Final Report:
Collaborative Research on the Natural History of the Enigmatic Spot-tailed Earless Lizard (*Holbrookia lacerata*) in Texas

Prepared for the
Texas Comptroller of Public Accounts
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by

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ACKNOWLEDGMENTS

CHAPTER 1. INTRODUCTION

Travis J. LaDuc

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Objectives of research program for the Spot-tailed Earless Lizard (*Holbrookia lacerata*)

The goal of this multi-year research program, first initiated in July 2014, was to develop science to inform the U.S. Fish and Wildlife Service's listing determination for *Holbrookia lacerata* whether the species warrants protection under the Endangered Species Act with a formal designation as a threatened or endangered species. Thus, the objective of the studies presented in this document is to improve our understanding of (1) biology of the species, (2) current condition, and (3) future condition. The results of these studies are organized in a manner so that they may be incorporated into a Species Status Assessment for *Holbrookia lacerata*. As these data were developed as part of an open, transparent process involving stakeholders, this final report details the results of the varied research program studies that were proposed over the course of the initial RFP (July 2014) and two iterative contract amendments (April 2015; February 2016), each expanding on the previous proposed work with the timeline to a listing decision by USFWS being continually pushed back to its current date in 2020 (USFWS 2016). A second separate contract focused wholly on radio telemetry work was signed (May 2017) to cover field work across 2017–2019, concluding prior to the current listing decision date.

Our results to date have begun to fill in gaps in our knowledge of this species (Figure 1.1). Road surveys across 57 counties within the historical range revealed populations of this species in 19 counties, including populations from both subspecies. Walking surveys were successful, but with lower detection rates than road/driving surveys. When found, this species often occupied early successional, disturbed habitats. Diet analyses of museum specimens indicate this species is an opportunistic generalist, with grasshoppers comprising over 1/3 of their diet; subsequent insect surveys in currently occupied STEL habitat demonstrate insect abundances match lizard diets. Initial genetic work using two genes supported the recognition of two separate species, elevating the subspecies to the species level: *Holbrookia lacerata* (north) and *Holbrookia subcaudalis* (south). A subsequent larger and more comprehensive molecular analysis supported these findings; morphological analyses found the same pattern with a division between the two taxa. With our knowledge of current day distributions elucidated by survey work, significant gaps remain in our understanding of habitat use, home range size, and behavior in these taxa. Radio telemetry work initiated under a separate contract in July 2017 demonstrated the effectiveness of small (0.2 g) transmitters for this small lizard (<6.0 g). An additional telemetry technique (harmonic radar) has been added to the radio telemetry protocol and both are being used at multiple field sites within the range of both taxa during both the 2018 and 2019 field seasons.

The research topics under this contract have grown and evolved during the 42 months of the contract. Work contracted under the initial RFP included quantifying habitat availability within the species' native range, compiling vegetation datasets, mapping landscape alteration resulting from oil and gas infrastructure development, and using this habitat assessment to direct on-the-

ground surveys to discover new populations. Work was conducted primarily by two groups at The University of Texas at Austin (Biodiversity Collections, College of Natural Sciences and the Bureau of Economic Geology, Jackson School of Geosciences); fieldwork was subcontracted with Mike Duran (The Nature Conservancy). The original December 2016 deadline for contract completion was driven by the need to accommodate the USFWS timetable for a FY 2017 listing decision for *Holbrookia lacerata*. The listing decision timetable was subsequently shown to be pushed back, allowing our group to submit a contract amendment to perform additional research tasks not originally considered because USFWS timetable. We proposed seven new tasks, including a significant expansion in field (survey) work and a novel proposal for genetic work, with both the field and genetic tasks subcontracted with the Institute for Renewable Natural Resources at Texas A&M University. We also proposed projects using museum voucher specimens to investigate both morphological differences between populations and elucidating the diet of this lizard species by examining preserved specimen gut contents. Three new modeling projects were also proposed: mapping effects of agriculture, roads, and urbanization on habitat fragmentation; a connectivity analysis (between northern and southern populations); forecasting future ecological impacts caused by urbanization and energy development in the Eagle Ford play. The contract amendment was approved in April 2015.

Work accelerated through 2015, buoyed in large part due to the survey success achieved by our Texas A&M and Nature Conservancy collaborators. Over 170 *Holbrookia lacerata* were seen during 274 surveys conducted in 2015, which was significant because of the paucity of sightings during the last range wide survey in 2008–2010 (Duran and Axtell 2010). These surveys not only documented the species' persistence in south Texas (southern population; individuals not having been seen for ~15 years) and the Permian Basin (northern population) but specimens collected provided important tissue samples for genetic analyses. Three analysis units were identified (N, SW, SE) by the end of 2015; the presence of these three separate units influenced decisions made by the Spot-tailed Earless Lizard working group (convened by Dr. Robert Gulley of the Texas Comptroller of Public Accounts and comprised of interested stakeholders) and directions of our subsequent research in 2016 and 2017.

At the encouragement of both the USFWS and the Spot-tailed Earless Lizard working group, our group collaboratively produced an influence diagram in 2015 (Chapter 9, Figure 9.5) to better understand our hypotheses for what factors are important to the survival of *Holbrookia lacerata*. We used the influence diagram to identify data gaps in the current understanding of *H. lacerata* to inform the development of additional scientific studies to elucidate how each source may affect the species, ultimately leading to a proposal for the final contract amendment in 2016. Additionally, the USFWS timetable for listing decisions pushed back the decision date to FY 2020 (USFWS 2016). The tasks in this last amendment were focused on these data gaps in an effort to provide data integral for the construction of a Population Viability Analysis (PVA), and ultimately to provide data in support of a Species Status Assessment (SSA) for *Holbrookia lacerata* that, for a period of time in 2015–2016, had been proposed to be collaboratively written by our group and USFWS. Ultimately, this relationship was never formally codified but this idea drove many of the tasks proposed in the final amendment and we anticipated products from this work would provide decision makers and natural resource managers a sound framework to proceed to a full PVA and population model. In this final contract amendment, we proposed several steps towards gathering the data needed for a PVA including: updating the habitat model

based on the presence of three analysis units; quantifying current and future landscape threats; field surveys and population genetic approaches to provide density and abundance estimates; insect surveys and mark-recapture studies to determine survival and fertility rates.

Field research under this contract concluded in July 2017 at the end of the field season. Unfortunately, despite continuing to see lizards at survey sites, the mark-recapture surveys did not provide adequate numbers of recaptures to facilitate reliable population size estimates. Funding and support for the PVA was withdrawn in 2017, partially on the basis of inadequate field data to integrate into the analyses. Connectivity analyses were also cancelled because of collective decisions made internally and by the Working Group to focus model efforts towards separate analyses for each of the three units. Further, genetic and morphological results supporting the recognition of two separate species, rather than a single species, provided additional reasons not to pursue connectivity analyses.

This final report provides the results and deliverables for tasks from the original contract and the two successive amendments. Four chapters of this final report have been published as peer-reviewed journal articles, one manuscript is currently in revisions, and at least three additional manuscripts are in development (climate change, diet of *Holbrookia lacerata*, insect survey data). Manuscripts published and in revisions are:

Wolaver, B.D., Pierre, J.P., Labay, B.L., LaDuc, T.J., Duran, C.M., Ryberg, W.A., Hibbitts, T.J. (2018a) An approach for evaluating changes in land-use from energy sprawl and other anthropogenic activities with implications for biotic resource management. Environmental Earth Sciences, https://doi.org/10.1007/s12665-018-7323-8.

Pierre, J.P., Wolaver, B. D., Labay, B. J., LaDuc, T. J., Duran, C. M., Ryberg, W. A., Hibbitts, T. J. and Andrews, J. R. (2018) Comparison of recent oil and gas, wind energy, and other anthropogenic landscape alteration factors in Texas through 2014. Environmental Management, https://doi.org/10.1007/s00267-018-1000-2. doi: 10.1007/s00267-018-1000-2.

Wolaver, B. D., J. P. Pierre, S. A. Ikonnikova, J. R. Andrews, G. McDaid, W. A. Ryberg, T. J. Hibbitts, C. M. Duran, B. J. Labay, and T. J. LaDuc, 2018b, An improved approach for forecasting ecological impacts from future drilling in unconventional shale oil and gas plays: Environmental Management. http://dx.doi.org/10.1007/s00267-018-1042-5.

Roelke, C. E., J. A. Maldonado, B. W. Pope, T. J. Firneno Jr., T. J. LaDuc, T. J. Hibbitts, W. A. Ryberg, N. D. Rains, and M. K. Fujita. 2018. Mitochondrial genetic variation within and between *Holbrookia lacerata lacerata* and *Holbrookia lacerata subcaudalis*, the spot-tailed earless lizards of Texas. Journal of Natural History 2018 [11 pp.]. https://doi.org/10.1080/00222933.2018.1436726.

Hibbitts, T. J., W. A. Ryberg, J. Harvey, G. Voelker, M. Lawing, C. S. Adams, D. B. Neuharth, D. E. Dittmer, C. M. Duran, B. D. Wolaver, J. P. Pierre, B. J. Labay, T. J. LaDuc. Phylogenetic relationships within *Holbrookia lacerata* (Cope 1880) (Squamata: Phrynosomatidae). Submitted to Zootaxa, reviewed and returned for revisions.

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GIS data sets from analyses shown in Chapters 9, 10, and 11 (Wolaver et al., 2018a, Pierre et al., 2018, and Wolaver et al., 2018b listed above) are available online at Texas Data Repository at: https://dataverse.tdl.org/dataverse/stel. If you download and use these mapping products, please cite the corresponding publication.

Additional datasets used as inputs that included confidential and/or proprietary data were delivered separately to the office of the Texas Comptroller of Public Accounts, and included raw data files for manuscripts currently in preparation (e.g. diet analyses).

Literature Cited

Axtell, R. W. 1998. *Holbrookia lacerata*. Interpretive Atlas of Texas Lizards 20:1–11.

Duran, C. M. and R. W. Axtell. 2010. A rangewide inventory and habitat model for the spot-tailed earless lizard (*Holbrookia lacerata*). Report to Texas Parks and Wildlife, Austin, Texas. 37 pp.

U.S. Fish and Wildlife Service (USFWS). 2016. National Listing Workplan: 7-Year Workplan (September 2016 Version). Available at https://www.fws.gov/endangered/esa-library/pdf/Listing%207-Year%20Workplan%20Sept%202016.pdf. Archived by WebCite at http://www.webcitation.org/6yMXZs0mq on 1 April 2018.
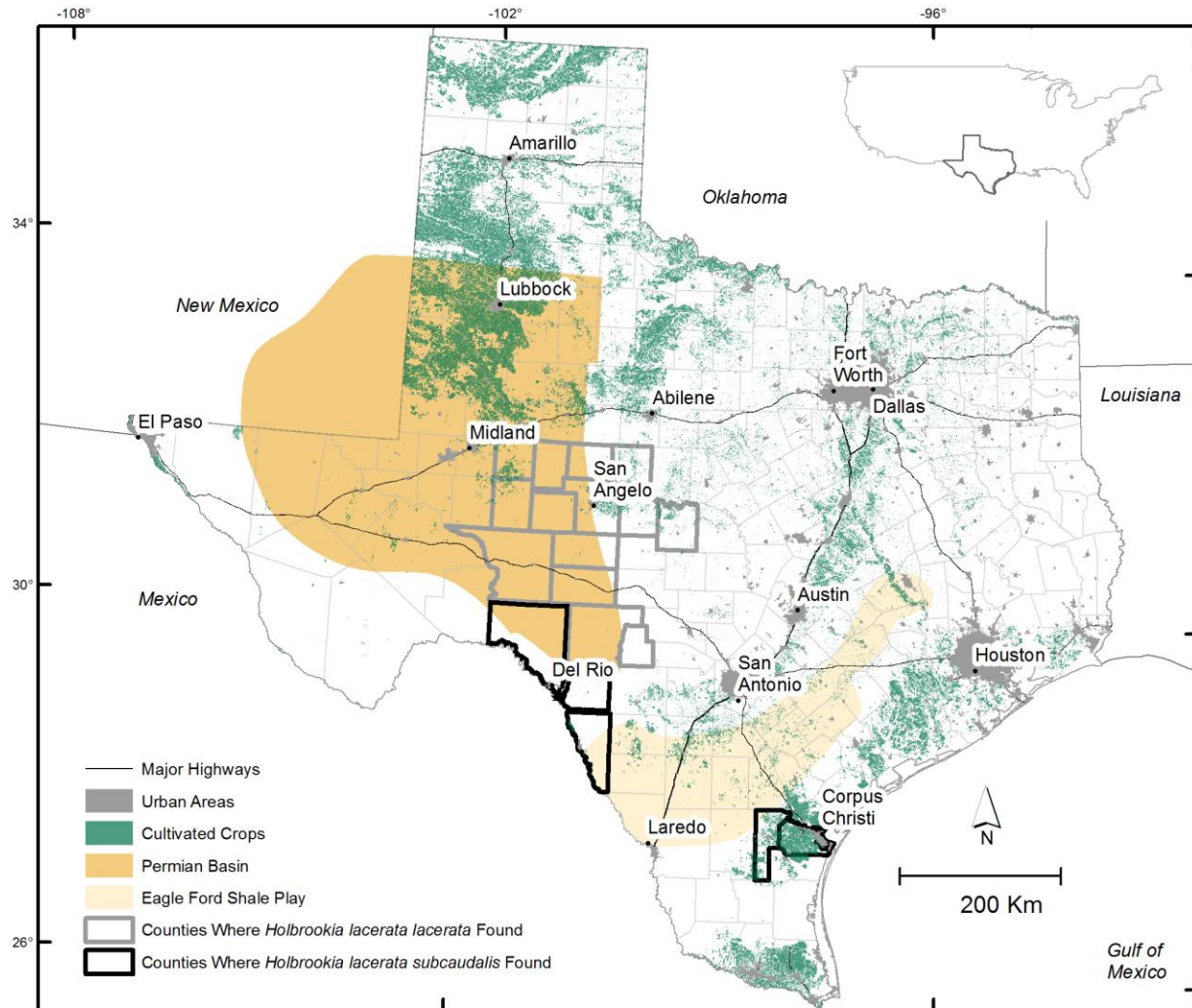
Figure 1.1. Distribution of Spot-tailed Earless Lizard (*Holbrookia lacerata*) based on survey data collected 2015–2017.

CHAPTER 2. SURVEY RESULTS FOR THE SPOT-TAILED EARLESS LIZARD (*HOLBROOKIA LACERATA*) IN TEXAS (2015-2017)

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Methods

Distribution Surveys

Historical records, aerial imagery and distribution models (created by University of Texas on this project) were used to select sites for Spot-tailed Earless Lizard (STEL; *Holbrookia lacerata*) distribution surveys beginning in 2015 and continuing through 2017. Surveys were conducted by driving along roads at slow speeds (e.g., 15 mph). These road surveys were timed and in many cases the same stretch of road was passed over several times. Some surveys were conducted on foot when access to private land was available. These were also timed in the same way as driving surveys. Both driving and walking surveys were conducted in each of the three survey units (e.g., North, Southwest, and Southeast). For 15 surveys in 2017, driving and walking survey methods were combined to survey areas in the Southwest unit containing locations where driving was temporarily prohibited.

Mark-recapture Data

In addition to improving our knowledge of the current distribution of STEL populations, our surveys were used to conduct a mark-recapture study aimed at estimating survival and recruitment of the species. To create encounter histories for the mark-recapture study, we used two different methods to identify recaptured STEL. The traditional toe-clipping method was employed whenever lizards were in hand. This method provides each individual STEL captured with a unique and permanent mark by clipping toes according to an established numerical marking scheme. Whenever lizards were seen but could not be captured, we took photographs of them from multiple angles with a Canon Powershot SX60 HS. This camera was chosen because its 65x optical zoom which gave us the ability to "capture" clear pictures of each STEL at long distances. Each photo was sorted into a database by location and date and given an ID number to compare between each individual within the given site. Photos were then compared side-by-side to check for similarities in colors, patterns, and shapes of blotches on individuals.

Results

Distribution Surveys

Male, female, and juvenile STEL were frequently observed basking on dirt, caliche, and paved roads during driving surveys in all three survey units (Fig. 2.1). Typical habitats where STEL was observed included relatively undisturbed, but grazed, grasslands with little woody

encroachment (Fig. 2.2) and heavily disturbed agricultural fields (i.e., plowed fields; Fig. 2.3). Male, female, and juvenile STEL were also observed, albeit less frequently, during walking surveys targeting similar grassland and agricultural habitats in all three survey units. Detailed results for each survey method across all three years are described below.

Figure 2.1. Male (top) and gravid female (bottom) basking on caliche/dirt road in Schleicher County, Texas.

Figure 2.2. Relatively undisturbed, but grazed, grassland habitat where STEL individuals were detected on a road in Schleicher County, Texas.

Figure 2.3. Heavily disturbed agricultural fields where STEL individuals were detected on roads in Nueces (top) and Glasscock (bottom) Counties, Texas.

2015 Surveys

Between April 22 and September 24, 2015, we conducted 295 surveys in 57 Texas counties (Fig 2.4, Table 2.1). We observed STEL on 46 surveys in 18 counties. A total of 172 STEL were observed. Overall we surveyed for 623.1 hours and found 0.284 lizards per hour on average. We also found that driving surveys (0.305 per hour) were more efficient than walking surveys (0.122 per hour) on average. Although we did surveys over six months, the majority of successful surveys were in April through June (37 successful out of 138 surveys) with far fewer successful surveys in the hotter drier parts of the summer (9 successful out of 136 surveys). We surveyed almost equally in the distribution of the northern subspecies (148 surveys) as the southern subspecies (147 surveys) and had slightly more successful surveys in the range of the northern subspecies (26 successful surveys compared to 20). Although survey number was almost equal between the north and the south, the amount of time spent surveying was higher in the south (375.9 hours) than it was in the north (247.2 hours). This is likely a result of the number of lizards captured per hour being much higher in the north (0.35 per hour) than in the south (0.23 per hour).

2016 Surveys

Between April 6 and September 28, 2016, we conducted 170 surveys across 27 Texas counties (Fig. 2.5, Table 2.2). A total of 170 STEL were observed on 53 surveys in 7 counties. Overall, we surveyed for 383.7 hours and found 0.24 lizards per hour on average. As we discovered in 2015, driving surveys (0.30 STEL per hour) were more efficient than walking surveys (0.04 STEL per hour) on average. Additionally, although we did surveys over six months, the majority of successful surveys were in April through June (40 successful out of 118 surveys, 34%) with far fewer successful surveys in the hotter, drier parts of the summer (12 successful out of 53 surveys, 23%). We conducted fewer surveys and spent less time surveying within the distribution of the northern subspecies (75 surveys, 155.7 hours) than the southern subspecies (95 surveys, 228.0 hours), but we had slightly more successful surveys in the range of the northern subspecies (30 successful surveys compared to 23, or 40% compared to 24%). Indeed, the number of lizards captured per hour was much higher in the north (0.67 STEL per hour) than in the south (0.28 STEL per hour). These patterns are similar to those observed in 2015.

2017 Surveys

We conducted 116 surveys for STEL between February 21 and August 18, 2017 (Fig. 2.6, Table 2.3). Overall, we surveyed for 246.3 hours and observed 67 STEL yielding an observation rate of 0.48 lizards per hour on average. Driving surveys (0.49 STEL per hour) were again more efficient than walking (0.04 STEL per hour) or combination (0.11 STEL per hour) surveys on average. Unlike previous years, the majority of successful surveys were *not* in April through June (19 successful out of 67 surveys, 28%), but instead in the hotter, drier months (17 successful out of 49 surveys, 35%). This is most likely due to the early survey start in February this year. Like 2016, we conducted fewer surveys and spent less time surveying within the distribution of the northern subspecies (39 surveys, 66.8 hours) than the southern subspecies (77 surveys, 179.5 hours); however unlike 2016, we had equal survey success in the range of both subspecies (12 of 39 northern and 24 of 77 southern, or 31%). That said, the number of lizards

captured per hour was much higher in the north (0.45 STEL per hour) than in the south (0.21 STEL per hour).

Table 2.1. Spot-tailed Earless Lizard 2015 survey effort and success by county. Survey number, time, lizards observed, and observation rate are listed by survey type (drive vs. walk).

County	Surveys			Time (hours)			Lizards Observed			Observation Rate (#/hour)		
	Drive	Walk	Total	Drive	Walk	Total	Drive	Walk	Total	Drive	Walk	Total
Atascosa	1		1	2.0		2.0				0.000		0.000
Bee	6		6	9.6		9.6				0.000		0.000
Bexar	2		2	2.4		2.4				0.000		0.000
Blanco	1		1	3.4		3.4				0.000		0.000
Coke	15		15	15.1		15.1	1		1	0.066		0.066
Comal	1		1	1.2		1.2				0.000		0.000
Concho	9		9	11.9		11.9	29		29	2.446		2.446
Crockett	6		6	9.3		9.3	5		5	0.538		0.538
Dimmit	11		11	15.1		15.1				0.000		0.000
Duval	14		14	27.7		27.7				0.000		0.000
Ector	1		1	0.8		0.8				0.000		0.000
Edwards	5		5	8.9		8.9	1		1	0.112		0.112
Frio	2		2	8.7		8.7				0.000		0.000
Gillespie	2		2	7.9		7.9				0.000		0.000
Glasscock	4		4	4.7		4.7	4		4	0.854		0.854
Goliad	1		1	1.9		1.9				0.000		0.000
Hays	1		1	2.1		2.1				0.000		0.000
Howard	7		7	10.2		10.2				0.000		0.000
Irion	5		5	10.8		10.8	1		1	0.093		0.093
Jim Hogg	1		1	2.8		2.8				0.000		0.000
Jim Wells	8		8	14.1		14.1	8		8	0.566		0.566
Karnes	2		2	3.1		3.1				0.000		0.000
Kendall	2		2	2.5		2.5				0.000		0.000
Kerr	4		4	5.4		5.4				0.000		0.000
Kimble	4	3	7	7.7	14.4	22.1				0.000	0.000	0.000
Kinney	7	2	9	20.5	24.6	45.1	42	1	43	2.047	0.041	0.953
Kleberg	5		5	9.7		9.7				0.000		0.000
La Salle	10		10	19.1		19.1				0.000		0.000
Live Oak	4		4	10.0		10.0				0.000		0.000
Martin	1		1	1.8		1.8				0.000		0.000

Table 2.1. (continued)

County	Surveys			Time (hours)			Lizards Observed			Observation Rate (#/hour)		
	Drive	Walk	Total	Drive	Walk	Total	Drive	Walk	Total	Drive	Walk	Total
Maverick	3	1	4	1.8	9.4	11.2		4	4	0.000	0.426	0.357
McCulloch	7		7	21.4		21.4	1		1	0.047		0.047
McMullen	4		4	11.4		11.4				0.000		0.000
Medina	6		6	11.1		11.1				0.000		0.000
Menard	14		14	20.5		20.5				0.000		0.000
Midland	4		4	4.4		4.4				0.000		0.000
Mitchell	15		15	22.3		22.3				0.000		0.000
Nueces	10		10	21.2		21.2	19		19	0.897		0.283
Reagan	4		4	4.6		4.6	4		4	0.876		0.876
Real	2		2	1.8		1.8	1		1	0.561		0.561
Refugio	3		3	7.9		7.9				0.000		0.000
Runnels	2		2	4.0		4.0	8		8	1.996		1.996
San Patricio	9		9	23.0		23.0				0.000		0.000
San Saba	2		2	7.1		7.1				0.000		0.000
Schleicher	1		1	1.5		1.5	5		5	3.279		3.279
Starr	3		3	4.9		4.9				0.000		0.000
Sterling	5		5	4.8		4.8	4		4	0.836		0.836
Sutton	10		10	14.0		14.0				0.000		0.000
Tom Green	6		6	10.6		10.6	23		23	2.173		2.173
Travis	1		1	0.7		0.7				0.000		0.000
Upton	3	1	4	5.0	1.0	6.0				0.000	0.000	0.000
Uvalde	4		4	2.5		2.5				0.000		0.000
Val Verde	1	7	8	0.0	70.3	70.3	1	10	11	0.000	0.142	0.157
Ward	1		1	3.0		3.0				0.000		0.000
Webb	9		9	26.7		26.7				0.000		0.000
Zapata	1		1	2.6		2.6				0.000		0.000
Zavala	9		9	14.4		14.4				0.000		0.000
Total = 57	**281**	**14**	**295**	**503.4**	**119.7**	**623.1**	**157**	**15**	**172**	**Avg 0.305**	**Avg 0.122**	**Avg 0.284**

Table 2.2. Spot-tailed Earless Lizard 2016 survey effort and success by county. Survey number, time, lizards observed, and observation rate are listed by survey type (drive vs. walk).

County	Surveys			Time (hours)			Lizards Observed			Observation Rate (#/hour)		
	Drive	Walk	Total	Drive	Walk	Total	Drive	Walk	Total	Drive	Walk	Total
Bee	1		1	1.3		1.3				0.00		0.00
Blanco	7	1	8	6.8	3.8	10.6				0.00	0.00	0.00
Coke	1		1	1.1		1.1				0.00		0.00
Crockett	2	25	27	4.1	72.1	76.2	3	2	5	0.74	0.03	0.07
Dimmit	1		1	11.6		11.6				0.00		0.00
Duval	1		1	2.0		2.0				0.00		0.00
Edwards	1		1	1.2		1.2	1		1	0.86		0.86
Jim Hogg	1		1	1.9		1.9				0.00		0.00
Jim Wells	22	1	23	32.9	2.4	35.3	37		37	1.12	0.00	1.05
Karnes	2		2	3.0		3.0				0.00		0.00
Kimble	1		1	0.6		0.6				0.00		0.00
Kinney	12		12	25.8		25.8				0.00		0.00
Kleberg	2	3	5	2.0	14.5	16.4				0.00	0.00	0.00
Live Oak	1		1	3.3		3.3				0.00		0.00
Maverick		2	2	0.0	16.6	16.6					0.00	0.00
McCulloch	1		1	0.6		0.6				0.00		0.00
McMullen	2		2	8.7		8.7				0.00		0.00
Menard	3		3	2.3		2.3				0.00		0.00
Nueces	5	1	6	3.0	3.9	6.8				0.00	0.00	0.00
San Patricio	1		1	1.8		1.8				0.00		0.00
Schleicher	12		12	26.5		26.5	42		42	1.58		1.58
Sutton	1		1	1.8		1.8	2		2	1.13		1.13
Tom Green	22		22	31.7		31.7	55		55	1.73		1.73
Val Verde	12	19	31	17.6	69.2	86.8	12	16	28	0.80	0.23	0.32
Ward	1		1	3.3		3.3				0.00		0.00
Webb	2		2	5.1		5.1				0.00		0.00
Zapata	1		1	1.5		1.5				0.00		0.00
Total = 27	**118**	**52**	**170**	**201.3**	**182.4**	**383.7**	**152**	**18**	**170**	**Avg 0.30**	**Avg 0.04**	**Avg 0.24**

Table 2.3. Spot-tailed Earless Lizard 2017 survey effort and success by county. Survey number, time, lizards observed, and observation rate are listed by survey type (drive vs. walk vs. comb = combined).

