	0.05
Grasshopper Sparrow [b]							
Presence	*H.contortus*	-6	-56	40	65	-0.29	0.78
	site				65	1.55	0.13
	motte area				65	-1.78	0.08
	motte height				65	-1.46	0.15
Density	*H.contortus*	0	-27	37	23	0.03	0.98
	site				23	0.89	0.38
	motte area				23	-1.21	0.24
	motte height				23	0.22	0.83
Eastern Meadowlark							
Presence	year×*H.contortus*				64	1.70	0.09
	2010	45	7	98			
	2011	9	-17	44			
	year				66	-2.92	0.005
	site				66	-1.37	0.17
	motte area				66	-1.40	0.17
	motte height				66	-0.51	0.61
Density	*H.contortus*	1	-7	11	31	0.32	0.75
	2010	0.06	0.05	0.08	31	-3.00	0.005
	2011	0.09	0.07	0.11			
	site				50	-0.50	0.62
	motte area				50	-1.51	0.14
	motte height				50	0.75	0.46

Grassland status, species, and variable	Effect	Estimate	95% CI		df	t	P
Facultative Grassland Species							
Northern Bobwhite							
Presence	*H.contortus*	-9	-29	17	65	-0.76	0.45
	2010	97%	88%	99%	65	4.12	0.0001
	2011	60%	46%	72%			
	site				66	1.2	0.24
	motte area				66	0.94	0.35
	motte height				66	-0.96	0.34
Density	*H.contortus*	1	-6	8	39	-0.36	0.80
	2010	0.10	0.09	0.13	39	-5.11	< 0.0001
	2011	0.20	0.16	0.25			
	site				65	-0.16	0.87
	motte area				65	0.81	0.42
	motte height				65	-0.35	0.72
Common Ground-dove							
Presence	*H.contortus*	-6	-23	14	65	-0.65	0.52
	2010	39%	27%	54%	65	0.05	0.96
	2011	39%	27%	53%			
	site				66	-0.67	0.50
	motte area				66	-1.25	0.22
	motte height				66	0.01	0.99
Mourning Dove							
Presence	*H.contortus*	2	-23	38	65	0.20	0.84
	2010	87%	74%	94%	65	1.48	0.14
	2011	75%	61%	85%			
	site				66	2.64	0.01
	motte area				66	-1.69	0.10
	motte height				66	0.84	0.41
Density	year×*H.contortus*				45	2.65	0.01
	2010	10	1	21			
	2011	-3	-11	5			
	year				45	-0.17	0.87
	site				65	-0.42	0.67
	motte area				65	1.49	0.14
	motte height				65	-1.49	0.14

Grassland status, species, and variable	Effect	Estimate	95% CI		df	t	P
Ash-throated Flycatcher							
Presence	*H.contortus*	4	-14	27	65	0.45	0.65
	2010	30%	18%	46%	65	0.15	0.88
	2011	29%	18%	45%			
	site				66	3.19	0.002
	motte area				66	-0.25	0.81
	motte height				66	0.28	0.78
Density	*H.contortus*	-2	-8	4	10	-0.91	0.38
	2010	0.05	0.04	0.07	10	0.58	0.57
	2011	0.05	0.04	0.06			
	site				39	1.21	0.23
	motte area				39	1.86	0.07
	motte height				39	0.77	0.45
Scissor-tailed Flycatcher							
Presence	*H.contortus*	-19	-35	3	65	-1.77	0.08
	2010	72%	57%	83%	65	1.72	0.09
	2011	56%	42%	69%			
	site				66	3.22	0.002
	motte area				66	-1.97	0.05
	motte height				66	-0.20	0.84
Density	year×*H.contortus*				30	2.79	0.01
	2010	4	-5	15			
	2011	-10	-18	-2			
	year				30	-1.05	0.30
	site				59	3.03	0.004
	motte area				59	-3.83	0.003
	motte height				59	-1.73	0.09
Western Kingbird [b]							
Presence	*H.contortus*	33	-18	116	65	1.20	0.23
	site				65	0.20	0.84
	motte area				65	-0.83	0.41
	motte height				65	-0.07	0.95
Lark Sparrow							
Presence	*H.contortus*	27	-4	69	65	1.71	0.09
	2010	17%	9%	31%	65	0.06	0.95
	2011	17%	9%	30%			
	site				66	1.31	0.20
	motte area				66	-1.60	0.11
	motte height	0.63	0.36	1.10	64	-1.67	0.10
Brown-headed Cowbird							
Presence	year×*H.contortus*				64	2.70	0.009
	2010	27	-9	76			
	2011	-34	-54	-4			
	year				64	-1.81	0.07
	site				66	1.23	0.22
	motte area				66	2.16	0.03
	motte height				66	-0.12	0.90

[a] Estimates and 95% CI for tanglehead are back-transformed to show a multiplicative change (%) for every 10% increase of *H. contortus* cover and for year to show annual changes.

[b] Analyzed only in 2010.

Appendix H. Multiplicative in presence and density of breeding birds with *H. contortus*, as well as 95% confidence intervals, test statistics, and *P*-values, after accounting for covariates, *n* = 70 plots, Jim Hogg County, Texas, winter 2010-2011. Where I detected interactions, I provide estimates for the effect of *H. contortus* in each year. Least squared means provided for year responses are the percent of plots occupied for presence or the estimated density per ha. Means are not provided for year×*H. contortus* interactions. [a]

Grassland status, species, and variable tested	Effect	Estimate [a]	95% CI		df	t	P
Obligate Grassland Species							
Northern Harrier							
Presence	*H.contortus*	44	6	94	65	2.40	0.02
	2010	11%	4%	23%	65	-0.65	0.52
	2011	15%	7%	29%			
	site				66	-1.64	0.11
	motte area				66	-0.94	0.35
	motte height				66	-0.13	0.90
Sedge Wren[b]							
Presence	*H.contortus*	-10	-40	35	62	-0.52	0.61
	site				62	-0.63	0.53
	motte area				62	0.61	0.54
	motte height				62	0.83	0.41
Sprague's Pipit[c]							
Presence							
	H.contortus	22	-14	72	65	1.15	0.26
	site				65	0.28	0.78
	motte area				65	-1.18	0.24
	motte height				65	-0.04	0.96
Cassin's Sparrow							
Presence	*H.contortus*	27	1	59	65	2.09	0.04
	2010	24%	13%	40%	65	2.34	0.02
	2011	10%	4%	22%			
	site				66	1.72	0.09
	motte area				66	0.97	0.33
	motte height				66	-0.93	0.36
Lark Bunting[b]							
Presence	*H.contortus*	3	-32	57	62	0.16	0.87
	site				62	1.08	0.28
	motte area				62	0.19	0.85
	motte height				62	-0.02	0.98

Appendix H Continued

Grassland status, species, and variable tested	Effect	Estimate [a]	95% CI		df	t	P
Savannah Sparrow							
Presence	*H.contortus*	-9	-25	.11	65	-0.94	0.35
	2010	62%	48%	74%	65	0.37	0.71
	2011	58%	44%	71%			
	site				66	1.14	0.26
	motte area				66	-1.54	0.69
	motte height				66	-0.17	0.86
Density	year×*H.contortus*				24	3.22	0.004
	2010	3	-8	14			
	2011	-18	-27	-8			
	site				24	-12.08	<0.0001
	motte area				56	-1.79	0.08
	motte height				56	-1.70	0.09
Grasshopper Sparrow							
Presence	year×*H.contortus*				64	2.52	0.01
	2010	08	-19	44			
	2011	-40	-59	-13			
	year				64	-4.37	<0.0001
	site				66	-1.40	0.17
	motte area				66	1.49	0.14
	motte height				66	-1.48	0.14
Density [b]	*H.contortus*	-19	-27	-10	46	-4.04	0.0002
	site				46	3.64	0.0007
	motte area				46	2.09	0.04
	motte height				46	-1.27	0.21
Eastern Meadowlark							
Presence	year×*H.contortus*				64	2.35	0.02
	2010	22	-6	56			
	2011	-30	-52	1			
	year				64	-0.46	0.64
	site				66	-2.48	0.02
	motte area				66	-0.69	0.49
	motte height				66	-0.19	0.85
Density	*H.contortus*	4	-6	14	8	0.88	0.40
	2010	1.66	0.91	3.02	65	2.94	0.005
	2011	0.50	0.27	0.93			
	site				41	-2.28	0.03
	motte area				41	-0.08	0.94
	motte height				41	1.18	0.24