County	Surveys				Time (hours)				Lizards Observed				Observation Rate (#/hour)			
	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total
Crockett	1	13		14	2.4	24.8		27.2					0.00	0.00		0.00
Jim Wells	7			7	10.8			10.8	1			1	0.09			0.09
Kinney	3			3	2.5			2.5					0.00			0.00
Kleberg		5		5		10.3		10.3						0.00		0.00
Nueces	4			4	2.5			2.5	2			2	0.80			0.80
Schleicher	8	1		9	1.8	12.2		14.0	3			3	1.67	0.00		1.67
Tom Green	16			16	25.6			25.6	27			27	1.05			1.05
Val Verde	36	7	15	58	90.5	17.6	45.3	153.4	26	3	5	34	0.29	0.17	0.11	0.22
Total = 8	**75**	**26**	**15**	**116**	**136.1**	**64.9**	**45.3**	**246.3**	**59**	**3**	**5**	**67**	**Avg 0.49**	**Avg 0.04**	**Avg 0.11**	**Avg 0.48**

Table 2.4. Spot-tailed Earless Lizard 2015-17 survey effort and success by county. Survey number, time, lizards observed, and observation rate are listed by survey type (drive vs. walk vs. comb = combined).

County	Surveys				Time (hours)				Lizards Observed				Observation Rate (#/hour)			
	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total
Atascosa	1			1	2			2					0.00			0.00
Bee	7			7	10.9			10.9					0.00			0.00
Bexar	2			2	2.4			2.4					0.00			0.00
Blanco	8	1		9	10.2	3.8		14					0.00	0.00		0.00
Coke	16			16	16.2			16.2	1			1	0.06			0.06
Comal	1			1	1.2			1.2					0.00			0.00
Concho	9			9	11.9			11.9	29			29	2.44			2.44
Crockett	9	38		47	15.8	96.9		112.7	8	2		10	0.51	0.02		0.09
Dimmit	12			12	26.7			26.7					0.00			0.00
Duval	16			16	31.6			31.6					0.00			0.00
Ector	1			1	0.8			0.8					0.00			0.00
Edwards	6			6	10.1			10.1	2			2	0.20			0.20
Frio	2			2	8.7			8.7					0.00			0.00
Gillespie	2			2	7.9			7.9					0.00			0.00
Glasscock	4			4	4.7			4.7	4			4	0.85			0.85
Goliad	1			1	1.9			1.9					0.00			0.00
Hays	1			1	2.1			2.1					0.00			0.00
Howard	7			7	10.2			10.2					0.00			0.00
Irion	5			5	10.8			10.8	1			1	0.09			0.09
Jim Hogg	2			2	4.7			4.7					0.00			0.00
Jim Wells	37	1		38	57.8	2.4		60.2	46			46	0.80	0.00		0.76
Karnes	4			4	6.1			6.1					0.00			0.00
Kendall	2			2	2.5			2.5					0.00			0.00
Kerr	4			4	5.4			5.4					0.00			0.00
Kimble	5	3		8	8.3	14.4		22.7					0.00	0.00		0.00
Kinney	22	2		24	48.8	24.6		73.4	42	1		43	0.86	0.04		0.59
Kleberg	7	8		15	11.7	24.8		36.4					0.00	0.00		0.00
La Salle	10			10	19.1			19.1					0.00			0.00
Live Oak	5			5	13.3			13.3					0.00			0.00

Table 2.4. (continued)

County	Surveys				Time (hours)				Lizards Observed				Observation Rate (#/hour)			
	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total
Martin	1			1	1.8			1.8					0.00			0.00
Maverick	3	3		6	1.8	26		27.8		4		4	0.00	0.15		0.14
McCulloch	8			8	22			22	1			1	0.05			0.05
McMullen	6			6	20.1			20.1					0.00			0.00
Medina	6			6	11.1			11.1					0.00			0.00
Menard	17			17	22.8			22.8					0.00			0.00
Midland	4			4	4.4			4.4					0.00			0.00
Mitchell	15			15	22.3			22.3					0.00			0.00
Nueces	19	1		20	26.7	3.9		30.6	21			21	0.79	0.00		0.69
Reagan	4			4	4.6			4.6	4			4	0.87			0.87
Real	2			2	1.8			1.8	1			1	0.56			0.56
Refugio	3			3	7.9			7.9					0.00			0.00
Runnels	2			2	4			4	8			8	2.00			2.00
San Patricio	10			10	24.8			24.8					0.00			0.00
San Saba	2			2	7.1			7.1					0.00			0.00
Schleicher	21	1		22	29.8	12.2		42.0	50			50	1.68	0.00		1.19
Starr	3			3	4.9			4.9					0.00			0.00
Sterling	5			5	4.8			4.8	4			4	0.83			0.83
Sutton	11			11	15.8			15.8	2			2	0.13			0.13
Tom Green	44			44	67.9			67.9	105			105	1.55			1.55
Travis	1			1	0.7			0.7					0.00			0.00
Upton	3	1		4	5	1		6					0.00	0.00		0.00
Uvalde	4			4	2.5			2.5					0.00			0.00
Val Verde	49	33	15	97	108.1	157.1	45.3	310.5	39	29	5	73	0.36	0.18	0.11	0.24
Ward	2			2	6.3			6.3					0.00			0.00
Webb	11			11	31.8			31.8					0.00			0.00
Zapata	2			2	4.1			4.1					0.00			0.00
Zavala	9			9	14.4			14.4					0.00			0.00

Table 2.4. (continued)

| Total = 57 | 475 | 92 | 15 | 582 | 843.0 | 367.1 | 45.3 | 1255.2 | 368 | 36 | 5 | 409 | Avg 0.26 | Avg 0.04 | Avg 0.11 | Avg 0.23 |
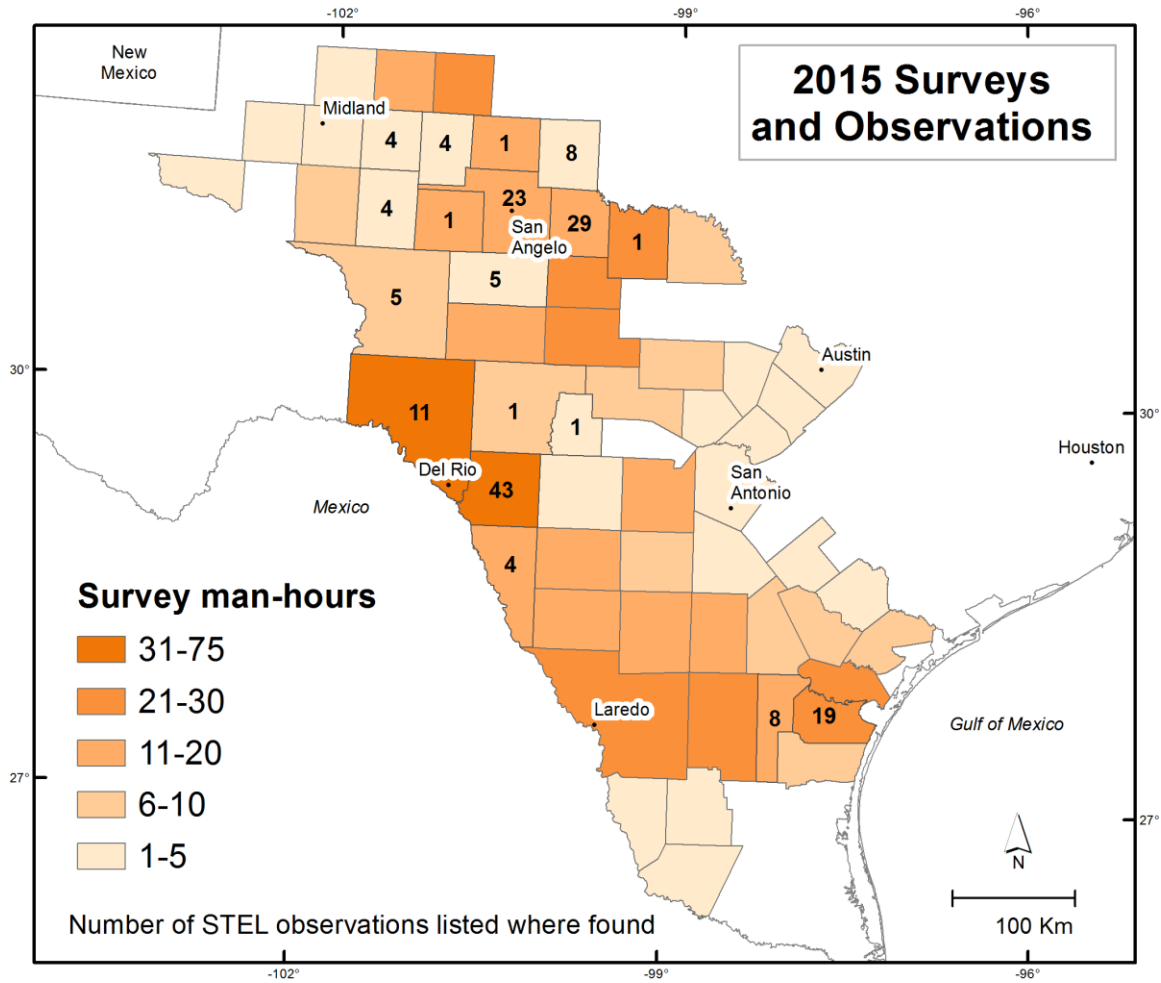
Figure 2.4. 2015 Spot-tailed Earless Lizard (*Holbrookia lacerata*) survey effort and results.
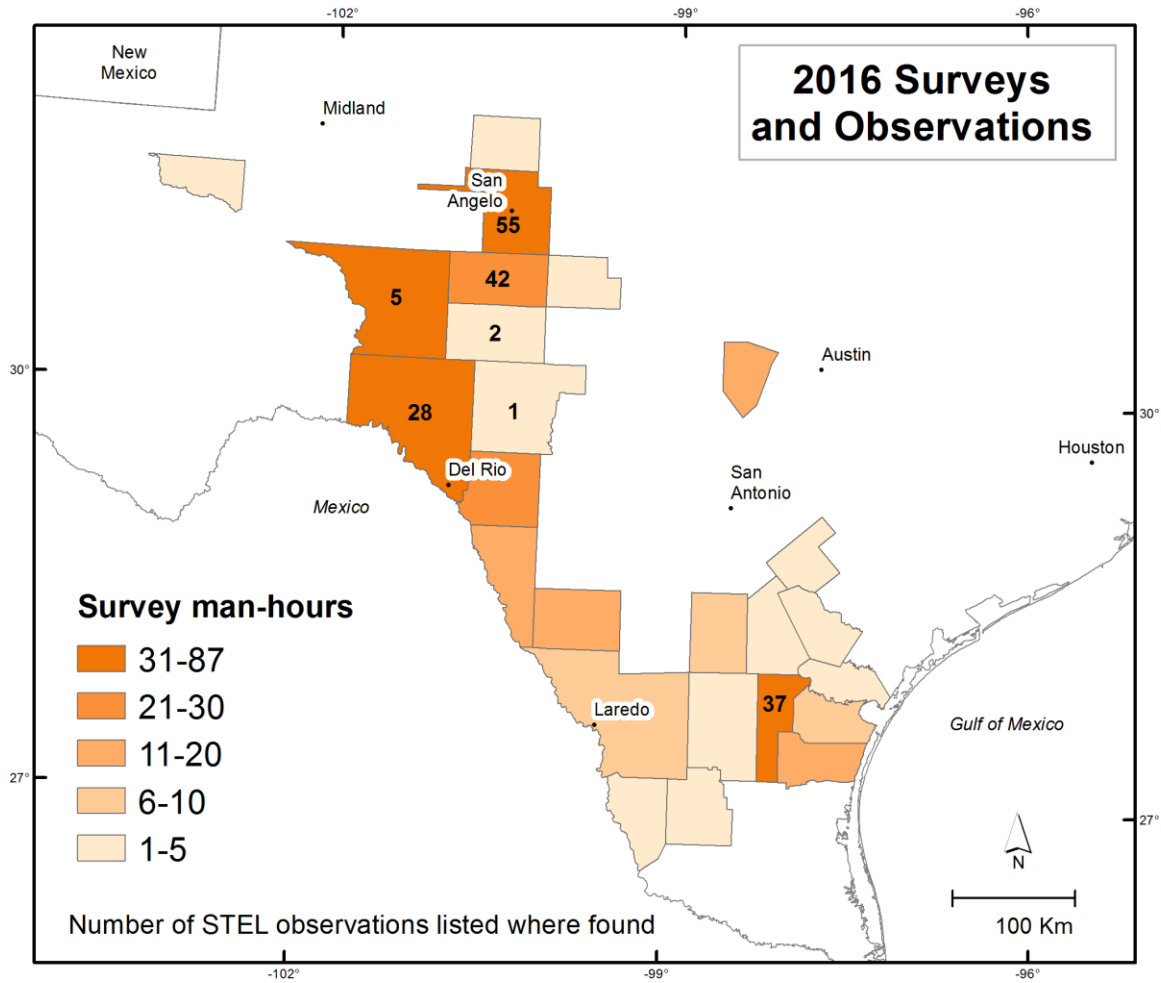
Figure 2.5. 2016 Spot-tailed Earless Lizard (*Holbrookia lacerata*) survey effort and results.
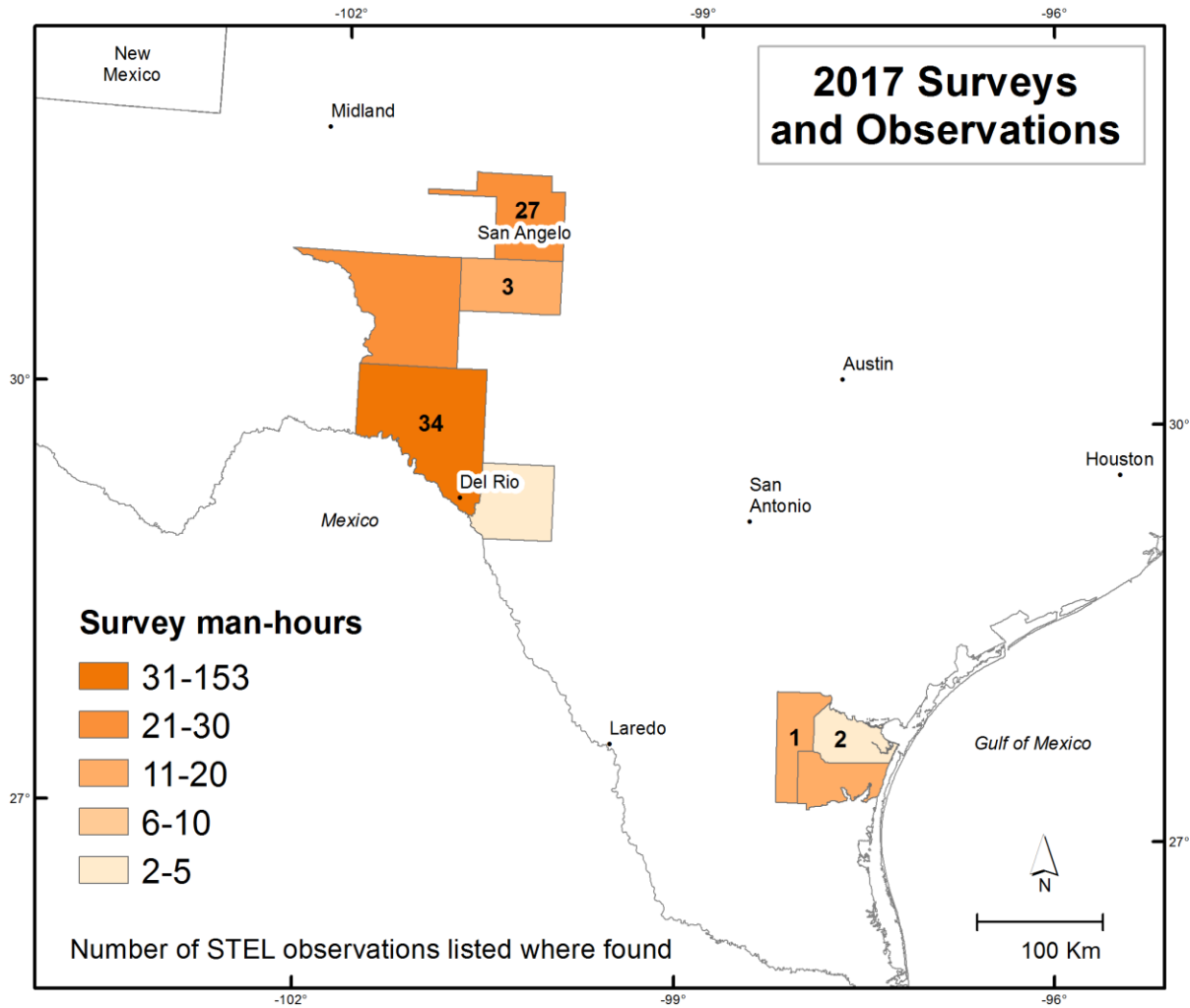
Figure 2.6. 2017 Spot-tailed Earless Lizard (*Holbrookia lacerata*) survey effort and results.

2015-17 Survey Man-Hours

- ■ 1 - 5
- ■ 6 - 10
- ■ 11 - 20
- ■ 21 - 30
- ■ 31 - 310

Number of STEL observations listed where found

○ Minimum bounding circle, 2000-2015 *Holbrookia lacerata* localities

0   100 km
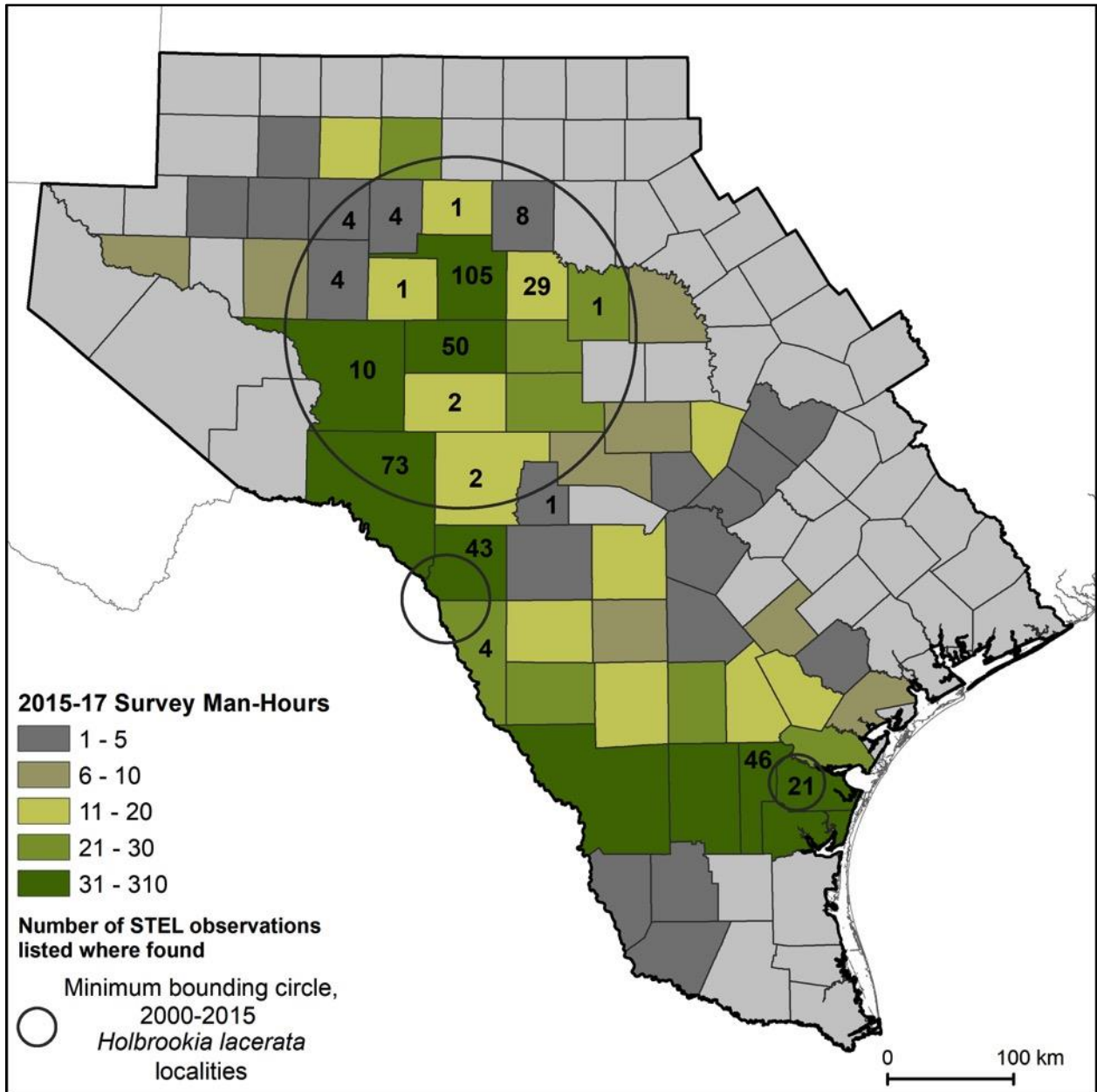
Figure 2.7. Spatial distribution of Spot-tailed Earless Lizard 2015-17 survey effort (in hours) and success by county.
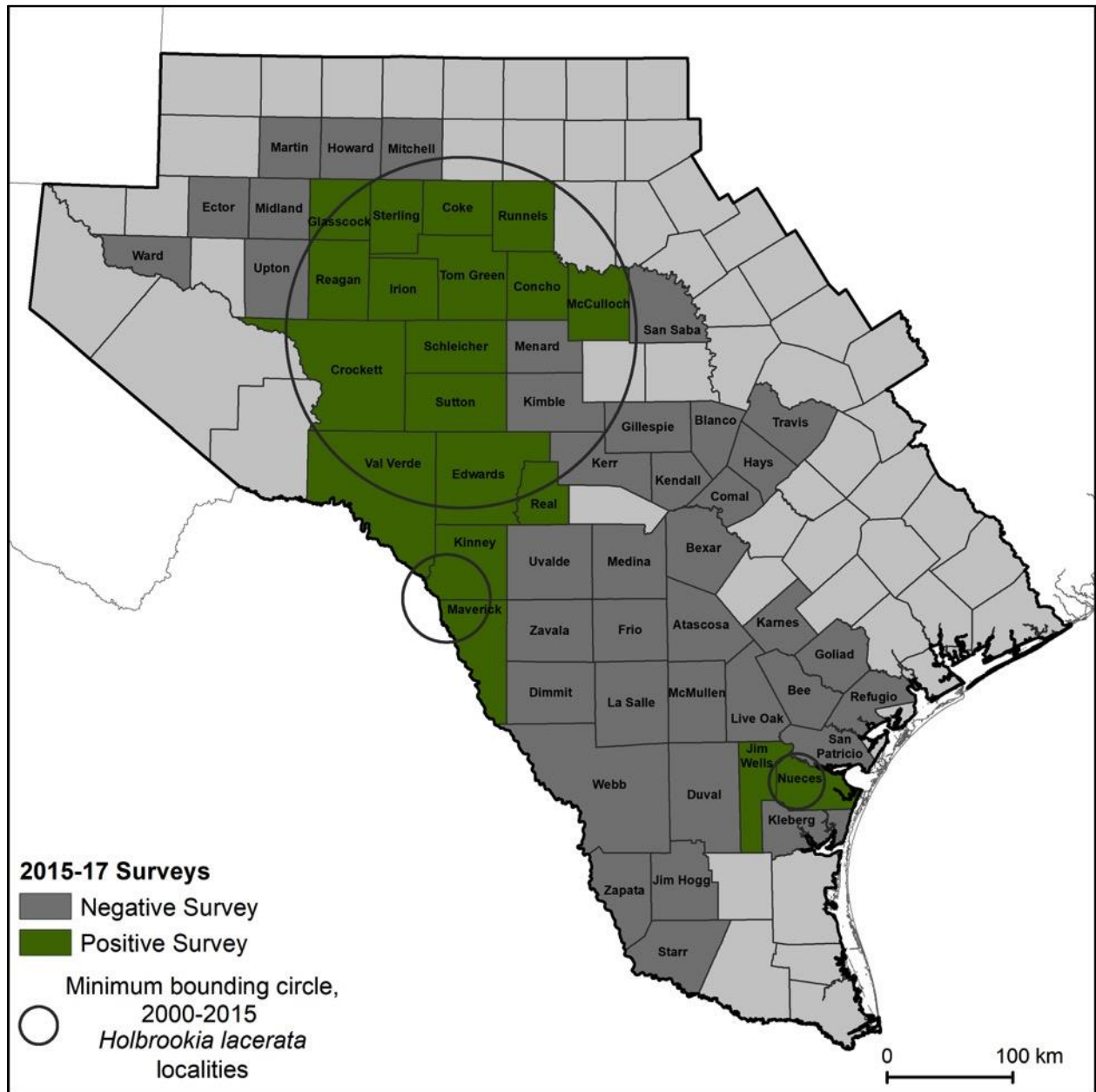
Figure 2.8. Positive and negative Spot-tailed Earless Lizard 2015-17 surveys by county.

All Surveys (2015-17)

We conducted 582 surveys for STEL across 57 Texas counties between April 22, 2015 and August 18, 2017 (Table 2.4; Fig. 2.7). A total of 409 STEL were observed on 135 surveys in 19 counties (Fig. 2.8). Overall, we surveyed for 1,255.2 hours and found 0.23 lizards per hour on average. Driving surveys (0.26 STEL per hour) were more efficient than walking (0.04 STEL per hour) and combination (0.11 STEL per hour) surveys on average. We conducted fewer surveys and spent less time surveying within the distribution of the northern subspecies (262 surveys, 469.7 hours) than the southern subspecies (319 surveys, 783.4 hours), but we had slightly more successful surveys in the range of the northern subspecies (68 successful surveys compared to 67, or 26% compared to 21%, respectively). Indeed, the number of lizards captured per hour was much higher in the north (0.47 STEL per hour) than in the south (0.24 STEL per hour).

Across all years, the earliest STEL detected was on 6 April and the latest detected was on 23 September (Fig. 2.9). The earliest gravid female detected was also on 6 April and the latest detected was on 20 July. Juveniles were detected as early as 14 June and as late as 23 September.
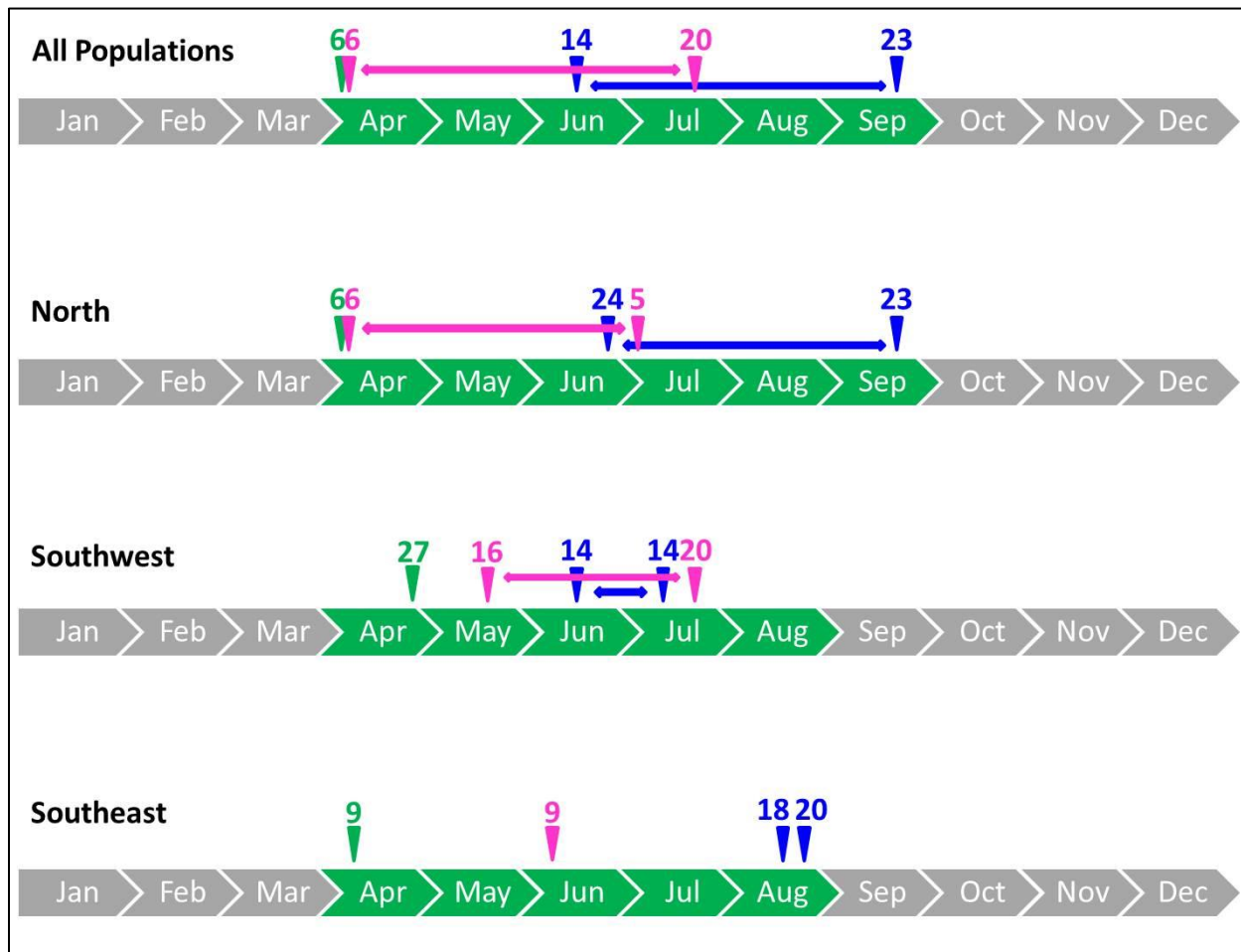
Figure 2.9. Summary of earliest and latest detections for all STEL (green), gravid females (pink), and juveniles (blue) across all populations and each survey unit.

Table 2.5. Spot-tailed Earless Lizard recaptures by survey unit, county, survey site, year, and survey type (drive vs. walk vs. comb = combined).

Survey Unit (lizards marked)	County	Survey Site	2016 Surveys				2017 Surveys				All Surveys			
			Drive	Walk	Comb	Total	Drive	Walk	Comb	Total	Drive	Walk	Comb	Total
North (47 marked)	Crockett	Barnhart 1												
	Crockett	Barnhart 2												
	Crockett	Barnhart 3												
	Schleicher	CR 408												
	Tom Green	Crooks Rd	1			1					1			1
	Tom Green	Debus Rd					1			1	1			1
		Total	**1**	**0**	**0**	**1**	**1**	**0**	**0**	**1**	**2**	**0**	**0**	**2**
Southwest (35 marked)	Kinney	Standard Ln												
	Maverick	Maverick1												
	Val Verde	Laughlin AFB					1			1	1			1
		Total	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**1**	**0**	**0**	**1**
Southeast (6 marked)	Jim Wells	CR 331	1			1					1			1
	Jim Wells	Orange Grove												
	Kleberg	Kingsville NAS												
	Nueces	CR 103												
	Nueces	CR 36												
	Nueces	CR 18												
	Nueces	CR 10, 75, 6												
		Total	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**
		Grand Total	**2**	**0**	**0**	**2**	**2**	**0**	**0**	**2**	**4**	**0**	**0**	**4**

Mark-recapture Data

We toe-clipped 88 total individual STEL across each survey unit: 47 in the North, 35 in the Southwest, and 6 in the Southeast. We recaptured a total of 4 of these individuals over the entire study (Table 2.5). Two of these recaptures occurred in 2016. One occurred in the North survey unit on Crooks Road in Tom Green County, and the other in the Southeast survey unit on County Road 331 in Jim Wells County. Two of these recaptures also occurred in 2017. One occurred again in the North survey unit but on Debus Road in Tom Green County, and the other occurred in the Southwest survey unit on Laughlin Air Force Base in Val Verde County. Thus, at least one recapture occurred in each of the survey units. In addition, all recaptures occurred on driving surveys.

We also analyzed 355 photos taken of STEL during surveys to quantify "recaptures" from the unique blotching patterns on each individual lizard. A total of 91 unique STEL individuals were identified from the photos taken, but none of those individuals were "recaptured" using the photographic method. Several photos were taken of each individual STEL whenever possible in order to capture the blotching pattern of lizards from several angles. Thus, the large discrepancy between number of photos and number of unique individuals stems from the large number of photos taken per individual lizard.

Discussion

Populations

The STEL was detected in all population survey units each year of surveys. In addition, gravid females or juveniles were observed in all population survey units each year of surveys. Recapture rates were very low across all population survey units each year regardless of survey method used, but new unmarked individuals were frequently encountered in areas where repeated surveys occurred. Although no encounter histories can be made from these mark-recapture data to estimate population parameters, we can still draw preliminary conclusions about STEL populations. We believe that STEL populations are robust in those areas repeatedly surveyed with many new individual observations over time and no recaptures. Across this species' broad range, these distribution survey data indicate that the populations in our survey units are large, but potentially separated by extensive regions of unoccupied habitat, especially in the southern subspecies (Figs. 4 and 5). The factors determining occupancy of habitat in this species are unknown, but may be related to the successional status of the habitat (see below).

Habitat

The STEL appears to be an early successional species that thrives on disturbance (Fig. 3). The species seems to prefer areas of bare ground created by disturbance within their habitat matrix. Such disturbances could occur naturally from wildlife grazing and fire, but currently it appears as though these disturbances are frequently created through farming, mowing, and ranching activities. Different sources of these disturbances occur in each of the population survey units, so habitat focused conservation and management efforts for this species should reflect these regional differences.

CHAPTER 3. SURVEYS FOR THE SPOT-TAILED EARLESS LIZARD (*HOLBROOKIA LACERATA*)

Final Report for UT Subaward UTA14-000790
Mike Duran, Vertebrate Zoologist
The Nature Conservancy

Introduction

In 2008-2010 Duran and Axtell (2010) visited 220 historical localities of the Spot-tailed Earless Lizard (STEL; *Holbrookia lacerata*) and recorded data that described the current ecological conditions of the sites. We performed brief surveys at each site, but because we had to visit several sites per day on most days, many sites were visited during conditions unsuitable for observing the STEL. To determine where populations of the STEL were extant, we mostly solicited public participation, and coordinated the efforts of volunteers and cooperators. We determined that the northern STEL (*H. l. lacerata*) was present in 11 Edwards Plateau counties but found no evidence that the southern STEL (*H. l. subcaudalis*) was extant below the Balcones Escarpment. Later, Duran (2013) discovered a healthy population of the southern STEL in Val Verde County. For the current project, we proposed, at a minimum, to survey in eight areas in southern Texas, in Ward County near the site of an unusual and disjunct record, and in Val Verde and/or Kinney counties where the subspecies may intergrade. In combination with another project, we were able to conduct many more surveys than those to which we had committed. All of those results are reported herein.

Methodology

Sites were selected near historical localities mostly based on soils, slope, land use (Duran and Axtell 2010), and on the predictive models of Ben Labay and Jon Paul Pierre. Preferred soils are mostly loam, clayey loam, loamy clay, and clay. Preferred slope is less than 3% or less than a 10 ft rise or drop over 1 km.

Duran and Axtell (2010) observed that roadsides near historical localities in southern Texas are overrun by non-native grasses, mostly Kleberg bluestem (*Dicanthium annulatum*) and buffelgrass (*Pennisetum ciliare*). Those observations prompted the hypothesis that the STEL might still be present near those localities but might only be observed away from roads, where non-native grasses did not create such a dense ground cover. Therefore, for this project we proposed to survey for STELs by walking transects in suitable habitat away from roads for at least 6 man-hours.

We thought we might have success with that methodology because of the success we had with visual encounter surveys (VES) during 2012-2014 at Laughlin Air Force Base (LAFB) in Val Verde County and at several sites on the Edwards Plateau. The 2012-2014 observations were generally on properties that had 30-80% bare ground exposed due to drought and livestock grazing.

Two phenomena caused that methodology to be less effective than we had hoped:

Precipitation—rainfall during late winter and early spring 2015 was far above average. No surveys could be performed while it was raining, but more importantly, abundant rain promoted plant growth which created dense groundcover and shrub layer vegetation that lowered the likelihood of observing STELs during walking surveys. For example, rainfall in Cotulla, Texas, near the center of the range of the southern STEL, for the five months, February-May, 2015, was 12.2 inches, while the average for the previous two years was 3.7 inches per year.

Access—gaining access to private land was more difficult than we anticipated. We believe landowners' reluctance to grant permission for surveys is largely engendered by the negative media attention that followed the publication of a 90-day finding by USFW that listing the STEL as federally threatened or endangered may be warranted. Several landowners who granted permission for surveys in 2009 (Duran and Axtell 2010) denied access in 2015. We were able to gain access to enough properties to fulfill our commitment to survey eight properties near historical localities in southern Texas, but in some cases we had to settle for sites where habitat was not ideal for the target species. In Ward County, the University of Texas (UT Lands) owns all of the land near historical localities and leases that land for oil exploration and production— despite numerous attempts, we were denied access to UT lands; that left road and roadside surveys as the only option in Ward County. We have not found a landowner that will allow surveys in the hypothetical area of intergradation of the subspecies (*H. l. lacerata and H. l. subcaudalis*) in east-central Val Verde and/or west-central Kinney counties. We gained access to three more sites in 2016—we were able to survey one time each in Dimmit, Jim Hogg, and McMullen counties.

In addition to the surveys, we sent letters to the owners of all parcels surrounding historical localities and to owners of other ownership parcels that appeared to include STEL habitat (for the majority of counties that have digital data available). The responses to the letters were less than expected. In response to the letters, we gained access from three owners and received photos from two letter recipients.

Results

During spring 2015 TNC staff and volunteers surveyed at 18 sites and road-routes in 14 counties. We observed the spot-tailed earless lizard (STEL) at six sites in six counties (Table 3.1).

In 2016, we surveyed 19 sites/road-routes in 18 counties, which included revisits to 10 sites/road- routes (Table 3.2). We observed the STEL at two sites/road routes (Nueces and Jim Wells counties) where they had been observed in 2015, but observed fewer lizards at both sites. We made a possible but unverifiable observation in Dimmit County near Catarina. Out of the nine sites that were new for 2016, only in Glasscock County were three lizards observed along a road-route, but we did not observe STEL at any of the other eight sites that were new for 2016, save a possible but unverifiable observation in central Mitchell County.

It was not a priority in 2016 to revisit sites that 2015 surveys revealed to have apparent healthy STEL populations, so we did not revisit sites in Val Verde, Maverick, and Kinney counties. In 2016, we were able to gain access to three new sites in South Texas, in Jim Hogg, Dimmit, and McMullen counties.

The 2016 survey in Jim Hogg County was at the exact site of a 1991 STEL historical record. We did not observe the STEL at that site. Buffelgrass had been planted some years before and now forms a dense groundcover at the site of the historical locality and all of the surrounding land.

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The site in Dimmit County was a mile or so to the east and on sandier soils than the historical record, and probably was not a site we would have chosen to survey if there had been other options. The dirt roads where the lizard had been collected in Dimmit County in the 1950s had been converted to caliche and gravel by the time we cruised them in 2009 and have now been paved. Oil field traffic is extremely heavy on these roads, probably greater than one vehicle per minute during peak hours. Due to the new road surface and to the intense vehicular traffic, the likelihood of observing the lizard on the road is now probably near zero.

The site in McMullen County, the Roberts-Miller Ranch, was the only property where we were granted permission to survey in that county. While it was within a few miles of historical localities, habitat at that site appeared to be only marginally suitable for the species—the proximity of rivers and streams appears to be an important component of STEL habitat, but the Roberts-Miller property lies on a very flat alluvial terrace between tributaries of the Frio River and there is no moving water on the ranch.

Reports for all sites are illustrated in Figures 3.1–3.34.

Significant Findings 2015-2016

The 2015 findings in Val Verde County (20+) include 16 observations that were made in 2013 that have not been reported except in a note on the relationship between the STEL and ground squirrels at LAFB (Duran 2014). All observations in Val Verde County were on LAFB. Prior to 2013, the STEL had not been reported south of the Balcones Escarpment for 17 years. In 2013, the 16 lizards were observed during a moderately severe drought; in 2015, during a period of much higher rainfall and denser groundcover, our cooperators observed fewer lizards.

In Kinney County at least 20 lizards were observed by various observers on roads in the central part of the county in 2015. In 2016, despite numerous surveys, no lizards were observed. TNC staff and volunteers observed four STEL on the LAFB Auxiliary Airfield at Spofford (LAFBAAS) in southern Kinney County. Other than a 1991 observation at LAFBAAS, the STEL had not been reported from Kinney County in 50 years.

In 2015, TNC staff observed four STELs on flooded private property and one on a public road in south-central Nueces County. Subsequently, our collaborators observed eight on roads in the southeastern part of the county, which included the dirt road near where the type specimen for *H. l. subcaudalis* had been collected. Prior to 2015, the lizard had not been reported from Nueces County in 32 years and had been presumed to be extirpated (Axtell 1998; Duran and Axtell 2010).

Far fewer lizards were observed per man-hour in 2016.

The 2015 observations in Jim Wells County were also on roads surrounded by plowed and flooded fields. TNC staff conducted a walking survey at La Copita Ranch, about 7 miles south of Alice without success. After the La Copita survey we cruised Jim Wells County roads. We observed four STELs on a county road east of Alice. The lizard had not been reported from Jim Wells County in 31 years. We visited that site several more times in 2015 and in 2016 and observed lizards each time.

In 2015 our collaborators observed four lizards in Maverick County. Those observations were the first in that county in 47 years.

Table 3.1. Sites surveyed and STEL found during Spring 2015.

Sites Surveyed	Date(s) Surveyed	Type of Survey	# STEL Observed*	Man Hours
Laughlin AFB (Val Verde County; Figure 2, 3)	March, April, May 2013	Road, VES	18	24
Falcon State Park and Starr County Roads (Figure 4)	3/3/2015	Road, VES	0	8
Star Cactus Ranch (Starr Co.; Figure 5)	3/18/2015	Road, VES	0	9
TNC Las Estrellas Preserve (Starr Co.; Figure 6)	3/19/2015	VES	0	8
Jim Wells County Roads (Figure 7, 8)	24 March, 03 April 2015	Road	5	10
La Copita Ranch (Jim Wells Co.; Figure 9)	3/24/2015	Road, VES	0	8
Hixon Ranch (LaSalle County; Figure 10)	3/25/2015	VES	0	9
Chaparral WMA (LaSalle Co.; Figure 11)	2, 19 April 2015	Road, VES	0	12
Ward County Roads (Figure 12)	4/16/2015	Road	0	10
Devil's Sinkhole SNR (Edwards Co.; Figure 13, 14)	5/1/2015	VES	4	30
S. Llano River State Park (Kimble Co.; Figure 15, 16)	15, 25 April 2015	VES	1*	18
Laughlin AFB at Spofford (Kinney Co.; Figure 17, 18)	6/3/2015	Road, VES	2	9
Head of the River Ranch (Tom Green Co.; Figure 19)	29-30 April	Road, VES	2	12
Wright Ranch (Nueces County; Figure 20, 21)	04–05 June 2015	Road, VES	5	9
Nueces County Roads (Figure 22)	6/24/2015	Road		
San Patricio County Roads (Figure 23)	10/28/2015	Road	0	6
Atascosa/Live Oak County Roads (Figure 24)	10/16/2015	Road	0	6
McMullen County Roads (Figure 25)	10/18/2015	Road	0	6

✳ Photo from Laura Jelemensky at S. Llano River State Park taken on 06 May 2014 (Figure 3.16).

Table 3.2. Surveys for STEL conducted in 2016*

Sites Surveyed	Date(s) Surveyed	Type of survey	# STEL Observed*	Man Hours
Star Cactus Ranch (Starr Co.; Figure 5)	3/15/16	VES, Road	0	6
TNC Las Estrellas Preserve (Starr Co.; Figure 6)	3/16/16, 3/23/2016	VES, Road	0	12
Hixon Ranch (La Salle Co.; Figure 10)	04/27/16	VES, Road	0	6
La Copita Ranch (Jim Wells Co.; Figure 9)	5/5/16	VES, Road	0	6
Jim Wells County Roads (Jim Wells Co.; Figures 7, 8)	5/5/16, 6/22/16	Road	3	6
Ward County Roads (Ward Co.; Figure 12)	6/11/16	Road	0	6
Nueces County Roads (Figure 22)	6/22/16	Road	1	4
Wright Ranch (Nueces Co. Figures 20, 21)	6/23/16	VES, Road	1	3
Devil's Sinkhole SNA (Edwards Co.; Figures 13, 14)	6/28-29/16	VES, Road	1	12
McMullen County Roads (McMullen Co. Figure 25)	3/23/16	Road	0	3
NEW sites added in 2016				
Roberts/Miller Ranch (McMullen Co.) (Figure 26)	04/06, 06/26/16	VES, Road	0	12
Las Estrellas Ranch and Jim Hogg/Starr Co Roads (Figure 27)	3/14/16	VES, Road	0	6
La Salle County Roads (La Salle Co.; Figure 28)	04/26-27/16	Road	0	6
Dimmit/ Webb Co. Roads/Catarina (Figure 29)	4/28/16, 5/12/16	Roads	1?	8
Maverick/Webb Co Roads (Eagle Pass to Laredo Rd; Figure 30)	4/29/16	Roads	0	10
Shape Ranch and W. Dimmit Co Roads (Dimmit Co.; Figure 31)	05/10/16	VES, Road	0	12
Howard and Mitchell County Roads (Figure 32)	6/8-9/16	Road	1?	14
Corners of Upton/Glasscock/Reagan/Midland Cos (Figure 33)	6/9-10/16	Road	3	8
S. Central Live Oak County Roads (Figure 34)	06/23/16	Road	0	18

Discussion

Axtell (1958, 1998) observed boom and bust cycles in STEL populations. The year 2015 was apparently a boom year across most of the range. We believe that the boom can be largely explained by the extraordinary rainfall that resulted in dense ground-layer vegetation. Ironically, the same factors that contributed to the boom also made it nearly impossible to observe lizards away from roads.

Standing water in fields and pastures in rural areas of Nueces and Jim Wells counties may have contributed to the abundance of 2015 observations. The flooded fields may have forced lizards onto roads in search of the component(s) of their ecological requirements that they obtain by periodically occupying bare ground. In 2016, fields in survey areas were not flooded, and fewer or no observations were made at those previously flooded sites.

The 2015 rediscoveries in Nueces and Jim Wells were particularly significant because most of them occurred on roads surrounded by row crops. Duran and Axtell (2010) hypothesized that row- cropping was a major threat to the STEL based on the absence of records from farmland after 1971. The results of surveys under this grant and another grant appear to indicate that row-cropping is not the threat as we had presumed. We still believe further analysis may provide evidence that the STEL may be threatened by certain agricultural practices, such as the application of pesticides, and that historical populations may have been greatly reduced, fragmented, and locally extirpated by conversion of grasslands to row crops. Of the other presumed threats, there are considerable data indicating that urbanization is a severe threat, but evidence is lacking for most other presumed threats.

There are several examples that seem to support the hypothesis that STEL populations, like many other animal populations, experience boom/bust population densities. In Kinney County, the site of 20+ observations in 2015 produced no observations in 2016 as far as I know. Far fewer STEL were observed per man-hour in Nueces, and Jim Wells counties and on the Edwards Plateau, in Tom Green, Edwards, and other Edwards Plateau counties in 2016 than in 2015. The increase in observations in the past few years indicates that the lizard is not common, but somewhat more common than most experts had presumed. In general, we have seen that increased observations are roughly correlated with increased observation hours and that the lack of observations over the last 50 or so years is partly due to lack of looking.

It was not an objective of the project under the subcontract to The Nature Conservancy to analyze or characterized STEL habitat, but we have done so in previous projects and there are a few attributes that most experts can agree on: STEL habitat is flat with loamy soil, and it's fairly open with some bare ground. We don't know enough about STEL ecology to say with any degree of certainty what natural history or life cycle function each of these habitat components play. The fact that the STEL seeks bare ground if available appears to mimic some characteristics of an early successional species, but I don't think it is terribly accurate or helpful to label it as such. "Early successional species" implies or connotes that the STEL can migrate some distance to find an early successional landscape. No one can say for sure, but based on the home range sizes of similar species, the STEL probably has a home range size smaller than a circle with a diameter of 50 meters. The STEL seeks out bare ground *if available*, but there are undoubtedly periods of years when bare ground is mostly unavailable. The historical coastal prairie in San Patricio and Nueces County provides an example of a landscape, where the species has persisted for thousands of years, that might for years be covered in tall, lush grasslands with little bare ground for hundreds of square miles. The species didn't travel overland to find an early successional landscape, it persisted.

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Duran, C. M. and R. W. Axtell. 2010. A rangewide inventory and habitat model for the spot-tailed earless lizard (*Holbrookia lacerata*). Report to Texas Parks and Wildlife, 37 pp.

Duran, C. M. 2014. *Holbrookia lacerata subcaudalis* (Southern Spot-tailed Earless Lizard). Refugia and Commensalism. Herpetological Review 45 (3): 501-502.

Figure 3.1. Known Recent Distribution of the Spot-tailed Earless Lizard — August 31, 2016**.**

Distribution of the Spot-tailed Earless Lizard *(Holbrookia lacerata)*

- • Spot-tailed Earless Lizard Localities 1878-2012 (227)
- • Spot-tailed Earless Lizard Localities 2013-2016 (197)
- — Balcones Escarpment (rough)
- Counties with spot-tailed earless lizard records since 2001
- Both Northern and Southern Occur in different parts of these counties
- Northern Spot-tailed Earless Lizard
- Southern Spot-tailed Earless Lizard