Appendix H Continued

Grassland status, species, and variable tested	Effect	Estimate [a]	95% CI		df	t	P
Western Meadowlark							
Presence	*H.contortus*	11	-10	37	65	0.99	0.33
	2010	57%	43%	70%	65	3.84	0.0003
	2011	24%	14%	38%			
	site				66	-0.34	0.73
	motte area				66	-1.13	0.26
	motte height				66	0.53	0.60
Density [c]	*H.contortus*	3	-8	15	33	0.47	0.64
	site				33	-2.12	0.04
	motte area				33	-1.51	0.14
	motte height				33	-2.00	0.05
Facultative Grassland Species							
American Kestrel							
Presence	*H.contortus*	-7	-28	20	65	-0.59	0.56
	2010	15%	7%	27%	65	0.61	0.54
	2011	12%	5%	23%			
	site				66	0.95	0.34
	motte area				66	-2.03	0.05
	motte height				66	0.93	0.35
Northern Bobwhite							
Presence	*H.contortus*	-1	-23	26	65	-0.11	0.92
	2010	11%	5%	23%	65	-2.02	0.05
	2011	25%	15%	39%			
	site				66	-0.61	0.54
	motte area				66	1.56	0.12
	motte height				66	-1.28	0.21
Mourning Dove [c]							
Presence	*H.contortus*	-18	-37	36	65	0.16	0.88
	site				65	-0.38	0.71
	motte area				65	0.2	0.84
	motte height				65	-0.77	0.44

Appendix H Continued

Grassland status, species, and variable tested	Effect	Estimate [a]	95% CI		df	t	P
Loggerhead Shrike							
Presence	*H.contortus*	5	-15	29	65	0.43	0.67
	2010	63%	48%	75%	65	2.41	0.02
	2011	41%	28%	56%			
	site				66	2.56	0.01
	motte area				66	-2.69	0.009
	motte height				66	-0.31	0.76
Density							
	H.contortus	4	-1	9	23	1.54	0.14
	2010	0.11	0.09	0.12	23	1.04	0.31
	2011	0.09	0.08	0.11			
	site				52	0.88	0.38
	motte area				52	0.48	0.63
	motte height				52	1.06	0.29

[a] Estimates and 95% CI for tanglehead are back-transformed to show a change for every 10% increase of *H. contortus* cover, for year to show annual changes.

[b] Analyzed only in 2011.

[c] Analyzed only in 2010.

Appendix I. Bird species detected in winter; raw data used to determine which species to include in analyses, $n = 70$ plots, Jim Hogg County, Texas. Species only detected beyond 162 m or as flyovers are denoted with a ×.

	2010		2011	
Grassland status, resident type and species	% Plots	No. Detections	% Plots	No. Detections
Obligate Grassland Birds				
Permanent Resident				
Cassin's Sparrow (*Peucaea cassinii*)	33	39	17	14
Grasshopper Sparrow (*Ammodramus savannarum*) [a]	21	29	76	248
Eastern Meadowlark (*Sturnella magna*)	53	71	27	40
Winter Resident				
Northern Harrier (*Circus cyaneus*)	11	9	16	11
Long-billed Curlew (*Numenius americanus*)		×		×
Sedge Wren (*Cistothorus platensis*)			11	9
American Pipit (*Anthus rubescens*)		×		
Sprague's Pipit (*Anthus spragueii*)	16	13	1	1
Clay-colored Sparrow (*Spizella 114asser*)			7	6
Vesper Sparrow (*Pooecetes gramineus*)	6	8	7	7
Lark Bunting (*Calamospiza melanocorys*)	6	8	13	9
Savannah Sparrow (*Passerculus sandwichensis*)	64	98	63	204
Western Meadowlark (*Sturnella neglecta*)	57	139	26	29
Facultative Grassland Birds				
Permanent Resident				
Northern Bobwhite (*Colinus virginianus*)	13	11	24	23
Turkey Vulture (*Cathartes aura*)		×		×
White-tailed Hawk (*Buteo albicaudatus*)	1	1		
Crested Caracara (*Caracara cheriway*)			1	1
Mourning Dove (*Zenaida macroura*)	13	15	6	5
Common Ground-Dove (*Columbina 114asserine*)	3	2		
Ash-throated Flycatcher (*Myiarchus cinerascens*) [b]			1	1
Lark Sparrow (*Chondestes grammacus*) [e]	1	1		
Brown-headed Cowbird (*Molothrus ater*)	3	3	3	3
Winter Resident				
Greater White-fronted Goose (*Anser albifrons*)		×		×
American Kestrel (*Falco sparverius*)	20	19	14	13
Sandhill Crane (*Grus asserine*)				×
Killdeer (*Charadrius vociferous*) [c]		×		×
Chihuahuan Raven (*Corvus cryptoleucus*) [c]		×		
Loggerhead Shrike (*Lanius ludovicianus*) [c]	69	93	54	49
Say's Phoebe (*Sayornis saya*)	3	2	6	5