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Figure 3.2. Spot-tailed Earless Lizard Survey Rt. at Laughlin AFB, Del Rio, Texas (2013).
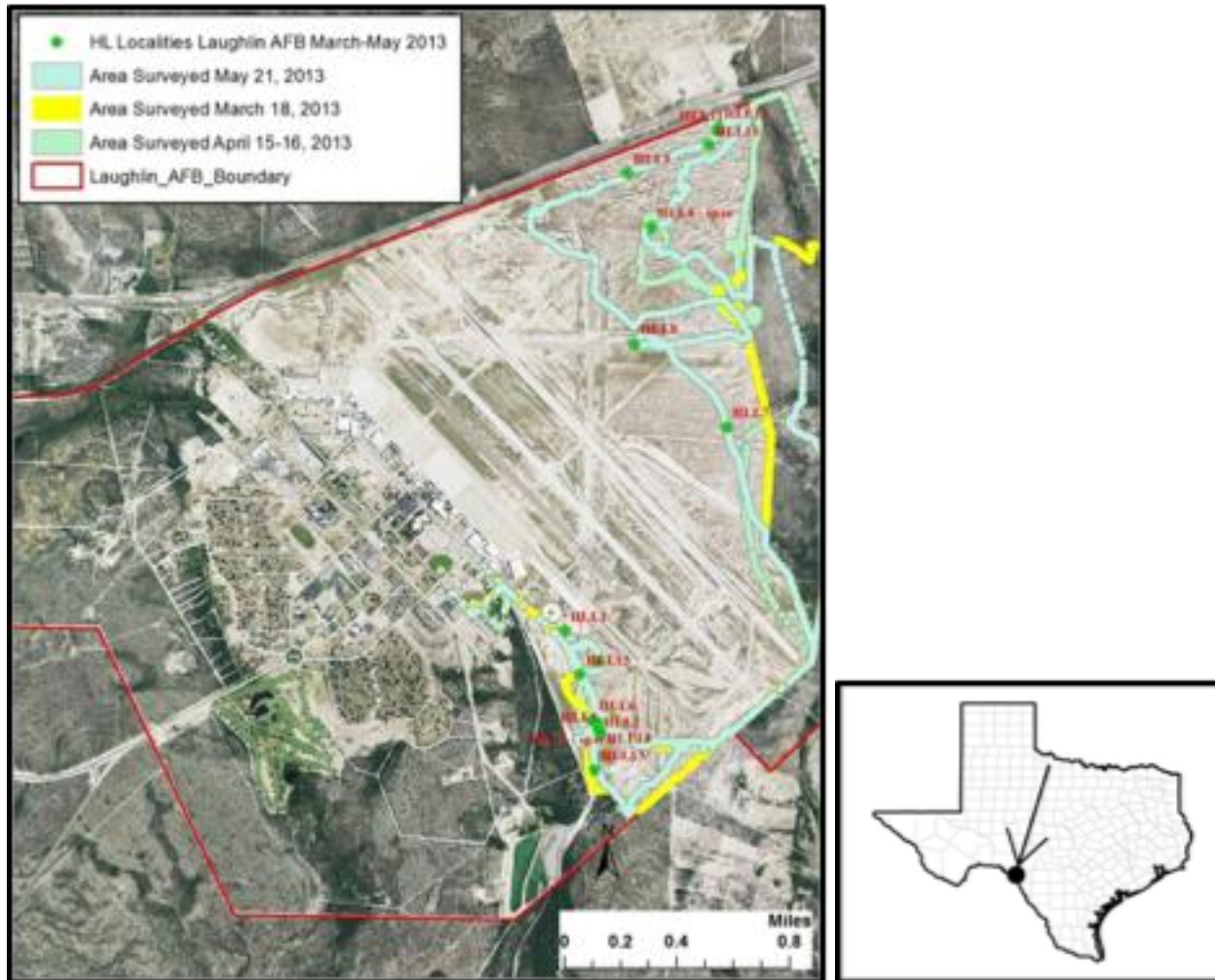
Figure 3.3. Spot-tailed Earless Lizard Survey route. at Laughlin AFB, Del Rio, Texas (2013)**.**
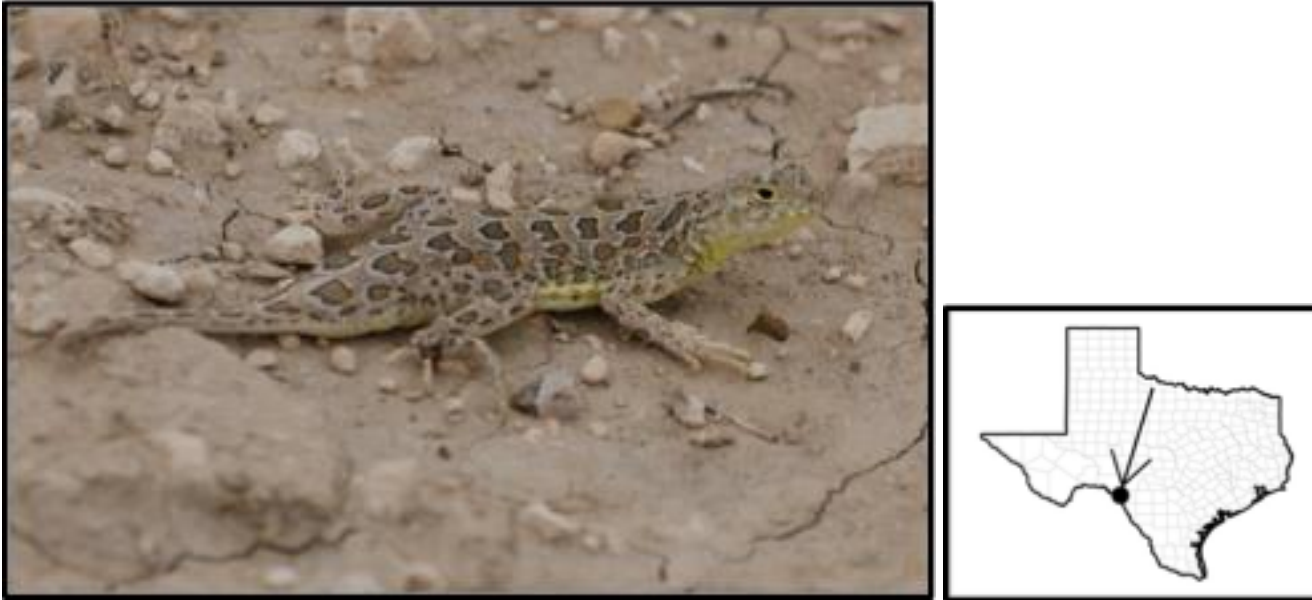
Figure 3.4. Falcon State Park and vicinity Spot-tailed Earless Lizard Survey Map — 03 March 2015.
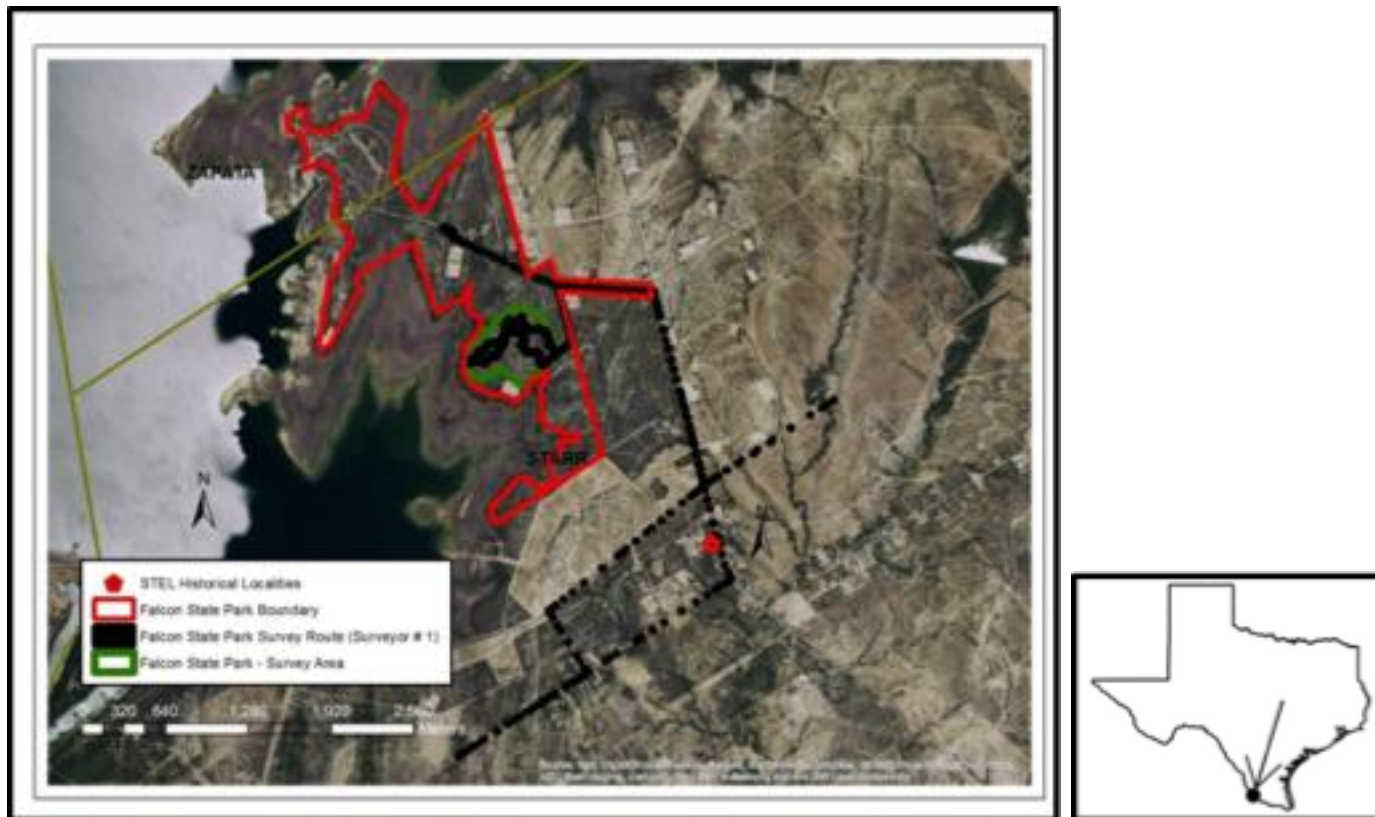
Figure 3.5. Star Cactus Ranch Spot-tailed Earless Lizard survey map, 18 March 2015 and 15 March 2016.

Figure 3.6. TNC Las Estrellas Preserve STEL survey map, 19 March 2015 and 14 March 2016.
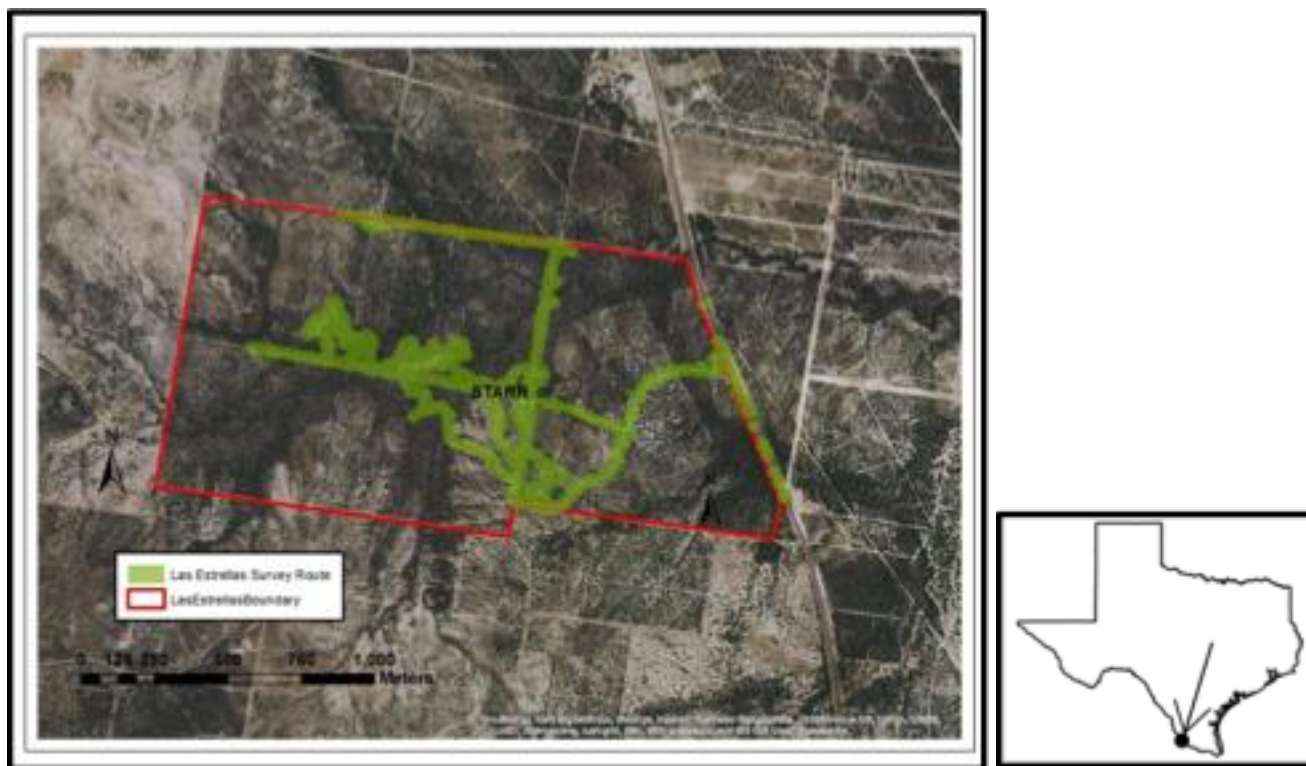
Figure 3.7. Jim Wells County Road Surveys – 03 March, 03 April 2015; 05 May and 22 June 2016.
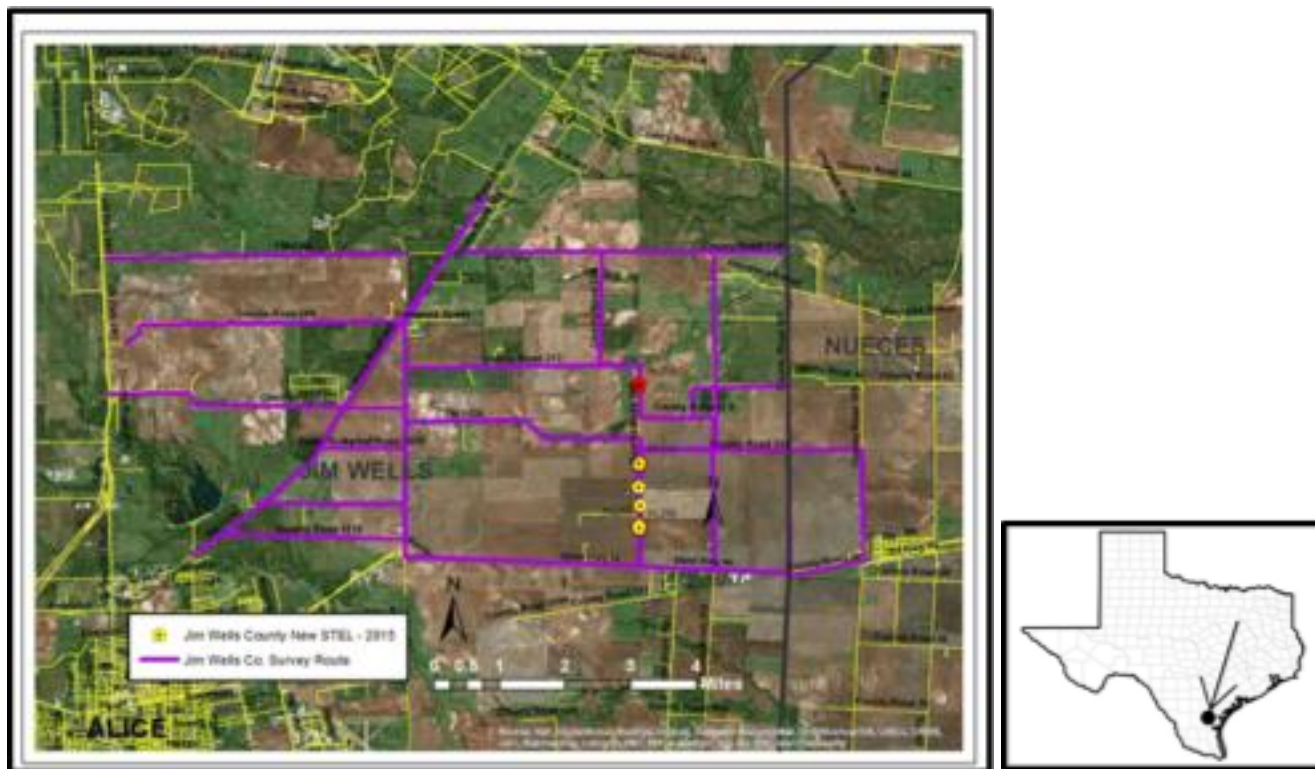
Figure 3.8. A Spot-tailed Earless Lizard found in NW Jim Wells County — 24 March 2015.
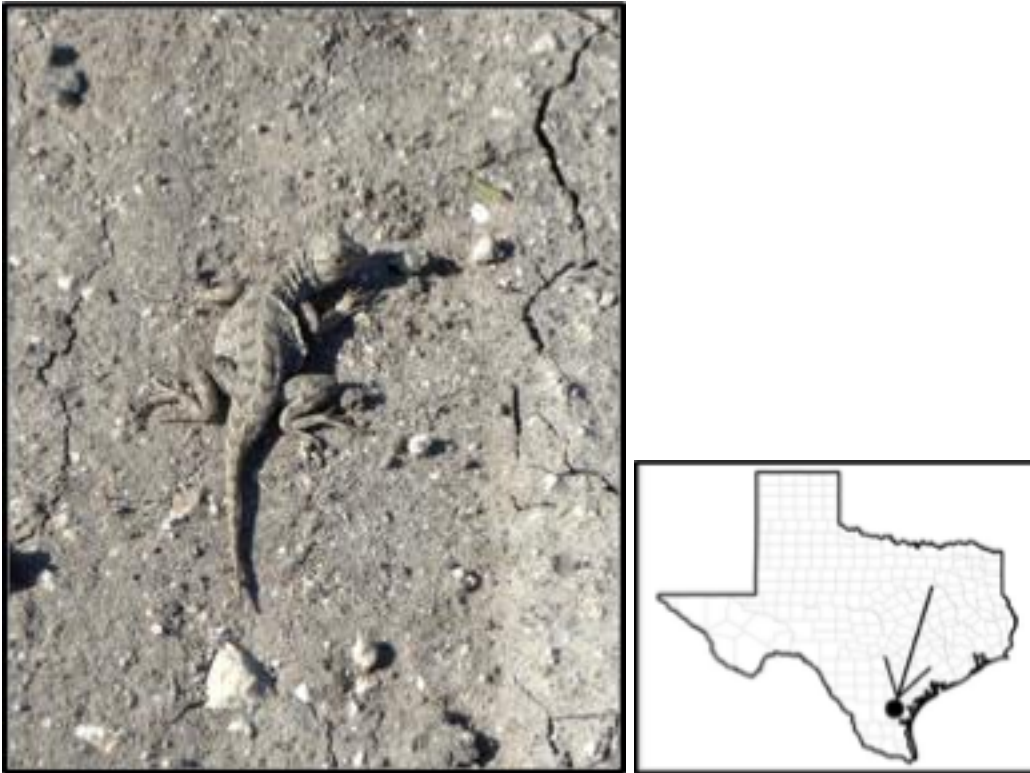
Figure 3.9. La Copita Ranch Survey Map — 24 March 2015 and 05 May 2016.
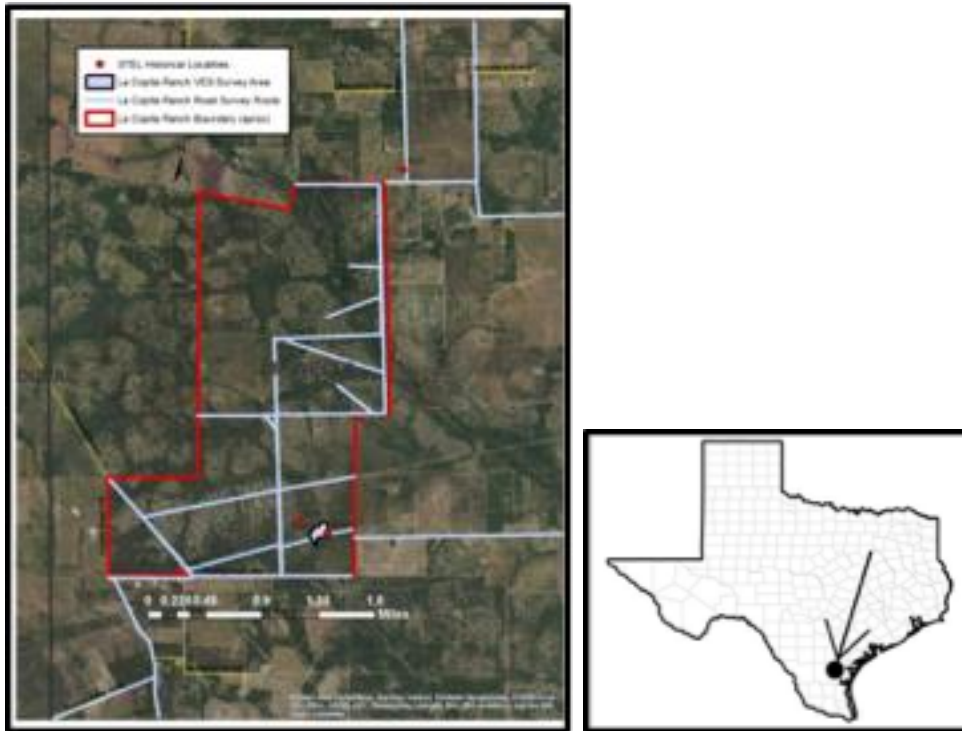
Figure 3.10. Hixon Ranch Survey Map — 25 March 2015.
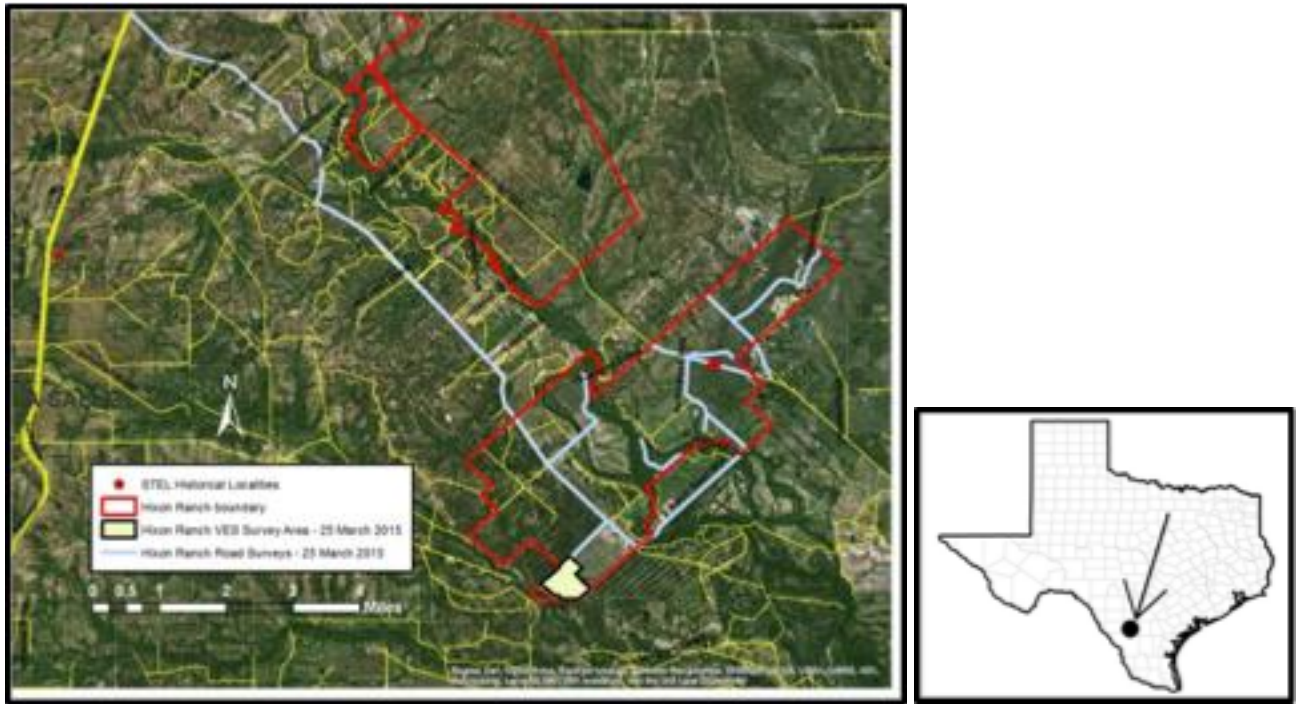
Figure 3.11. Chaparral WMA Survey Map — 02 April and 01 May 2015.
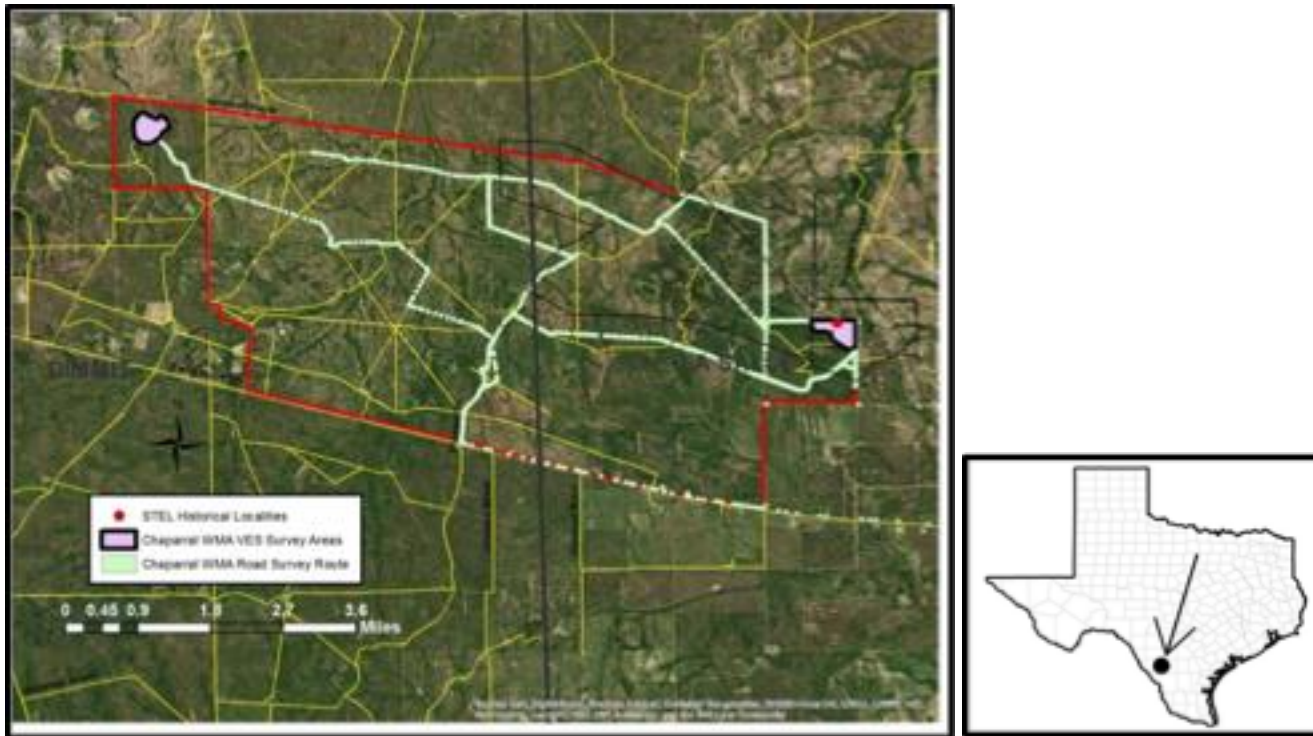
Figure 3.12. Ward County Road Survey Map — 16 April 2015 and 11 June 2016.
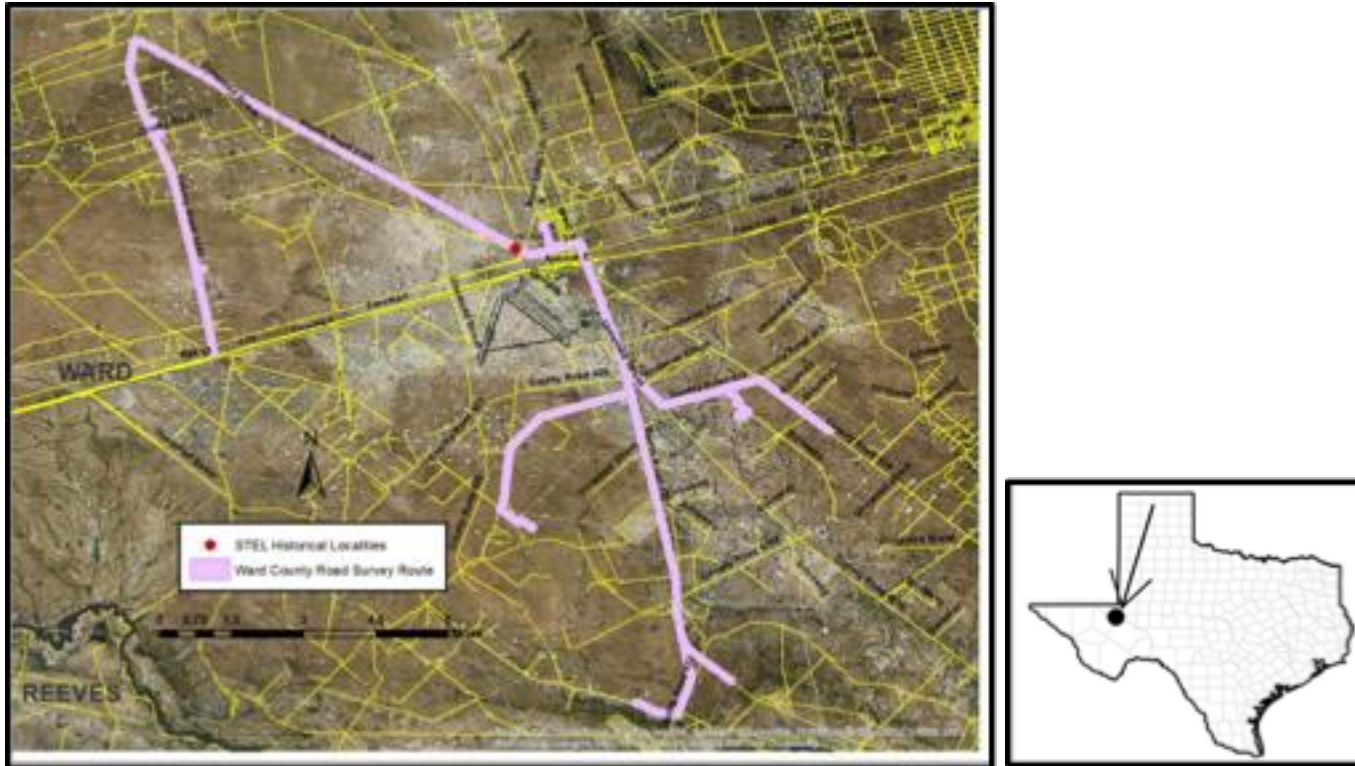
Figure 3.13. Devil's Sinkhole Survey Map—01 May 2015, 28-29 June 2016.
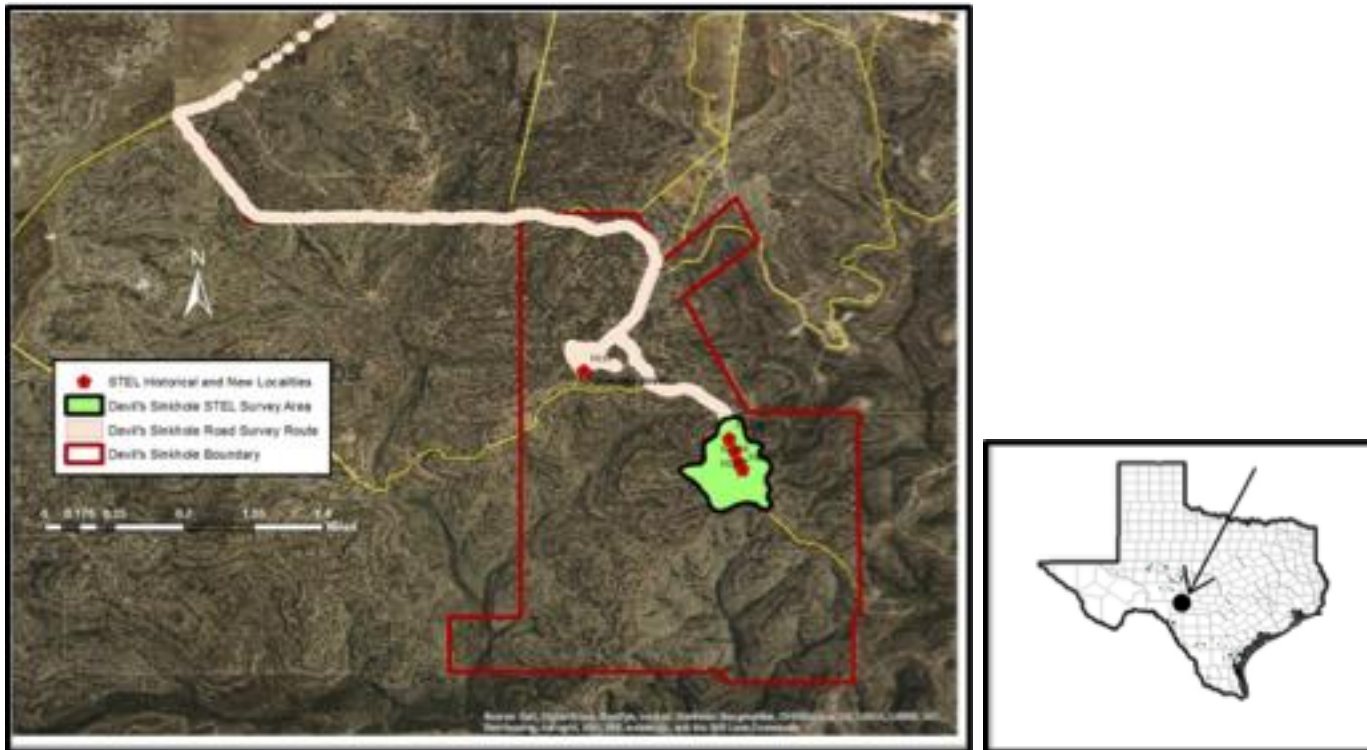
Figure 3.14. A Spot-tailed Earless Lizard observed at Devil's Sinkhole SNA – 01 May 2015.

Figure 3.15. South Llano River State Park Survey Map – 15 and 25 April 2015.
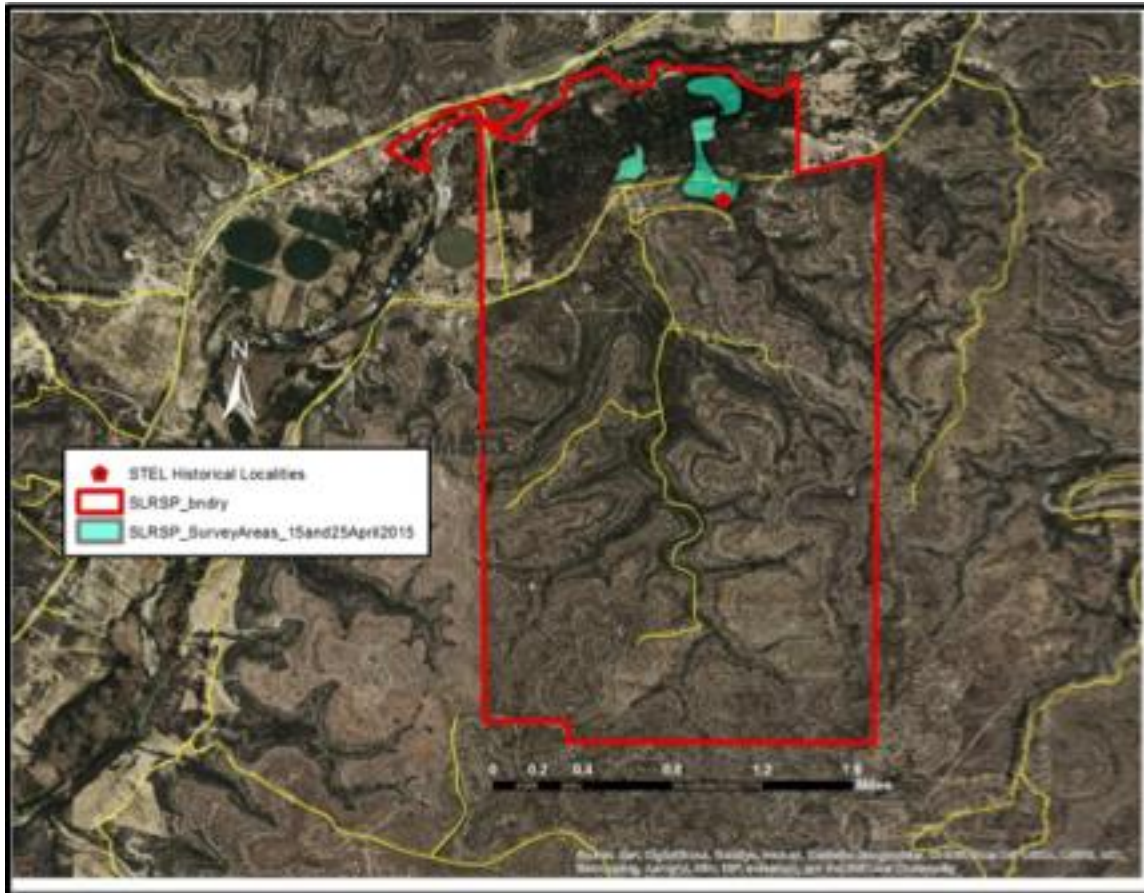
Figure 3.16. Spot-tailed Earless Lizard at South Llano River SP – 06 May 2014 (Laura Jelemensky).

Figure 3.17. Laughlin AFB Auxiliary Airfield at Spofford STEL Survey Map 03 June 2015.
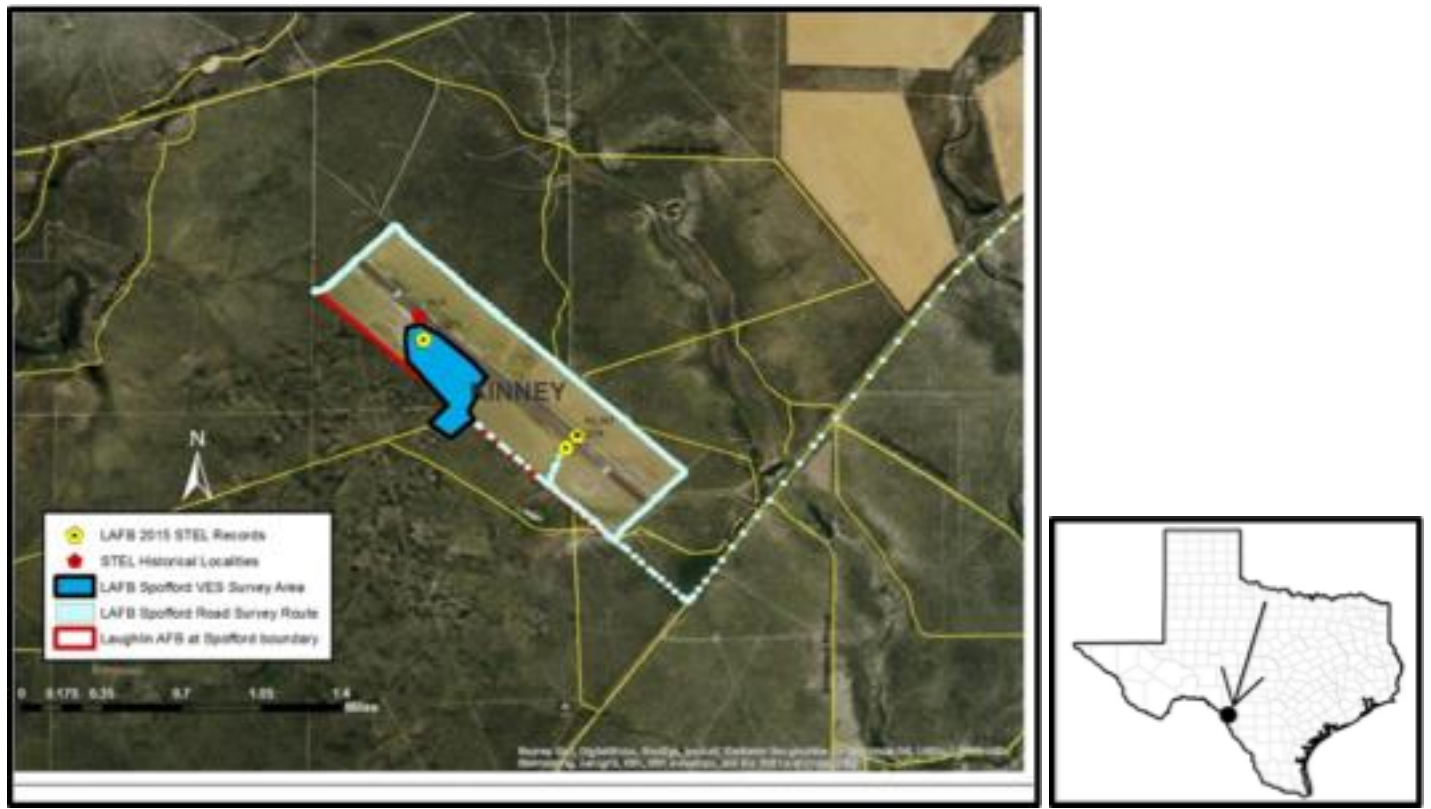
Figure 3.18. A Spot-tailed Earless Lizard at Laughlin AFB Airfield, Spofford, 03 June 2015.
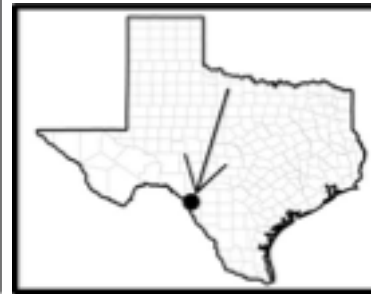
Figure 3.19. Head of the River Ranch Spot-tailed Earless Lizard Survey Map – 29-30 April 2015.

Figure 3.20. Wright Ranch, Nueces Co. Spot-tailed Earless Lizard survey map 4-5 June 2015 and 23 June 2016.

Figure 3.21. Spot-tailed Earless Lizards found on Wright Ranch, Nueces Co. – 05 June 2015.
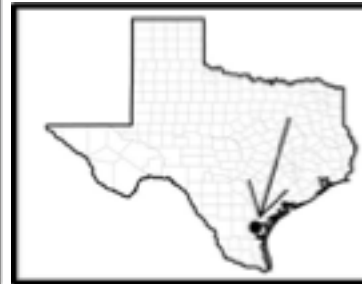
Figure 3.22. Nueces County Road Spot-tailed Earless Lizard Survey Map – 09 April and 03 June 2015.
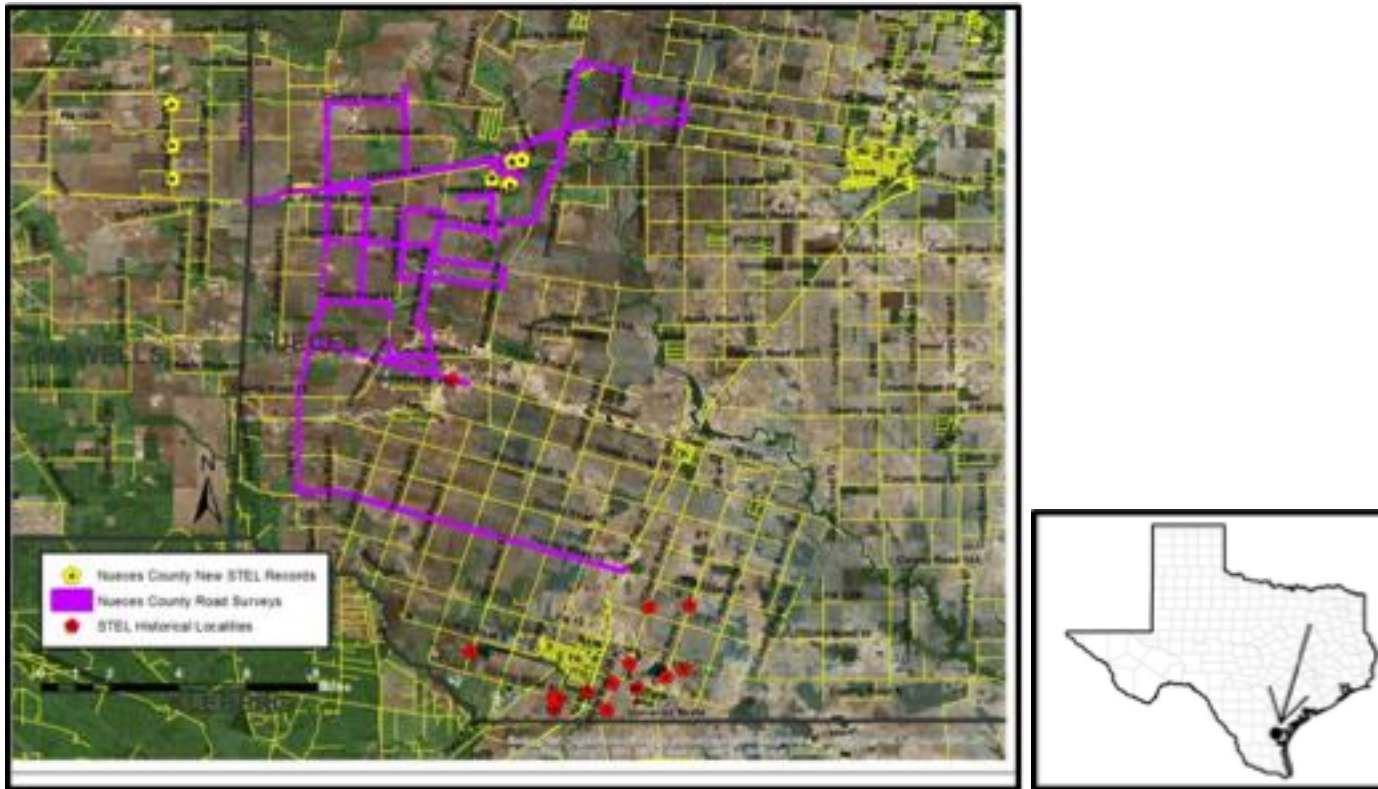
Figure 3.23. San Patricio County Spot-tailed Earless Lizard Road Survey Map 28 October 2015.

Figure 3.24. Atascosa, Bee, Karnes, Live Oak, Spot-tailed Earless Lizard Road Survey Map 16 October 2015.
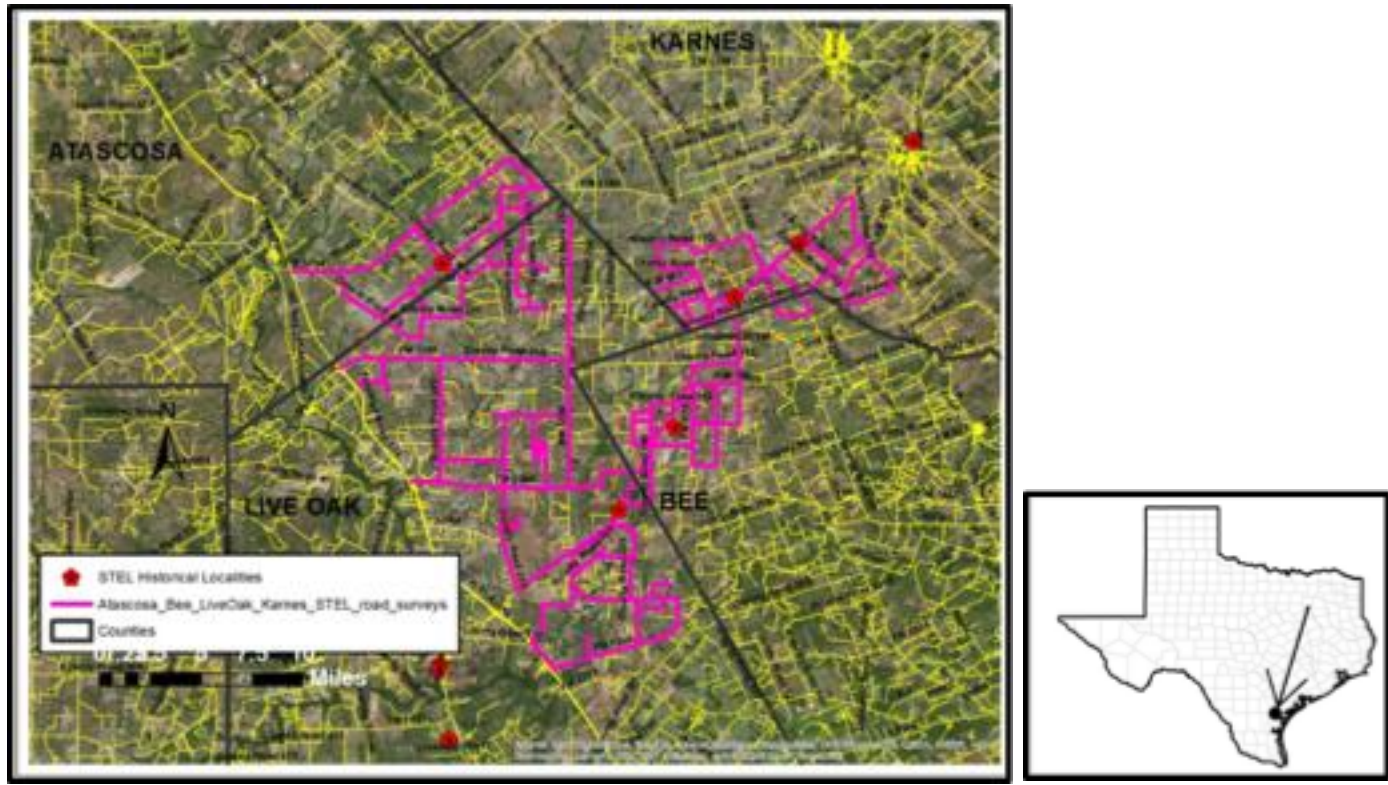
Figure 3.25. McMullen County Spot-tailed Earless Lizard road survey map - 18 October 2015, 23 March 2016.
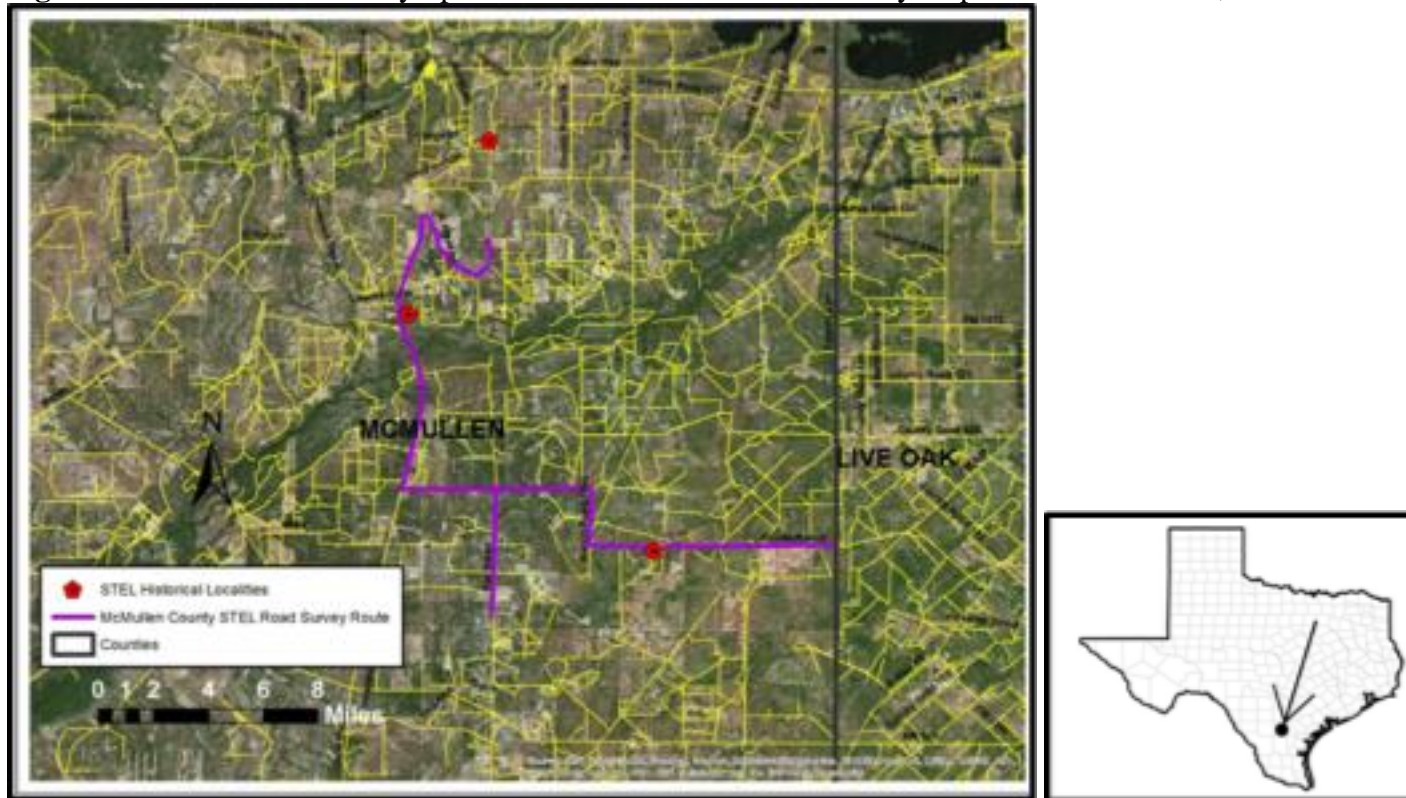
Sites Added for 2016 Only

Figure 3.26. Roberts-Miller Ranch (Dimmit Co.) 28 April and 26 June 2016.
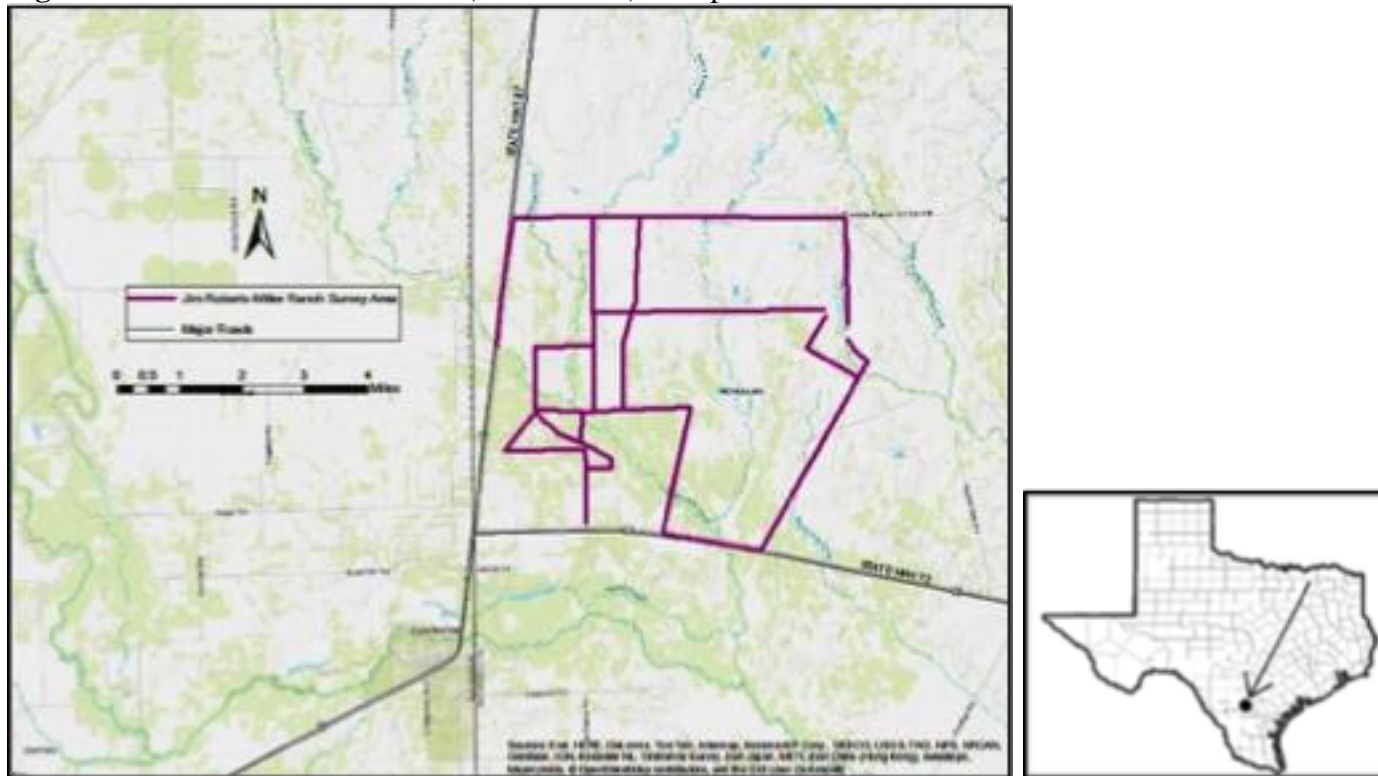
Figure 3.27. Las Estrellas Ranch Area and Jim Hogg/Starr County Roads – 13, 14, 22 March 2016.