Grassland status, resident type and species	2010		2011	
	% Plots	No. Detections	% Plots	No. Detections
Brewer's Blackbird (*Euphagus cyanocephalus*)	1	2	3	5
Non-Grassland Birds				
Permanent Resident				
Great Blue Heron (*Ardea herodias*) [c]		×		
Cooper's Hawk (*Accipiter cooperii*)		×		×
Red-tailed Hawk (*Buteo jamaicensis*)	4	3		×
Eurasian Collared-Dove (*Streptopelia decaocto*)		×		×
White-tipped Dove (*Leptotila verreauxi*)		×		
Rock Pigeon (*Columba liva*)				×
Greater Roadrunner (*Geococcyx californianus*)	1	1	1	1
Great Horned Owl (*Bubo virginianus*)	4	3		×
Golden-fronted Woodpecker (*Melanerpes aurifrons*)	49	67	25	20
Ladder-backed Woodpecker (*Picoides scalaris*)	29	25	23	18
Great Kiskadee (*Pitangus sulphuratus*)			1	1
Green Jay (*Cyanocorax yncas*)	4	3		×
White-eyed Vireo (*Vireo griseus*)		×	4	4
Black-crested Titmouse (*Baeolohus atricristatus*)	1	1	3	2
Verdin (*Auriparus flaviceps*)	21	17	20	17
Bewick's Wren (*Thryomanes bewickii*)	31	28	46	50
Blue-gray Gnatcatcher (*Polioptila caerulea*)	11	8	1	1
Northern Mockingbird (*Mimus polyglottos*)	81	125	27	35
Long-billed Thrasher (*Toxostoma longirostre*)		×	6	5
Curve-billed Thrasher (*Toxostoma curvirostre*)	7	5	6	4
Olive Sparrow (*Arremonops rufivirgatus*)			1	1
Black-throated Sparrow (*Amphispiza billineata*)	1	4		
Northern Cardinal (*Cardinalis cardinalis*)	59	95	67	114
Pyrrhuloxia (*Cardinalis sinuatus*)	97	301	81	178
Audubon's Oriole (*Icterus graduacauda*)			1	2
Winter Resident				
Yellow-bellied Sapsucker (*Sphyrapicus varius*)			1	1
Eastern Phoebe (*Sayornis phoebe*) [d]	89	179	61	61
House Wren (*Troglodytes aedon*) [d]	50	60	57	63
Ruby-crowned Kinglet (*Regulus calendula*)	23	18	21	17
Cedar Waxwing (*Bombycilla cedrorum*)	1	1		
Orange-crowned Warbler (*Oreothlypis celata*)	70	88	67	81
Yellow-rumped Warbler (*Setophaga 115asserin*)	1	1		
Field Sparrow (*Spizella pusilla*) [d]	17	30	27	28
Chipping Sparrow (*Spizella 115asserine*)	1	7		

Grassland status, resident type and species	2010		2011	
	% Plots	No. Detections	% Plots	No. Detections
White-crowned Sparrow (*Zonotrichia leucophrys*)			1	1
Lincoln Sparrow (*Melospiza lincolnii*)			14	11
Red-winged Blackbird (*Agelaius phoeniceus*)		×		
Great-tailed Grackle (*Quiscalus mexicanus*)		×		×

[a] Permanent resident only in wet summers.

[b] Data from Christmas Bird Counts indicate this species can be qualified as a permanent resident because individuals will winter in the region.

[c] Did not breed on the ranches but may breed within the county.

[d] Included in presence and density analyses, but not richness.

[e] Withdrawals from grasslands to mowed or burned areas on the ranch in winter

VITA

Brian J. Bielfelt graduated, with honors, from Florida State University, receiving a B.S. in Biological Sciences in 2005. He is an avid birder that spent 4 years post-college working for multiple field jobs throughout the United States, performing migration and point count surveys. Notably, Mr. Bielfelt worked for two local chapters of the National Audubon Society from 2006 to 2009, serving as a bio-blitz coordinator, hawk migration specialist, science intern, and teacher naturalist. While at Audubon, he served as a volunteer coordinator, developed educational material for numerous school children, identified insects, organized dragonfly surveys, restored native ecosystems, and many other duties. In 2009, he married his beautiful wife Melissa in Nyack, NY. Within weeks after their honeymoon, they drove to southern Texas to begin pursuing a Master's degree at Texas A&M University-Kingsville. He served as a volunteer at the local Corpus Christi hawk watch for three seasons. In 2011, Brian and Melissa moved to Santa Clarita, California to begin work as a biological consultant for Sapphos Environmental, Inc. As a consultant, he serves as the link between hard science and application, development and conservation. He uses his skills in statistics, methodology, avian ecology, botany, and entomology to enhance work products produced by this company. In 2012, Brian and Melissa welcomed their first child, a daughter named Autumn 'Iolana. Aside from his passion for birds, insects, and hiking, he is driven by his faith in God.