Figure 3.28. La Salle County Roads. 26, 27 April 2015.

Figure 3.29. Dimmit and extreme NE Webb county roads, Catarina 28 April and 12 May 2016.
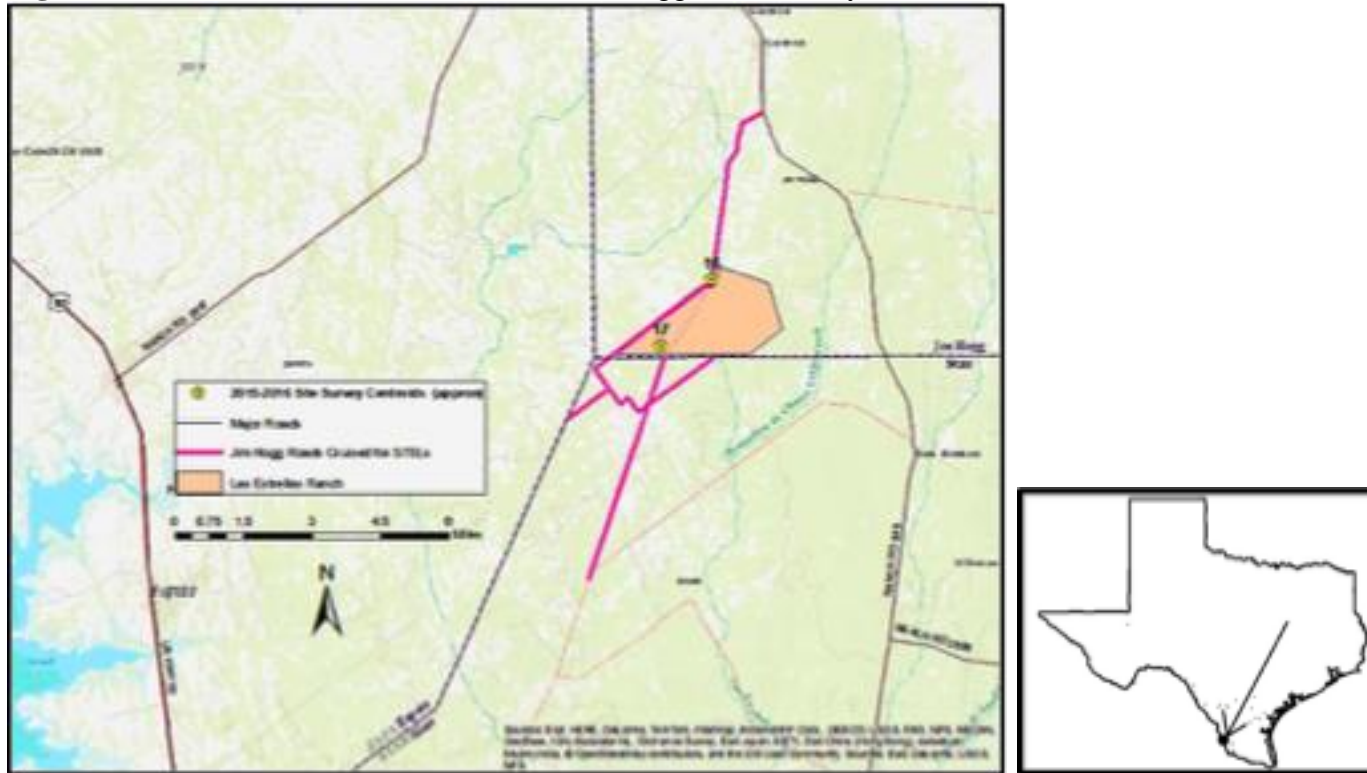
Figure 3.30. Maverick/Webb Co Roads (Eagle Pass to Laredo Road).
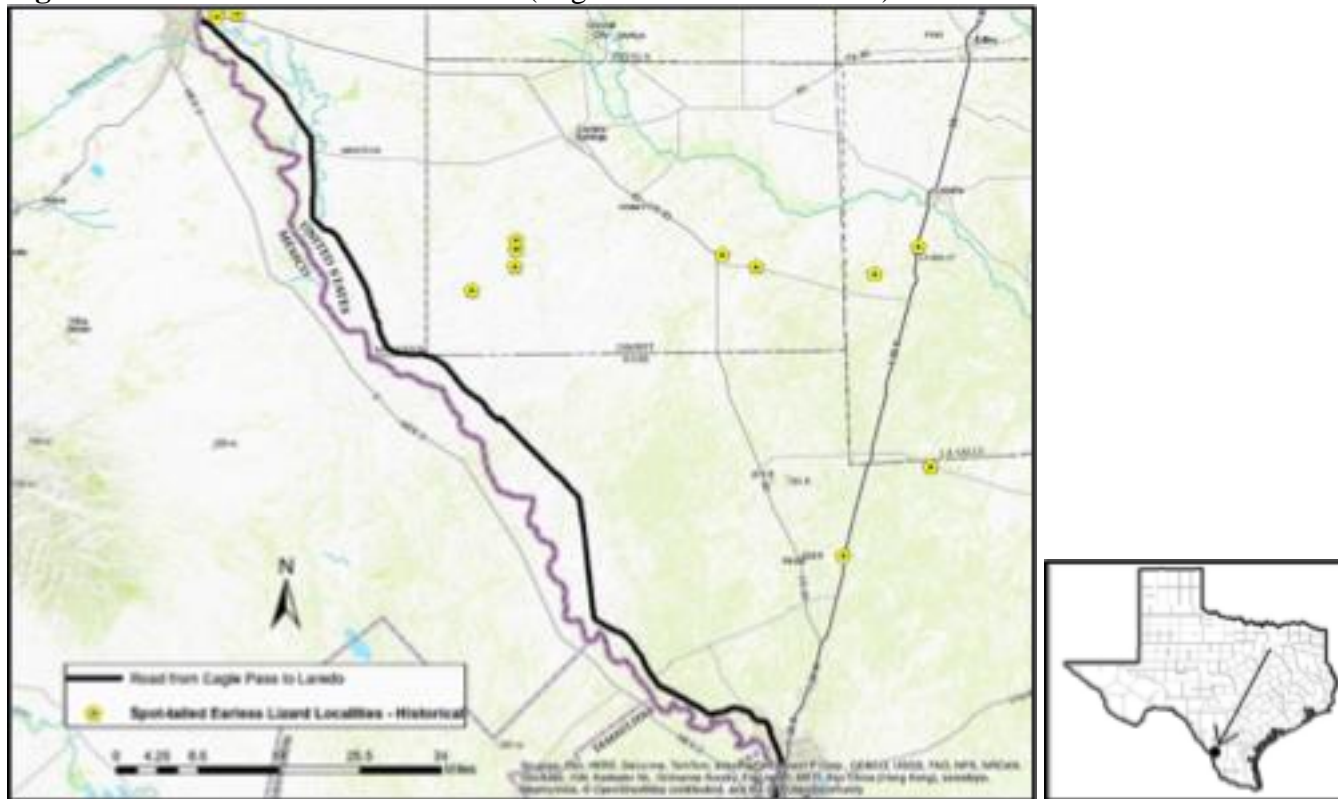
Figure 3.31. Shape Ranch and W. Dimmit Co. Roads 10 May 2016.
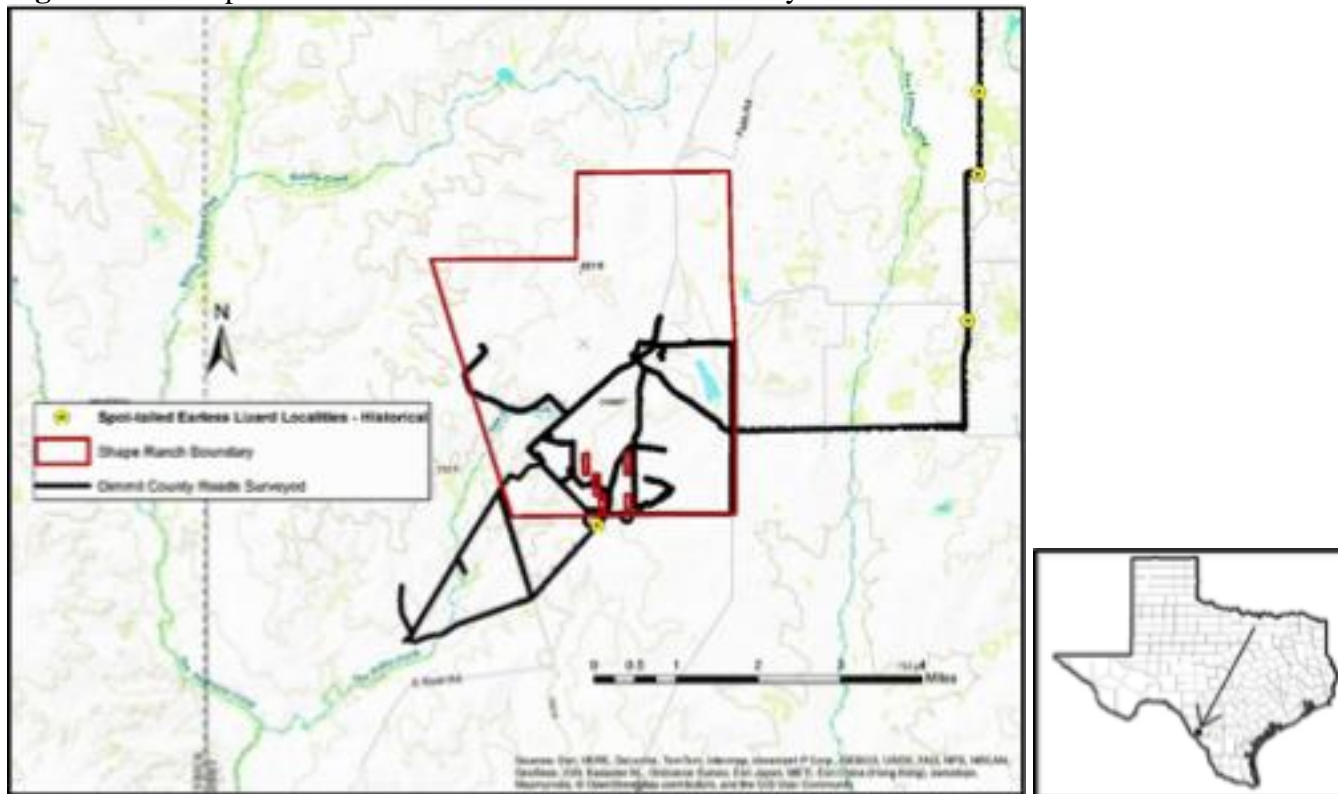
Figure 3.32. Howard and Mitchell county roads 8, 9 June 2016.
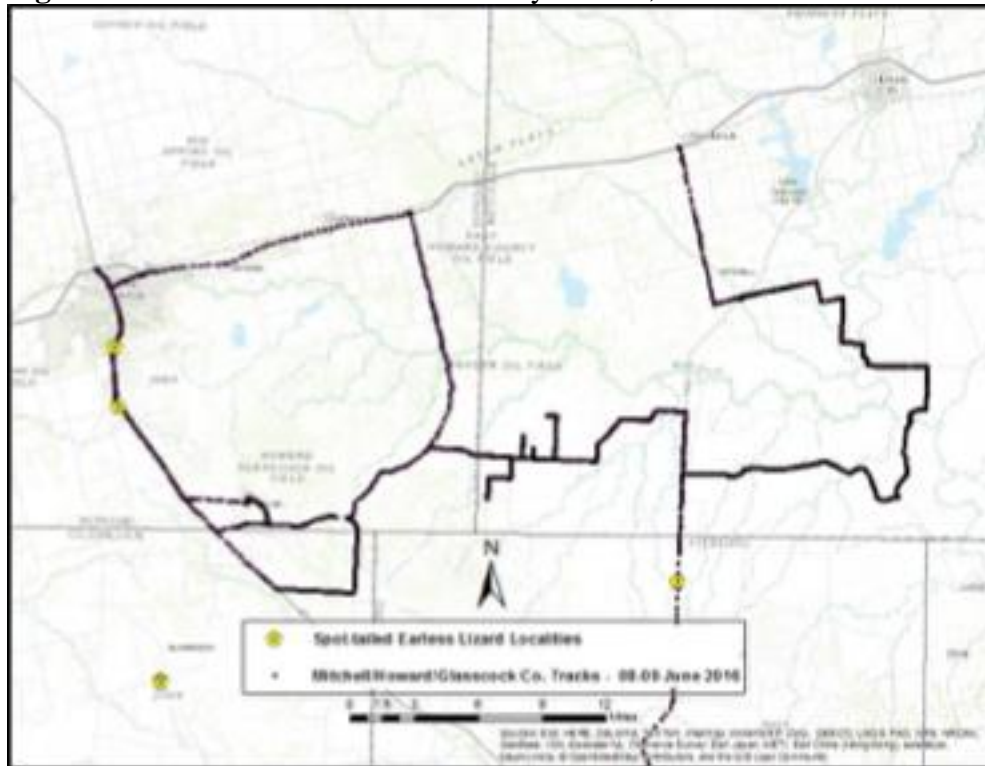
Figure 3.33. Corners of Midland/Upton/Reagan/Glasscock county roads 9, 10 June 2016.

Figure 3.34. South-central Live Oak Co. roads 23 June 2016.
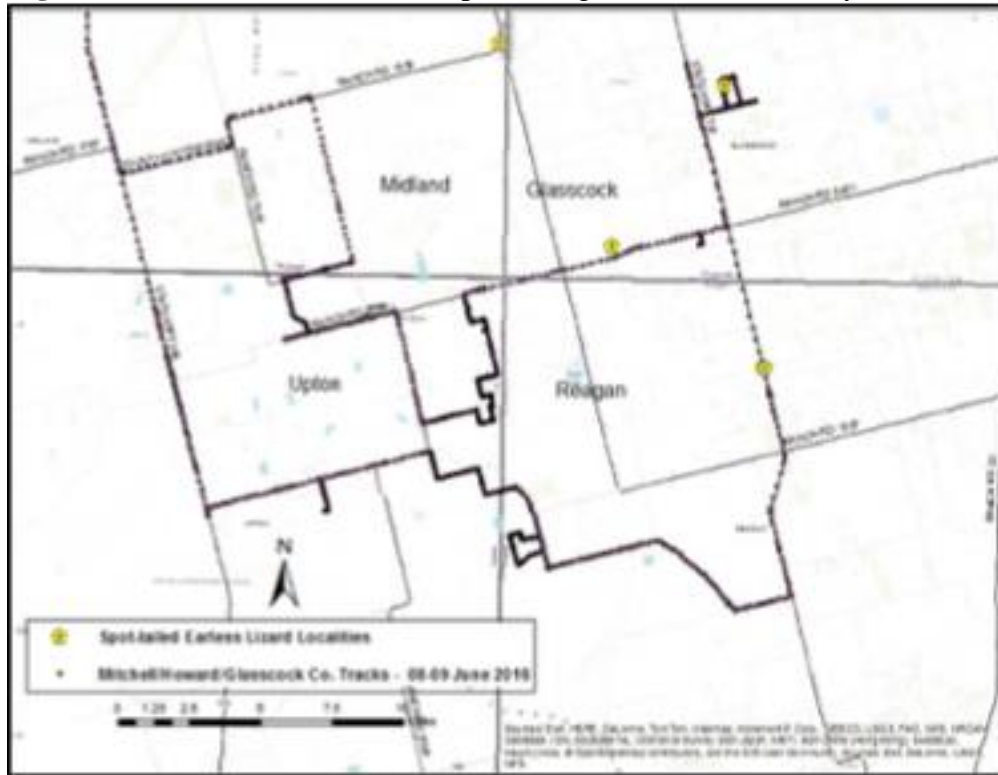
CHAPTER 4. THE DIET OF THE SPOT-TAILED EARLESS LIZARD (*HOLBROOKIA LACERATA*) AND FIELD AVAILABILITY OF INSECTS AS PREY ITEMS

Ian M. Wright and Travis J. LaDuc

Diet can be an important indicator of population health and competition in lizards (Suarez and Case 2002). The type and quality of prey a lizard eats can have a significant impact on its growth rate and, potentially, on population-level reproduction and persistence rates as well (Suarez and Case 2002). Consequently, the description of diet breadth and preference can have important implications for management of species in decline. Optimal prey selection depends in part on prey availability in the surrounding habitat, with higher quality habitats typically holding more diverse and abundant prey (Bolger et al. 2000, Flanders et al. 2006). *Holbrookia lacerata* (the Spot-tailed Earless Lizard) is a species of conservation concern (TPWD 2012) and may be in decline throughout its distribution in Texas. Little is currently known about the natural history of this species, including significant data gaps in diet and feeding ecology (Hibbitts and Hibbitts 2015).

Holbrookia lacerata was named as a priority species in the Texas Wildlife Action Plan (TPWD 2012), and on May 24, 2011, the U.S. Fish and Wildlife Service (USFWS) issued a 90-day finding that states listing the species as threatened or endangered may be warranted. The timeline for a listing decision by USFWS is FY 2020 (USFWS 2016). At the inception of the initial contract in 2014, the understanding of distribution and status of *Holbrookia lacerata* was based on 2009–2010 studies that surveyed museum collections and literature, interviewed collectors, conducted seminars, solicited volunteer support, and methodically surveyed sites where the species has occurred historically (Duran and Axtell 2010; Duran et al. 2011). *Holbrookia lacerata* were observed and vouchered by specimens and/or photos in the general vicinity of historical localities in 12 counties. The species was located in two more counties near historical localities subsequent to the 2009–2010 work.

Holbrookia lacerata consists of two subspecies, *Holbrookia lacerata lacerata* (the Northern Spot-tailed Earless Lizard), which occurs mainly on the Edwards Plateau, and *Holbrookia lacerata subcaudalis* (the Southern Spot-tailed Earless Lizard), which occurs below the Balcones Escarpment, mainly in the South Texas Plains. The species formerly occurred in the Gulf Coastal Prairies, and appeared to be extirpated from many counties in the southeastern part of the range, as well as from the urbanized counties of Bexar, Comal, Hayes, and Travis (Axtell 1968, 1998; Duran and Axtell 2010). The taxonomy of this species is stable (Axtell 1956, 1958, 1998) but little work had been done on the genetic diversity within the species before this contract had started (Schulte and de Queiroz 1998), likely due to the paucity of recent specimens and tissues. Basic natural history information on aspects, such as reproduction and diet, is limited (Axtell 1956, 1958, 1968), though recently, limited numbers of *Holbrookia lacerata* have been brought into captivity and maintained with limited success at the Fort Worth Zoo (Diane Barber, personal communication).

At the initiation of this project in 2014, virtually nothing was known about the diet or natural history of *Holbrookia lacerata* save a brief mention by Axtell (1954).

Dietary records were restricted to brief notes in the unpublished thesis of Axtell (1954): p. 42, *Holbrookia lacerata lacerata*: "Food consists of small flying or hopping insects. Moths were taken in captivity. Movement of the prey is essential for the procurement of food." and p. 49, *Holbrookia lacerata subcaudalis*: "Probably less is known about the food habits of this subspecies than of any other subspecies of *Holbrookia*. Only a few stomachs have been examined, and these contained fragments of grasshoppers, spiders, wasps, and lepidopteraus [sic]. This subspecies apparently prefers small soft-bodied insects." This data gap was noted by the STEL Working Group during a meeting of that committee and, at their urging, one task was added to each of two subsequent contract amendments to address this data gap.

The first diet task was to provide a comprehensive description of stomach contents from preserved museum specimens of *Holbrookia lacerata* and a comparison of lizard diet to recent published literature surveys for arthropod communities in south Texas. To determine the diet of *Holbrookia lacerata*, museum specimens were borrowed and stomach contents identified. Diet studies utilizing museum voucher specimens are a common avenue of research for reptiles, particularly snakes (e.g., Rodriguez-Robles and Greene 1999; Rodriguez-Robles 2002), however, to our knowledge no diet study had ever been conducted on museum specimens for any species of *Holbrookia*. Additionally, neither historic nor recent multi-taxa arthropod surveys could be found from areas with current or former populations of *Holbrookia*. Thus, we can make few inferences regarding prey availability. Our multi-taxa study of potential prey arthropods serves as a crucial baseline in any future comparative work identifying the microhabitat utilization of *Holbrookia lacerata*.

The second diet task was to describe prey arthropod availability from a portion of the range of *Holbrookia lacerata*. In order to further understand how this lizard species utilizes its habitat, we initiated a field arthropod survey in the hopes of assessing prey availability on the ground. We adapted common methods for sampling insect diversity to target those arthropods that lizards could feasibly consume and to focus our effort on the taxa most commonly encountered in lizard gut contents.

Results of this first diet study would provide important natural history data for a species for which little is known. Identifying arthropod prey species and interpreting those arthropod phenologies and specific microhabitats could help provide greater detail in understanding habitat specificity and phenology for *Holbrookia lacerata*. In turn, this information can be used to develop better models to describe and predict lizard distributions. By comparing the diet of *Holbrookia lacerata* from the 1950s and 1960s with those of current arthropod communities, we could provide another clue towards understanding why this species is no longer extant at so many historical localities or, conversely, why *Holbrookia lacerata* continues to persist at other localities.

Results of the second diet study will serve as a baseline of habitat quality in the future and give us some insight into the selectivity these lizards employ in the foraging of the landscape they are likely to face. These data can be used in conjunction with previously funded work on the diet of *Holbrookia lacerata* to assess variability around diet preferences and to establish metrics for use in habitat quality assessment and rates of survival, persistence, and reproductive quality. Thus, understanding the diet preferences of this species would help us better gauge its use of habitat and habitat quality. These data will also help us interpret individual survival rates and population-level persistence

rates.

Diet study using museum voucher specimens of *Holbrookia lacerata*

Materials and Methods:

Lizard specimens were obtained through loans from the Biodiversity Research and Teaching Collections at Texas A&M University, the University of Kansas, and the Natural History Museum of Los Angeles County, in addition to specimens available from the Biodiversity Collections at The University of Texas at Austin. This yielded a total of 145 lizards with collection localities across one state in Mexico and 25 counties in west and south Texas from 1905 to 2009. Specimens were collected by various methods but all were preserved in 10% formalin and stored in 70% ethanol. Seventy-six of these specimens came from the northern population (*Holbrookia lacerata lacerata)*, 71 of which were dissected; 35 specimens came from the southern population (*Holbrookia lacerata subcaudalis*), 25 of which were dissected. An additional 33 specimens lacking specific locality data also were dissected.

Lizards were identified as male, female, or juvenile (of either sex) based in part on the presence of eggs or testes as well as by examining the post-anal scales. Some juveniles were intermediate in morphology and could not accurately be assigned male or female. Based on animals that could be identified male or female, a size cutoff of 37 mm snout-vent length (SVL) was used as the upper boundary for juveniles.

Snout-vent lengths and gape widths (defined as the widest point across the mouth opening) were measured to the nearest hundredth of a millimeter with digital vernier calipers prior to dissection. The stomach contents of 129 of these individuals were removed and stored in ethanol for later counting and identification by one author (IMW).

Arthropod prey items were sorted under a dissecting scope, identified to order and family, and counted. Length, width, and height measurements were taken using a piece of 1 mm-gridded graph paper placed under a petri dish and examined through the dissecting microscope. These measures were used later to calculate prey volumes using the formula for a prolate spheroid (Vitt and Morato de Carvalho 1992).

We used total abundance and volume scores to calculate relative abundance (percentage of total items in gut) and relative volumes (percentage of total food volume in gut) of each prey item.

Results:

Overall, the diet of *Holbrookia lacerata* (n = 129 stomachs examined) is largely generalist and consists mainly of insects as well as spiders (Table 1). Grasshoppers accounted for the most gut volume across all lizards followed by beetles and spiders. Next most important are lepidopteran larvae, hymenopterans (especially ants), true bugs, and termites in roughly equal measure. Six other arthropod orders were consumed but only rarely. Regarding abundance, termites were the most commonly eaten arthropods. However, individual termites are comparatively small insects and the bulk of *Holbrookia lacerata* gut volume was occupied by relatively few but large-bodied orthopterans.

Juvenile lizards showed the highest evenness of prey items taken compared to adult males and females (Figure 4.1). The majority of their prey also was grasshoppers by

volume, but other arthropod orders were present in roughly equal amounts. By abundance, juveniles ate the greatest number of termites and small hemipterans, though these did not constitute the bulk of prey volume as each individual was small.

Adult lizards also show high proportions of orthopterans in their diet but females consume fewer of these and more beetles than either males or juveniles. Male lizards show the most restricted diet breadth with nearly 65% of their prey volume coming from few, large grasshoppers and spiders.

Initial analyses indicate no major differences between northern and southern populations; however, the data for the southern population is less clear and more susceptible to large swings in representative diet due to low sample size.

Discussion:

This study, based on the gut contents of 129 lizards, is the first comprehensive description of the diet of *Holbrookia lacerata*. The results of this diet study indicate that *Holbrookia lacerata* likely is an opportunistic generalist, consuming a variety of small-bodied arthropods as they are encountered across the landscape. Grasshoppers constitute the largest source of food for these lizards by volume and are likely the most abundant and important piece of their feeding ecology. Moreover, orthopterans constitute more than a third of the diet of both juveniles and adult lizards suggesting their importance in maintaining and growing populations of these lizards through time. Beetles and spiders constitute the next most important prey for these lizards followed by caterpillars, ants, and true bugs.

Most of these prey items are likely to be encountered on open soil between patches of vegetation. Grasshoppers, especially, are cryptic when resting in or on branches or clumps of vegetation and are unlikely to catch the attention of visual hunters like *Holbrookia lacerata*. However, they often move between vegetation in short bursts of flight and land on open ground where they are more noticeable. When flushed, grasshoppers fly to the nearest patch of vegetation and take a considerable amount of time to recover from their ungainly landings. During this time their lizard predators could run them down and glean them from the vegetation. This gleaning behavior is also supported by the presence of many types of pollinators and vegetation specialists in moderate abundance throughout the gut samples. These prey, such as apid bees and chalcidoid wasps, rarely alight on open ground, instead preferring to land and move through vegetation. Crab spiders (Thomosidae), which rarely leave flower heads and stems, were also present throughout the samples. Prey types like these give further indication that *Holbrookia lacerata* is a versatile forager and match with previous speculations regarding the foraging behaviors of these lizards (Axtell 1954).

Additional, though anecdotal, guesses about the temporal spread of feeding behavior in these lizards can be inferred from the diet. Guts from this study contained portions of the legs of a sun spider (Solifugae) as well as several ants in the genus *Camponotus*. Both of these arthropod groups are crepuscular or nocturnal and are most often encountered on open ground during these times of the day. The presence of these taxa in the guts of *Holbrookia lacerata* indicate that these lizards may be actively foraging at dawn or dusk as well as throughout the heat of the day.

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Both ontogenetic and sex differences are present in the diet (Figure 4.1). Though these do not deviate much from the average diet across all lizards, some feeding ecology differences are worth noting. Juvenile lizards show a wide range of diet breadth despite the fact that grasshoppers account for nearly half of their prey volume. Juveniles, for example, eat a much larger proportion of collembolans and small opiliones than do adults. These groups are very small, ground-dwelling arthropods that are likely to be overlooked or ingested by accident by larger adult lizards, but which may represent a reliable, easy to catch food source for the much smaller juveniles. Juveniles also took no caterpillars and much fewer pollinator taxa than adults. This could indicate that juveniles are not as adept at climbing and foraging from low-lying vegetation and must rely more heavily on ground-dwelling and soil arthropods instead. These smaller-bodied taxa also accounted for the majority of the individual prey items eaten, suggesting that juveniles focus predominantly on small, easy to obtain prey but will take the occasional larger orthopteran when presented with an opportunity.

Females tend to take fewer orthopterans and more beetles than either juveniles or males. They also show the highest proportion of lepidopteran larvae in their guts. This could indicate that females spend more time gleaning prey from around vegetation than they spend foraging across open soil.

Why adult males seem to slightly specialize on orthopterans and spiders is unclear. These prey items would be most commonly encountered on bare ground between patches of vegetation and would have to be run down to be caught. This could indicate that males are traveling farther and spending more of their time moving across the landscape than females which would be expected if male territory and home range sizes are larger than those of females who might be more tied to burrows. We do not know if this pattern describes the behaviors of *Holbrookia lacerata*, however it does match the majority of phrynosomatid lizards (Pianka and Vitt 2003).

Additionally, 26% of lizards sampled had empty stomachs. While these lizards could have been kept in captivity until starvation, this figure is well within the reported range for field-captured lizards (Huey et al. 2001). This proportion of empty stomachs is perhaps another indication that these lizards will take prey opportunistically as they encounter it.

Together, these data present the first complete glimpse of the feeding ecology of *Holbrookia lacerata* across Texas. This study also provided guidance in establishing protocols for future fieldwork to understand diet availability in the habitats these lizards occupy [following study]. These results indicate that we need only assess prey population smaller than the maximum gape width of these lizards. Because of this study, we also appended standard insect sampling protocols to focus more on trapping methods and efforts that would elucidate patterns of diversity and abundance of ground- and vegetation-dwelling insects of the taxa most commonly observed in *Holbrookia lacerata* guts. In sum, this diet analysis has provided the first steps to understanding and accurately evaluating the foraging ecology of *Holbrookia lacerata* across Texas.

Field Availability of Arthropods as Potential Diet Items for *Holbrookia lacerata*

Materials and Methodology:

Field surveys for arthropods were conducted at two sites in west Texas during June and August of 2016. Each field survey lasted a total of seven days and employed a variety of traps and methodologies to accurately census arthropod diversity. We were initially going to include a third survey site in southeast Texas, however our field crew was unable to secure access to a site in this area with high enough densities of *Holbrookia lacerata* to be valuable to the study. The remaining field sites were chosen because they were in areas of probable high lizard densities and because field survey crews were in the process of conducing lizard surveys at these sites. This provided valuable on the ground help and experience as well as a baseline of lizard densities to correlate with any future arthropod availability surveys.

At each site and time point, five different arthropod capture methodologies were employed in order to provide the most complete understanding of the arthropod fauna available. Termite cover boards were constructed from 0.25m x 0.25m pieces of corrugated cardboard and staked down 5 meters apart from each other in a 3 x 3 grid at each site. The objective of these boards is to provide a source of fiber as a bait for termite recruitment. These were left in place for 7 days before being collected into ziplock bags for later dissection and examination in the lab. Nine pan traps were also laid out 5 meters apart in a 3 x 3 grid at each site. These consisted of a 2" deep, 14" x 10" yellow tray filled with an inch of water and a drop of liquid soap to break the water's surface tension. This traps and drowns insects, especially pollinators, which fly in as they are attracted by the color. These traps were held open for 24 hours during the first and seventh days of sampling at each field site and during each sampling period. The contents of these traps were then poured into ziplock bags for later analysis in the lab. Five rows of 10 pitfall traps were dug at each site, moving perpendicularly outward from a roadside. Rows were spaced 10 meters apart from one another and individual pitfall traps were spaced at 5 meter intervals along these rows. Phrynosomatid lizards do not tear their prey into pieces and thus are gape width limited with regard to prey size. Thus the pitfall traps used in this survey were 50 mL centrifuge tubes with a mouth diameter of roughly 1". These tubes were buried level with the ground, filled with 10 mL of antifreeze, and left open for 24 hours during the first and seventh days of each sampling period. Sweep samples were also conducted in sets of 10, 100-meter long transects perpendicular to roadsides and separated by 10 meters. Transects were swept in 2-meter wide arcs with a sweep net and contents of each sweep were dumped into a ziplock bag for later analysis in the lab. A set of the ten sweep transects was run during the first, second, and seventh days of each sampling period. Finally, malaise traps were set out in flyways within 50 meters of the nearest pitfall or sweep transect and held open for all seven days of each sampling event. Specimens caught by these traps were stored in 70% ethanol in a plastic vial until being analyzed in the lab. All together this yielded 100 pitfall samples, 30 sweep samples, 18 pan samples, 9 termite board samples, and 1 malaise sample from each of the four sampling events. Using the number of arthropod species present along with the relative abundance of each species, a Simpson's diversity index was calculated (Simpson 1949).

Field site descriptions:

LAFB Site: The LAFB site is a 16 km-square patch of managed rangeland within the Laughlin Air Force Base. It is bordered on all sides by high fence and on its north boundary by a highway. Less than 1 km to the southwest of the field site is an active runway. The site is in the southeastern corner of Val Verde County, Texas roughly 10 km east of the town of Del Rio. The field site itself is a highly managed mown grass field with no trees within roughly 2 km of its center. The vegetation is mostly a mix of native and introduced grasses with occasional flowering plants and forbs such as asters, devils bouquet, *Sabatia*, and milkweeds. The vegetation height here averaged 0.25 meters. While the diversity and structural complexity of vegetation here was lower than at the Flip site, it was still within a few kilometers of riparian corridors and tributaries to the Rio Grande river. This proximity to more complex habitat is a likely driver of the relatively high diversity found in this otherwise heavily managed site. This resulted in a variety of diverse arthropod taxa at least occupying the site and intercepted during dispersal.

"Flip" Site: The Flip site is an 8 km-square patch of unfenced scrubland bordered on two sides by dirt access roads with a power line access corridor along its southern edge. It is located roughly 13 km southeast of Barnhart, Texas in Crockett County. The site is surrounded for several miles on all sides by scrubland of similar composition, although much of the land is fenced off, used for cattle grazing, and/or under development for well pads. The vegetation height here averages 0.5 meters high, however there is a reasonable density of mesquite trees providing an array of complex structural habitat. The ground cover is moderately open with several bare patches of soil and rock covered in a patchwork of annual native grasses, mesquite, prickly pear cactus, and a variety of asters and forbs such as broomweed and goldenrod. This yields a diversity of structure and nectar resources for a wide variety of arthropod species as well as adequate bare ground cover for lizards to capture prey.

Results:

The results of a Simpson's index (S) calculated for all taxa collected across both time points show that the Flip site is much more diverse and species-even (S = 0.677) than the LAFB site (S = 0.351). However, it is worth noting that the LAFB site actually included greater total numbers of families and species of arthropods than did the Flip site and that a Simpson's index value of 0.351 still represents appreciable diversity, especially considering how heavily managed this field site is. Total abundance was also much higher at the Flip site (n = 12021 individual arthropods) than at the LAFB site (n = 3385). Most of this density is explained by a single taxon; hymenoptera. For example, nearly 81% of the density at the Flip site was accounted for by ants and other hymenopterans. Other taxa were found in much lower proportions as outlined below (Table 4.2).

Diversity and abundance at both sites decreased from the June sampling period to the August sampling period. This was most pronounced at the Flip site which saw a 72% decrease in abundance compared to a 38% decrease at the LAFB site. However, the lowest abundance totals from the Flip site were still 44% larger than the highest abundance totals at LAFB. Seasonality of arthropod reproduction and activity patterns likely contributed to some of the abundance decrease seen over the summer, however it is worth mentioning that the LAFB site sustained heavy and consistent rains before and during the August sampling period which likely drove down overall activity levels (especially flight movement and dispersal).

Hymenopterans were by far the most abundant taxa at each location and time point. Further, this abundance was primarily driven by ants. The majority of other taxa were rare and represented by only a handful of individuals. However, at both sites, beetles, flies, spiders, and grasshoppers were commonly encountered. These are all important diet items for *Holbrookia lacerata* as indicated by their relative percentages of volume found in gut contents (these taxa each account for at least 7% relative gut volume). Interestingly, when excluding the hyper-abundant hymenoptera as a variable, the relative abundances in the field are about equal to the relative abundances seen in gut contents. Thus the current diet availability at these sites nearly mirrors the diet preferences found in lizard guts in the first study with the exception of spiders, hemipterans, and termites. Spiders and hemipterans are more common in the field than would be predicted by gut contents and termites are vastly more common in lizard guts than they are in the field.

Discussion:

Diversity survey studies like this provide few concrete answers to testable questions, however they do highlight the overall diversity and abundance of a study area. This allows comparisons to be made across sites and times and provides insights, albeit speculative, to the ecology and natural history that must be at work.

From a diversity standpoint, the LAFB site is less diverse and less species-even than the Flip site. While the LAFB site contained a greater number of families and species than found at the Flip site, most of these taxa were represented by only one or a few individuals and would likely not be a consistent source of available food at the site. This disparity between the sites is likely due to the comparatively reduced structural complexity and diversity of the habitat around LAFB. Many insects are tied to certain types or even species of host plant and a site like Flip that is high in flowering plant diversity offers a variety of nectar and food resources for arthropods. The structural complexity at this site is also far more diverse than at the LAFB site. This structural complexity provides an array of perching, hiding, and thermoregulatory spots for arthropods as well traps more moisture and resources underneath bark or other vegetation for the arthropods to exploit. Thus, we would expect to find a greater diversity and greater abundance of arthropods across niche types at the Flip site. While the raw diversity numbers are similar, this result holds up when one considers that more of the taxa found at the Flip site were found in large numbers, presumably indicating consistent prey bases here.

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The diversity found at the LAFB site, however, is still quite respectable for such a heavily managed area. Many more arthropod species were found at the LAFB site than would be expected given the lack of habitat complexity. The increased diversity is likely explained by the sites proximity to riparian areas and wooded corridors. These areas likely serve as habitat for large and consistent populations of many arthropod species and the individuals collected during this study were likely a result of spillover of dispersing organisms. For example, a few individuals of the ant genus *Neoponera* were collected in sweep samples running through areas of sparse grass cover despite the fact that, in Texas, this group of ants tends to live mainly along riparian corridors. Their dispersal range is far enough that these ants were likely emigrating from nearby stable populations to the LAFB site. So while these ants and other taxa with similar patterns may not be a sustainable source of food for lizards, they certainly represent possibilities for opportunistic encounters.

Diversity and abundance both decreased over the sample period from June to August 2016 suggesting that prey availability decreases later in the season. Some of this seasonality is undoubtedly accounted for by heavy and persistent rains during the second sampling period at the LAFB site during the August sampling period and by the fact that the site was mowed between sampling periods. However, even without this the trend would still likely have been downward. We are unsure what this means for patterns of lizard activity and foraging. Lizards likely spend more time foraging and consuming prey items early in the season when these prey are more abundant. Conversely, lizard activity slows down as prey become less abundant and as temperatures begin to drop. Insects can still be found across west Texas during the winter months, outside the primary activity period of *Holbrookia lacerata* based on lizard survey work under this contract. Like other phrynosomatids, they likely spend more of the winter underground or under vegetation cover in a state of torpor and eat little if at all. This hypothesis is supported by the gut contents of the only four lizards collected in winter months that were examined in the gut content survey (one each from November, December, January, and February). Two of these lizards had empty stomachs and the two others each contained one prey item each accounting for an average volume of 18 mm^3. In comparison, lizards collected across all other months had an average gut content volume of 268.5 mm^3. Thus it seems probable that these lizards are foraging little if at all during the winter months perhaps only coming out of torpor on hot days to thermoregulate and eat.

Diversity and density varied greatly among the arthropod taxa collected at each site but especially of note was the abundance of hymenopterans, specifically ants. Hymenopterans dominated abundance counts at both field sites and at each time point. Especially dominant at the Flip site was one species of *Forelius* ant. Admittedly, these counts were raw abundance numbers and we did not take volumetric measures of prey size during this study. So, while these ants were numerous, a single large grasshopper might equal the volume and nutritional value of hundreds of ants. By reanalyzing the gut content data to look at relative abundances in the diet we can compare these numbers to numbers of arthropods observed in the field. By this measure, orthopterans are present in about equal proportions at each field site as they are in lizard guts. However, at both sites, spiders and hemipterans are more abundant and termites are less abundant than their gut content abundances would suggest. This could indicate that lizards somewhat avoid spiders and hemipterans which might be difficult to catch in favor of larger, relatively

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more valuable orthopterans. Other taxa found disproportionally in lizard guts compared to field samples could be explained by temporal variability in the availability of those prey items. Termites, for example, were found in much greater abundance in lizard guts than they were at either field site or time point. Termites spend much of their time buried under ground or underneath rocks and vegetation but can show seasonal spikes in above-ground abundance during mating flights just after rains. Termite predation by lizards might thus be facultative, following variable encounter rates and relative abundances, and/or we simply sampled at the wrong time of year or in the wrong microhabitats to accurately census this diet item. Another explanation could be that lizards are digging for termites or specifically foraging around vegetation bases or fallen dead branches to search for this particular prey type.

All together, these sites both seem indicative of good habitat quality and abundant forage for *Holbrookia lacerata*. Results from our gut content survey indicate that these lizards are opportunistic generalists that subsist on small prey items but which fill their guts with large grasshoppers when the opportunity presents itself. They also appear to glean insects from low-lying vegetation and, potentially, from bark, soil, and leaf litter. These habitats, and the arthropods that occupy them are abundant at both field sites, especially the Flip site. Both sites also show arthropod availability at roughly the same proportions that these arthropod types were represented in the diet of museum specimens. Both habitats also have a reasonable amount of bare ground cover for the lizards to chase down arthropod prey and to thermoregulate. This project highlights the importance of surveying not only the diet, but the prey availability for a given predator. From these data, we now better understand how these lizards utilize their habitat and what prey items are most important to the lizards, providing us an indication of how well an area suits the diet of this particular lizard.

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Appendix 1. Specimens Examined: Diet Analysis. *Holbrookia lacerata*: KU 476–478, 56080–56084, 61468–61469, 88105–88106, 88108, 126981, 317576–317577; LACM 4192–4193, 23364, 26942, 53611–53612; TCWC 15073, 18796–18799, 22783, 35142–35145, 36582, 37967–37970, 39945, 60398, 62347, 63435–63437, 63722–67326, 67329–67332, 67334–67336,, 68848, 68930–68931, 69753, 71164, 85869, 94087–94088, 100324, 100379, 100593, 100595–100596, 100659, 100695–100711, 100777–100782, 100830–100834; TNHC 28395, 30617–30620, 30629, 30633–30639, 30644, 31106, 33405–33406, 46148, 52030, 65263–65268, 70369–70389, 74704.

Figure 4.1. Relative volumes of prey types in guts of juvenile, female, and male *Holbrookia lacerata*.
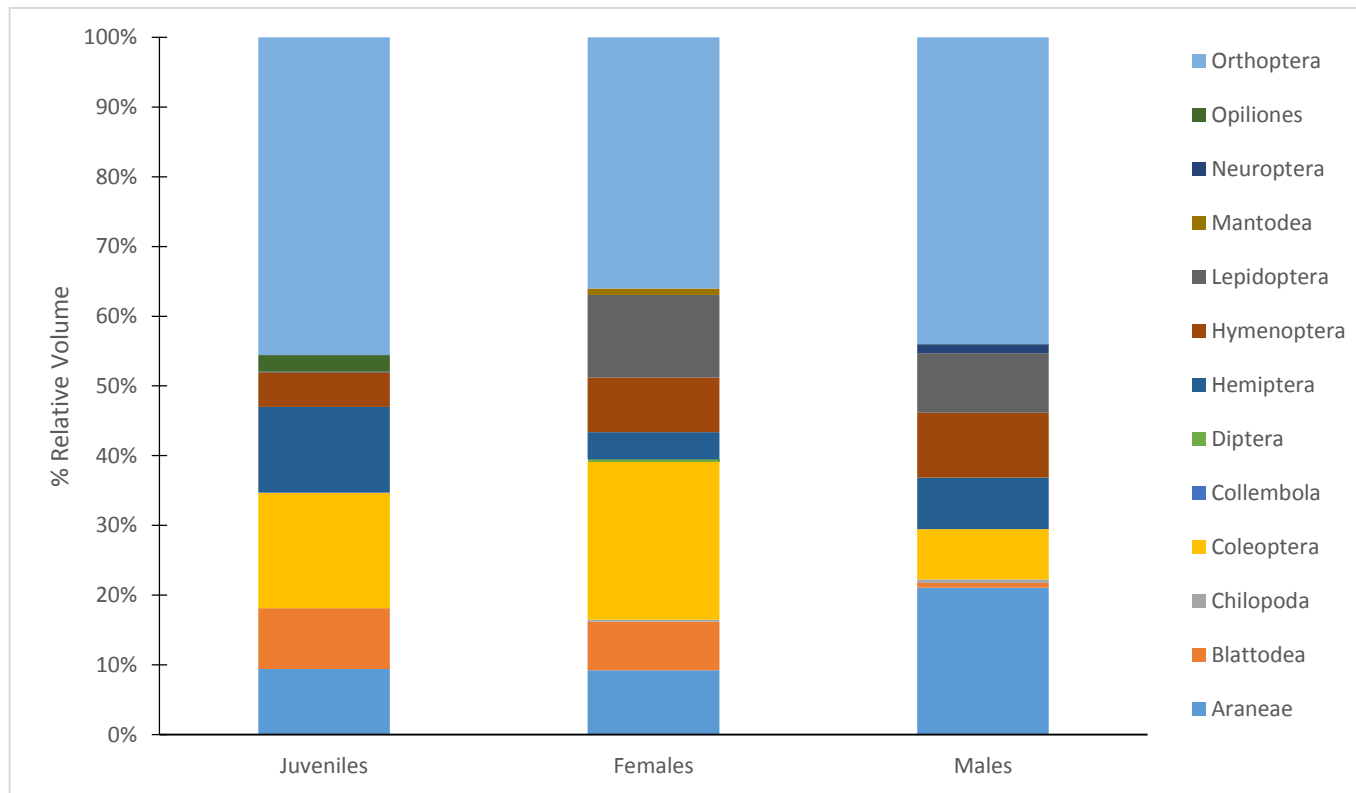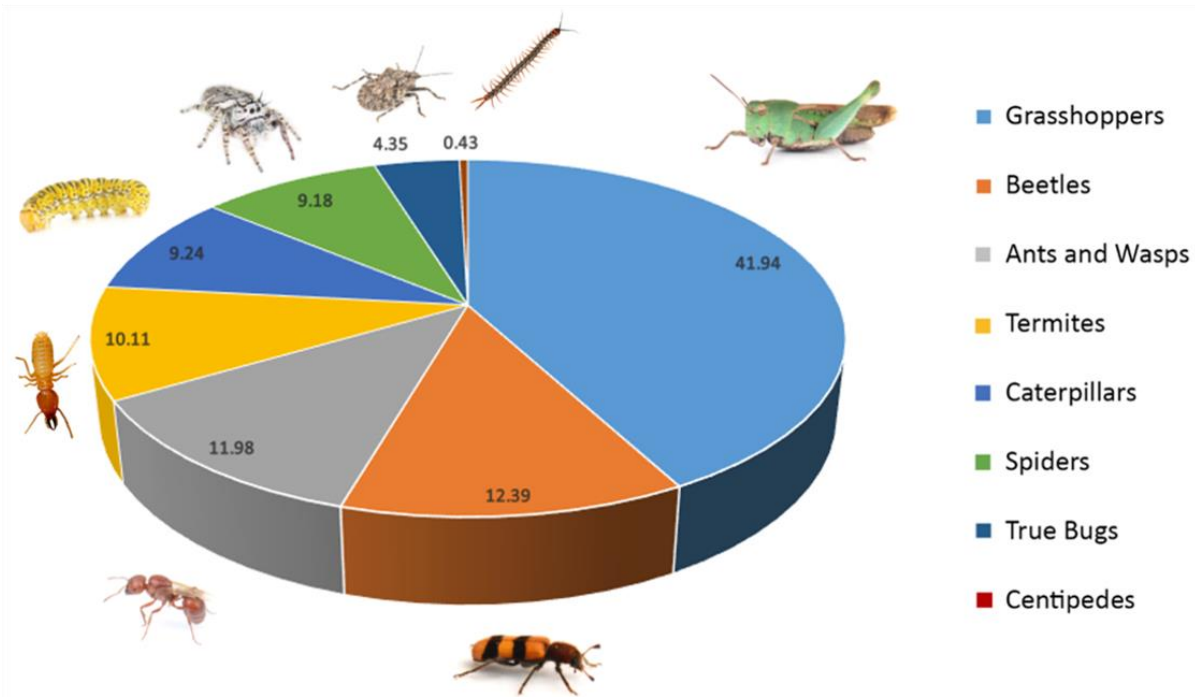
Figure 4.2. Diet of the Spot-tailed Earless Lizard (*Holbrookia lacerata*) by relative volume based on recovered stomach contents from 129 preserved museum specimens.

Table 4.1. Diets of juvenile, adult female, and adult male *Holbrookia lacerata*. Numbers of stomachs dissected are indicated in parentheses.

Prey Type (Order)	Juveniles (n = 19)			Females (n = 60)			Males (n = 50)		
	Total Count	% Relative Count	% Relative Volume	Total Count	% Relative Count	% Relative Volume	Total Count	% Relative Count	% Relative Volume
Araneae	15	8.57	9.41	35	7.48	9.23	36	18.56	21.08
Blattodea	44	25.14	8.73	215	45.94	6.95	8	4.12	0.67
Chilopoda	0	0.00	0.00	3	0.64	0.28	1	0.52	0.49
Coleoptera	14	8.00	16.52	117	25.00	22.61	40	20.62	7.24
Collembola	1	0.57	0.06	1	0.21	0.01	0	0.00	0.00
Diptera	0	0.00	0.00	2	0.43	0.35	0	0.00	0.00
Hemiptera	44	25.14	12.28	27	5.77	3.89	30	15.46	7.36
Hymenoptera	22	12.57	4.93	22	4.70	7.87	35	18.04	9.32
Lepidotera	0	0.00	0.00	15	3.21	11.81	10	5.15	8.51
Mantodea	0	0.00	0.00	1	0.21	0.94	1	0.52	0.01
Neuroptera	2	1.14	0.12	0	0.00	0.00	1	0.52	1.29
Opiliones	28	16.00	2.37	0	0.00	0.00	1	0.52	0.04
Orthoptera	5	2.86	45.57	30	6.41	36.00	31	15.98	43.99

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Table 4.2. Total and percent relative abundances of arthropod taxa collected at each field site and time point.

Order	LAFB Site				Flip Site			
	June		August		June		August	
	Total abundance	% Relative abundance	Total abundance	% Relative abundance	Total abundance	% Relative abundance	Total abundance	% Relative abundance
Araneae	58	3.67	70	7.11	482	4.93	173	6.17
Blattodea	2	0.13	3	0.30	4	0.04	0	0.00
Chilopoda	0	0	0	0	2	0.02	4	0.14
Coleoptera	113	7.15	165	16.77	85	0.87	77	2.74
Collembola	15	0.95	38	3.86	75	0.77	14	0.50
Diptera	98	6.20	47	4.78	74	0.76	55	1.96
Hemiptera	229	14.48	129	13.11	729	7.46	217	7.73
Hymenoptera	944	59.71	484	49.19	8104	82.90	2096	74.70
Isopoda	0	0	0	0	10	0.10	1	0.04
Lepidoptera	62	3.92	23	2.34	35	0.36	41	1.46
Mantodea	0	0.00	1	0.10	1	0.01	1	0.04
Mecoptera	0	0	0	0	3	0.03	0	0.00
Microcoryphia	0	0.00	2	0.20	0	0	0	0
Neuroptera	0	0	0	0	1	0.01	2	0.07
Odonata	0	0.00	1	0.10	1	0.01	0	0.00
Orthoptera	56	3.54	20	2.03	138	1.41	119	4.24
Phasmatodea	0	0.00	1	0.10	10	0.10	3	0.11
Psocoptera	3	0.19	0	0.00	21	0.21	1	0.04
Thysanoptera	1	0.06	0	0.00	1	0.01	2	0.07
Totals	1581	100.00	984	100.00	9776	100	2806	100

CHAPTER 5. PHYLOGENETIC RELATIONSHIPS WITHIN HOLBROOKIA LACERATA (COPE 1880) (SQUAMATA: PHRYNOSOMATIDAE)

[PI note: chapter text below is from manuscript currently in review at Zootaxa]

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Abstract

Species delimitation attempts to match species-level taxonomy with actual evolutionary lineages. Such taxonomic conclusions are typically, but not always, based on patterns of congruence across multiple data sources and methods of analyses. Here, we use this pluralistic approach to species delimitation to help resolve uncertainty in species boundaries of phrynosomatid sand lizards of the genus *Holbrookia*. Specifically, the Spot-tailed Earless Lizard (*H. lacerata*) was historically divided into a northern (*H. l. lacerata*) and southern (*H. l. subcaudalis*) subspecies based on differences in morphology and allopatry, but no research has been conducted evaluating genetic differences between these taxa. In this study, patterns in sequence data derived from two genes, one nuclear and one mitochondrial, for 66 individuals sampled across 18 counties in Texas revealed three strongly supported, reciprocally monophyletic lineages each comprised of individuals from a single geographic region. Distinct genetic variation evident across two of these regions corresponds with both the historical subspecies boundaries based on morphological variation and the presumed geographic barrier between them, the Balcones Escarpment. The combined evidence from genetics, morphology and distribution is sufficient to consider these subspecies as distinct species with the lizards north of the Balcones Escarpment retaining the name *Holbrookia lacerata*, and those south of the Balcones Escarpment being designated as *Holbrookia subcaudalis*.

Introduction

Delimiting species is a fundamental function of taxonomy. While many methods have been used for species delimitation (reviewed by Carstens et al. 2013), it is critically important to investigate

multiple sources of data for each potential species (Knowles & Carstens 2007; Schlick-Steiner et al. 2010). Congruence of all data sources is not necessary when delimiting species. For example, morphology is known to be conservative (and thus less informative) in many taxa with deep genetic divergences. However, congruence between genetic and non-genetic data sources (e.g., life history, distribution, morphology, ecology, and behavior) provides a compelling argument for concluding that populations or metapopulations are their own evolutionary lineage (General Lineage Concept—de Queiroz 1998).

Using multiple methods and criteria for species delimitation would be particularly helpful in resolving uncertainty in species boundaries of phrynosomatid sand lizards. This sand lizard group is comprised of 12 currently recognized species belonging to four different genera: *Uma, Callisaurus, Cophosaurus*, and *Holbrookia* (Schulte & de Queiroz 2008; Wilgenbusch & de Queiroz 2000). Although the monophyly of the sand lizard group, its relationships to other phyrnosomatid lizards, and the validity of the four genera listed above are well-supported (de Queiroz 1992; Schulte & de Queiroz 2008; Wiens et al. 2010; Wilgenbusch & de Queiroz, 2000), the taxonomic designation of lineages within some of those genera are unresolved. The genus *Holbrookia,* for example, contains the following four "earless" species (i.e., with a concealed tympanic membrane): *H. elegans* Bocourt (2 subspecies), *H. lacerata* Cope (2 subspecies), *H. maculata* Girard (5 subspecies), and *H. propinqua* Baird and Girard. Phylogenetic relationships, geography, and patterns of morphological variation suggest that some of the subspecies may warrant species rank (Wilgenbusch & de Queiroz, 2000).

For the Spot-tailed Earless Lizard (*Holbrookia lacerata*) in particular, two subspecies have been distinguished based on allopatry and morphology (Axtell 1956, 1958). The distributions of these subspecies are clearly separated by the southern edge of the Edwards Plateau or Balcones Escarpment (Fig. 1; Axtell 1956, 1958). The southern subspecies (*H. l. subcaudalis*) differs from the northern subspecies (*H. l. lacerata*) in average adult size (snout-vent length 62 mm vs. 54 mm, respectively) and average femoral-pore count (15.7 to 12.8, respectively). The southern subspecies also has unfused pairs of blotches on each side of the dorsal vertebral line and rounded blotches on the hind legs rather than fused dorsal blotches and dark bands on the hind legs found in the northern subspecies (Fig. 5.1). Despite these clear geographic and morphological differences, no research has been conducted to determine whether genetic differences between *H. lacerata* subspecies exist.

In this study, we evaluate the subspecies designations of *Holbrookia lacerata* using sequence data derived from two genes, one nuclear and one mitochondrial, morphological data, and ecological niche modeling. Our goal was to provide information about genetic diversity, morphological differentiation, and niche differences within *H. lacerata*. This will determine congruence among data types and provide empirical support for delimitation of *H. lacerata*. Results of this research have implications for future conservation and management of *H. lacerata* populations, as this species is currently being considered for listing by the U.S. Fish and Wildlife Service (FWS) under the Endangered Species Act (USFWS 2011).
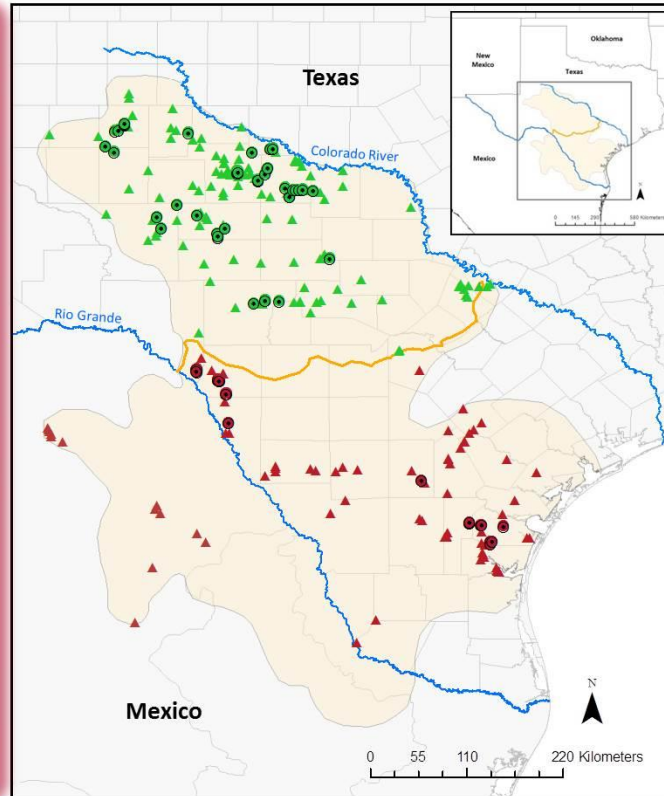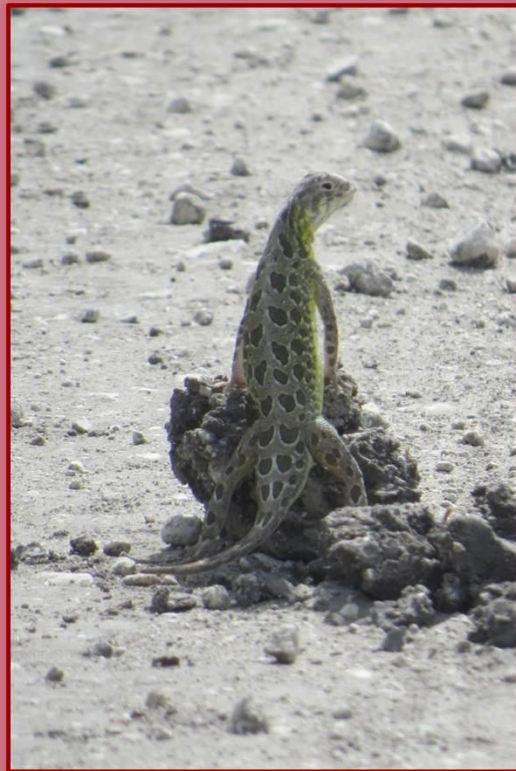
Figure 5.1. Shaded portion of the map depicts the historical distribution of *Holbrookia lacerata*
The green and red triangles are localities for the historically divided northern (*H. l. lacerata*) and southern *(H. l. subcaudalis)* subspecies, respectively. The samples collected for this study are depicted as red or green circles. The orange line represents the Balcones Escarpment. The photograph outlined in red is a male *Holbrookia subcaudalis* from Jim Wells County, Texas and the photograph outlined in green is a male *H. lacerata* from Schleicher County, Texas.

Methods

Phylogenetics

We collected tissue samples during 274 statewide surveys in Texas between April and September 2015. We did most of these surveys by driving roads, which has proven to be an effective method for collecting *Holbrookia lacerata* (TJH, WAR pers obs). We took liver samples from up to two specimens at each survey site. We also collected tail tips from additional captured lizards and collected tissues from lizards found dead on the road. We also contacted natural history collections and museums to supplement tissues collected from road searches. In total, we amassed 73 tissues from three *Holbrookia* species, which included 66 *H. lacerata* samples from 20 Texas counties.

We extracted whole genomic DNA from tissues, tail tips, and blood as available using the E.Z.N.A Tissue Extraction Kit and standard protocols (Omega Bio-Tek, Norcross, GA) for *Holbrookia lacerata* individuals as well as from two outgroups (*H. maculata* (n = 4) and *H. propinqua* (n = 3)). We used extracted DNA to sequence a mitochondrial and a nuclear gene. We selected the mitochondrial NADH dehydrogenase subunit 2 gene (ND2*)* as it was informative in reconstructing diversification patterns within the sand lizard clade (*Uma*, *Calliaurus*, *Cophosaurus*, and *Holbrookia*) of Phyrnosomatidae (Blaine 2008). We amplified 1,086 bp of ND2 using primers H4437 and Ala.r3 (Blaine 2008; Macey et al. 1997), for all samples. The nuclear gene amplified was Recombination Activating Gene 1 (*RAG-1*), which we amplified for 33 *Holbrookia* individuals (including one each of *H. maculata* and *H. propinqua* as outgroups) and 1,054bp using JRAG1f2 and JRAG1r3 (Leaché & McGuire 2006). We selected RAG-1 as it has proven phylogenetically informative in resolving relationships within other phyrnosomatid genera (Wiens et al. 2010).

We performed polymerase chain reactions (PCR) with GoTaq Flexi DNA polymerase (Promega). Automated sequencing was performed using BigDye (Applied Biosystems) and products were sequenced on an ABI PRISM 3730xl (Beckman Coulter, Danvers, MA). We verified and aligned sequences by eye using Geneious 6.1.8 (http://www.geneious.com, Kearse et al., 2012). We used PHASE 2.1 (Stephens et al. 2001) for haplotype reconstruction of diploid gametic alleles for the *RAG-1* gene as implemented in the DnaSP 5.10.1 package (Librado & Rozas 2009). We used a 1000 burn-in, 10 thinning intervals, and 1000 main iterations resulting in 66 sequences for 33 taxa.

Phylogenetic analyses were first conducted on single gene trees. The most appropriate models of evolution were determined using Partition Finder (Lanfear et al. 2012) for each single gene across all positions. For the *ND2* gene and RAG-1 gene, the most appropriate model selected using the Akaike information criterion (AIC) was GTR + G, whereas the Bayesian information criterion (BIC) criterion selected the HKY + G. For concatenated gene tree analysis the most appropriate models selected using AIC was 3 partitions, ND2 position 1+2 under GTR + I, ND2 position 3 under HKY + I, and Gene 2 under HKY + I. The most appropriate model selected using the BIC criterion was HKY + I + G for both genes across all position.

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Single-gene phylogenies and concatenated gene tree analyses were assessed using HKY + I for all. Bayesian inference (BI) was conducted using MrBayes 3.2.6 (Ronquist & Huelsenbeck 2003) and in two Monte Carlo Markov Chain (MCMC) analyses (Geyer 1991) which were run for 10 million generations and sampled every 1000. For ND2, we ran both AIC and BIC selected models, and for RAG-1, we ran the AIC and BIC selected model as well as a reversible jump (RJ) model. For all analyses, convergence and appropriate burn-in was assessed using Tracer (Rambaut 2007) and potential scale reduction factors were verified to have reached convergence values (PSRF=1.0). Maximum likelihood (ML) analysis was conducted using RAxML 7.2.7 (Stamatakis 2006) on the CIPRES Science Gateway Portal (Miller et al. 2010). Analyses were run under the GTRGamma model and all parameters were estimated. Rapid bootstrap support values were estimated with 10000 replicates.

For the concatenated analysis, model selection was run under both AIC and BIC model schemes determined in PartitionFinder. BI and ML analyses were run as the single gene analysis in MrBayes 3.2.6 and RAxML 7.2.7, respectively. For BI concatenated gene tree analysis, the most appropriate models selected using AIC was 3 partitions, ND2 position one under GTR + I, ND2 position three under HKY + I, and RAG1 all positions under HKY + I + G. The most appropriate model selected using the BIC criterion was HKY + I + G for both genes across all positions. RAxML 7.2.7 was run under the GTRGamma model with all parameters estimated and rapid bootstrap values estimated with 10000 replicates.

We constructed median-joining haplotype networks using Network 5.0 (Fluxus-engineering.com) to discern patterns across different haplotype genotypes. Uncorrected pair-wise sequence divergences among mtDNA haplotype groups was determined using MEGA7.0.14 (Kumar et al. 2016) for the ND2 gene.

Morphology

We amassed 157 *H. lacerata* specimens (*H. l. lacerata* = 112: *H. l. subcaudalis* = 45) from surveys and natural history museums. On each lizard we measured snout-vent length (SVL), tail length, head width, head depth, head length, upper arm length (humerus), lower arm length (from elbow to longest finger), upper leg length (femur), lower leg length (tibia), foot length (foot to longest toe), fourth toe length, and interlimb length to the nearest millimeter using digital calipers. We also counted the number of lateral spots, body blotches, connected blotches (between pelvic and pectoral girdles), femoral pores (left and right separately), and blotches on right leg (Fig. 5.2).
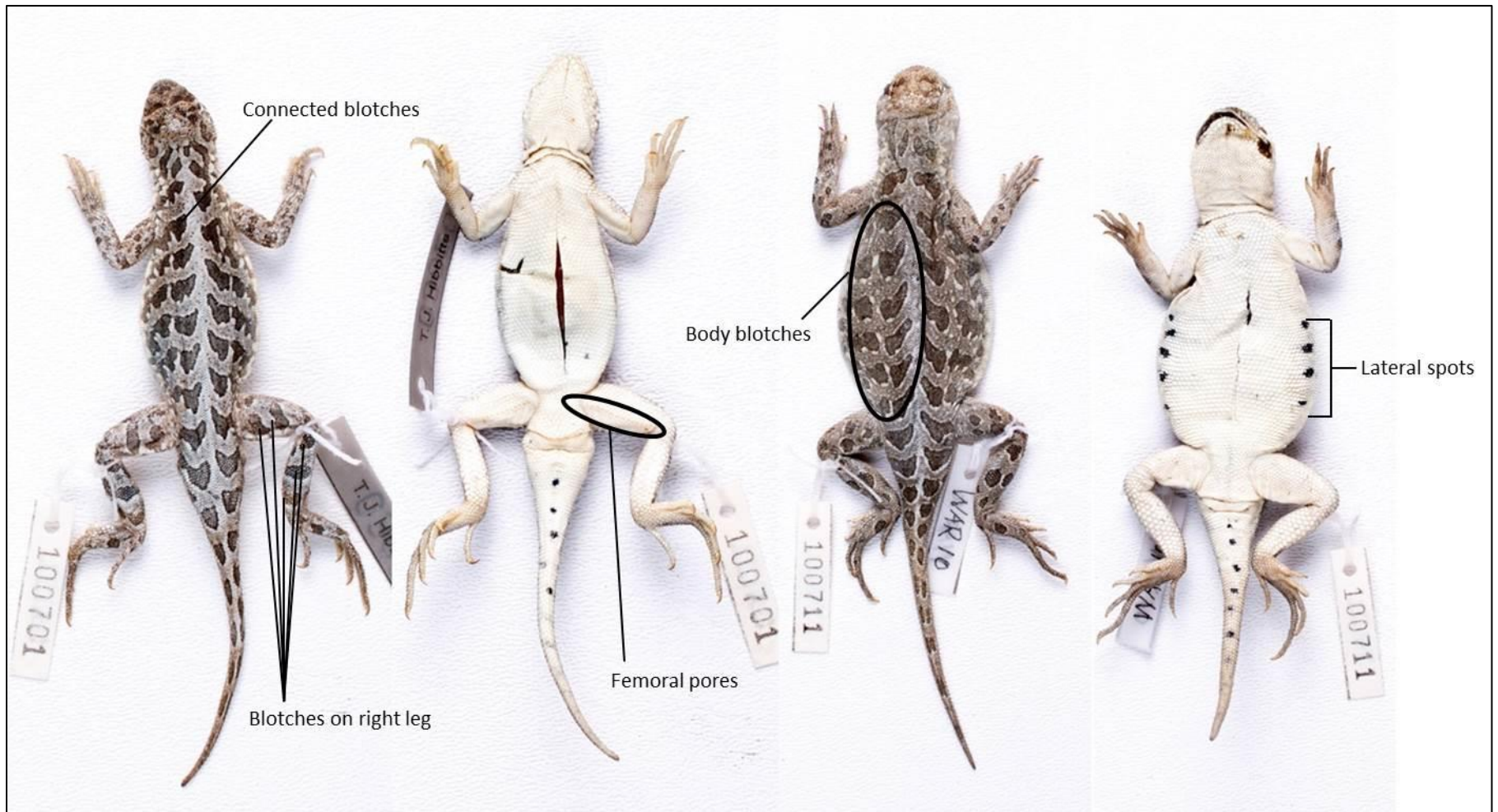
Figure 5.2. Morphological characters used to distinguish northern and southern subspecies from one another
The two images on the left are from a single northern (*H. l. lacerata*) male (dorsal and ventral view). The two images on the right are from a single southern (*H. l. subcaudalis*) female (dorsal and ventral view).

We removed the effects of body size by taking the residuals from linear regressions against SVL for all length measurements. We used these residuals in all subsequent analyses. We investigated morphological variables for multicollinearity. We found significant pairwise Pearson correlation between each of the leg variables (femur, tibia, foot, and fourth toe) and arm variables (humerus and lower arm), therefore we used only femur and humerus length in the analysis. We performed t-tests on the variables commonly associated with sexual dimorphism in phrynosomatid lizards (SVL, head width, head depth, head length, and interlimb length). We found that head width ($t = 2.19$, $p = 0.03$), head depth ($t = 2.28$, $p = 0.02$), and interlimb length ($t = -7.708$, $p < 0.001$) were all significantly different between sexes; therefore we did not use these sexually dimorphic characters in later analyses.

We used principle component analysis (PCA) to investigate the importance of morphometric variables and to visualize the morphospace occupied by the two *H. lacerata* subspecies. We used t-tests, with Bonferroni correction, to test for significance of each variable between subspecies. All statistical analyses were done in the program PAST 3.07 (Hammer and Harper, 2006).

Ecological Niche Correlates

To infer whether there is ecological divergence between the two subspecies of *H. lacerata*, we tested for niche equivalency and background similarity (Warren et al. 2008). Niche equivalency tests whether two modeled ecological niches are more different than expected if drawn from the same population. This test uses Schoener's (1968) statistic for niche overlap (D) and a similarity statistic (I) based on Hellinger distances (van der Vaart 1998). Both statistics range from 0 to 1, where 0 indicates no overlap and 1 indicates complete overlap. A randomization procedure partitions the occurrences from known groups into randomly assigned groups and then uses the groups to estimate ecological niche models. D and I are calculated for each permutation of this procedure and are compared to the original D and I for the known groups. Background similarity tests whether the difference between two modeled ecological niches are more similar than expected, given the difference between their backgrounds (i.e., available or accessible environments). We used 1000 permutations in both tests of niche equivalency and background similarity. Tests were performed in the R Statistical Programming Language with the packages ecospat (Di Cola et al. 2017), maxent (Phillips et al. 2017), SDMTools (VanDerWal et al. 2014), and dismo (Hijmans et al. 2017). We compiled occurrence data and climate variables to build ecological niche models for tests of niche equivalency and background similarity.

Occurrence data (n = 565) were compiled from all known locality records of *H. lacerata* (Fig. 5.1). Occurrences were separated into *H. l. lacerata* (n = 322) and *H. l. subcaudalis* (n = 243) based on morphology, genetics, and/or geographic location of sample. To account for spatial and collector bias in the occurrence data, we used an environmental filtering method that down samples occurrences based on gridding predictor variable space (Varela et al. 2014). The environmental filtering procedure randomly samples one occurrence point from each equidistant grid cell in predictor variable space. Each variable grid was based on equidistant spacing of grid cells. After applying the environmental filter, the occurrence dataset was reduced to 122 occurrences for *H. l. lacerata* and 64 occurrences for the *H. l. subcaudalis*.

Predictor variables included in the analysis were from a suite of bioclimatic variables in the Worldclim 2 database sampled at a 2.5 minute resolution (Fick and Hijmans 2017). Bioclimatic variables are meant to be biologically meaningful and represent means and extremes of temperature and precipitation at various temporal scales (monthly, quarterly, and yearly) (Nix 1986). We removed strongly correlated variables (r > 0.65 or r < -0.65) from the suite of nineteen bioclimatic variables to simplify interpretation of variable contribution and permutation importance results from ecological niche modeling, discussed below. Five predictor variables met the criteria: mean annual temperature (C), isothermality (%), maximum temperature of the warmest month (C), annual precipitation (mm), and precipitation seasonality (%). Isothermality is a ratio that compares the average day to night temperature differentials with annual temperature differentials; if the ratio is 1 (or 100%), then the difference in temperature during an average day or month is no different than the difference in temperature between seasons. Precipitation seasonality is the coefficient of variation of monthly precipitation. For detailed descriptions of the derivation of these five variables see Nix (1986).

We used Maxent version 3.4.1 to build ecological niche models of *H. l. lacerata* and *H. l. subcaudalis* (Phillips et al. 2017). We randomly sampled 20% of occurrence records after filtering for a testing dataset and used the remaining 80% of data for model training. Order of variable importance and amount of variable contribution was quantified for each model. We used area under the receiving operating characteristic curve (AUC) to evaluate training and testing datasets (Fielding and Bell 1997). In general, an AUC of 0.75 is considered informative (Elith et al. 2006); although, the higher the AUC, the better fit the model. Although ecological niche models will show whether there is projected overlap in the distributions of *H. l. lacerata* and *H. l. subcaudalis*, the results do not distinguish between background differences and their influence on the models. To consider this, we used tests for niche equivalency and background similarity.

Results

Phylogenetics

We recovered 2156 bp for both loci (1002 bp for ND2 and 1054 bp for RAG1). There were no gaps or indels found within amplicons. For ND2 mtDNA, BI analysis was run under HKY + I and GTR + I models of evolution and ML analysis was run under GTRGamma. These resulted in highly congruent phylogenies across BI and ML analyses. The topologies resolve two monophyletic, fully supported clades (posterior probability = 1.0, bootstrap support = 100; Fig. 5.3). These clades represent *H. lacerata* individuals from north of the Balcones Escarpment and *H. lacerata* individuals from south of the Balcones Escarpment. Within the southern clade, there were two subclades (posterior probability ≥ 0.95, bootstrap support ≤ 95; Fig. 5.3) corresponding to southwest and southeast Texas, respectively.

Haplotype network analysis for *H. lacerata* ND2 mtDNA gene indicated 38 unique haplotypes from 66 samples included in the analysis. These haplotypes cluster into three distinct haplogroups, which correspond to distinct geographic regions (north, southwest, southeast; Fig. 5.3). We observed no regions with shared haplotypes (Fig. 5.3). The northern haplotype group was over 90 mutational steps from the nearest southwestern haplotype, and over 70 from the

nearest southeastern haplotype. The southern haplotype groups differed by over 30 mutational steps.

Uncorrected pairwise (*p*) genetic distance, for the ND2 gene, between three clades/haplogroups was greatest between the north clade, and the southwest and southeast clades (8.70% and 7.60%, respectively). *P*-distance between the southwest and southeast clades was 3.20%.

The BI and ML analysis, run for selected models for *Holbrookia lacerata* RAG-1 nuclear DNA gene all resulted in highly supported polytomy (posterior probability $\geq$ 0.95, bootstrap support $\geq$ 95) uniting all *H. lacerata* individuals relative to outgroup taxa (Fig. 5.4). Topologies across all analysis were all concordant. The network analysis contained 66 phased sequences (in group taxa only) and resulted in 36 distinct haplotypes. Unlike our results for ND2, the RAG-1 gene does not show discrete clustering wherein all individuals were reciprocally monophyletic by geography (north, southwest, or southeast), although some internal clades do show some geographic structuring (Fig. 5.4). However, within these internal subclades, there is only one instance of a haplotype being shared between geographic regions (southwest + southeast; Fig. 5.4).
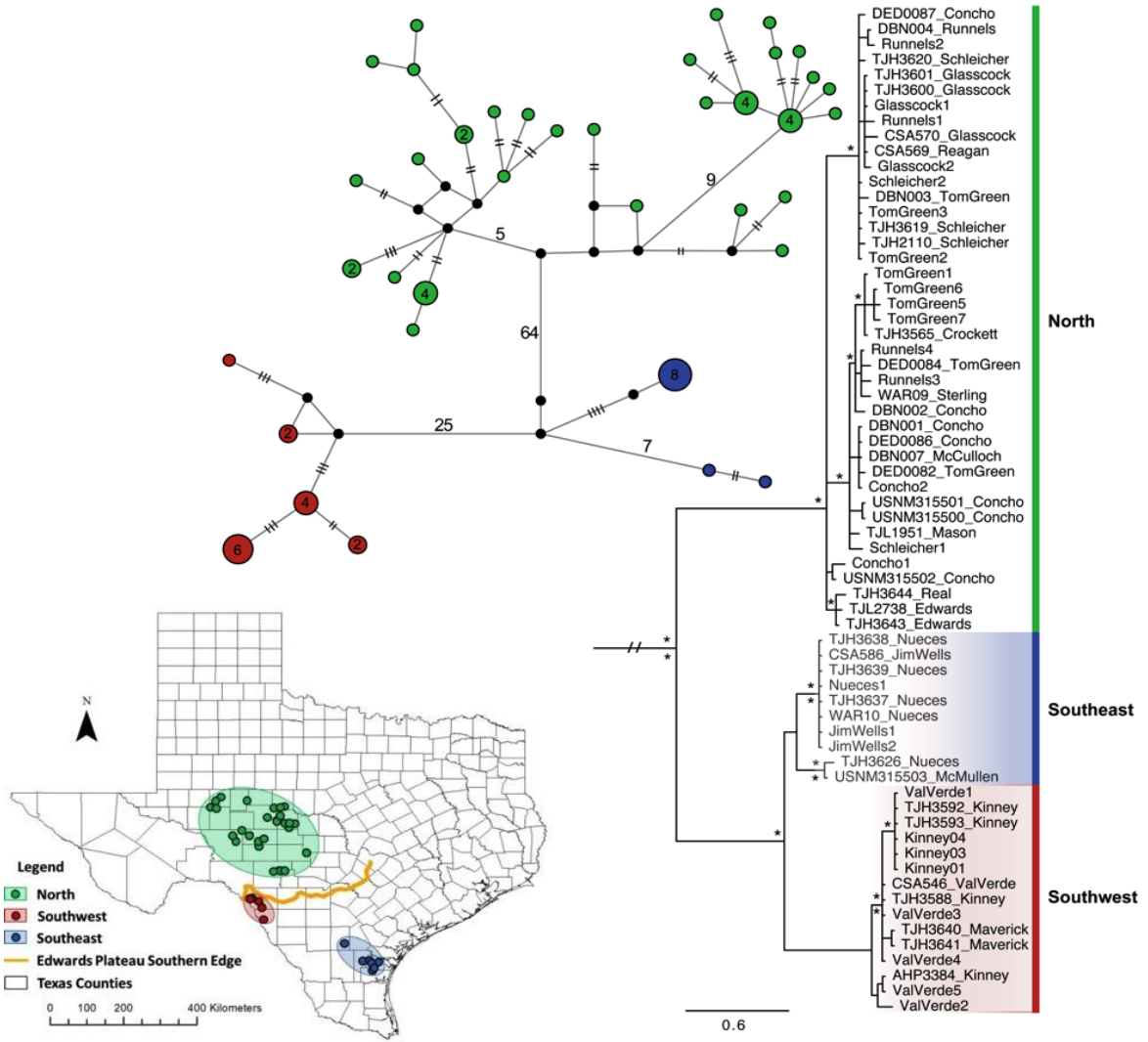
Figure 5.3. Locations of tissue samples of Holbrookia lacerata used in the analysis

In all cases the northern species (*Holbrookia lacerata*) is green. The southwestern population of the southern species (*Holbrookia subcaudalis*) is red and the southeastern population of the southern species is blue. Median-joining network (left) of the observed 38 haplotypes for ND2 mtDNA gene sequences of 66 spot-tailed earless lizard individuals. Circle sizes are proportional to frequencies of haplotypes. Black circles indicate missing intermediates (unsampled). Cross-hatches represent mutational steps with all greater than four denoted by the number of steps. Bayesian analysis of the mtDNA ND2 gene (right). Numbers at the nodes are posterior probability values. Asterisks indicate values = 1.

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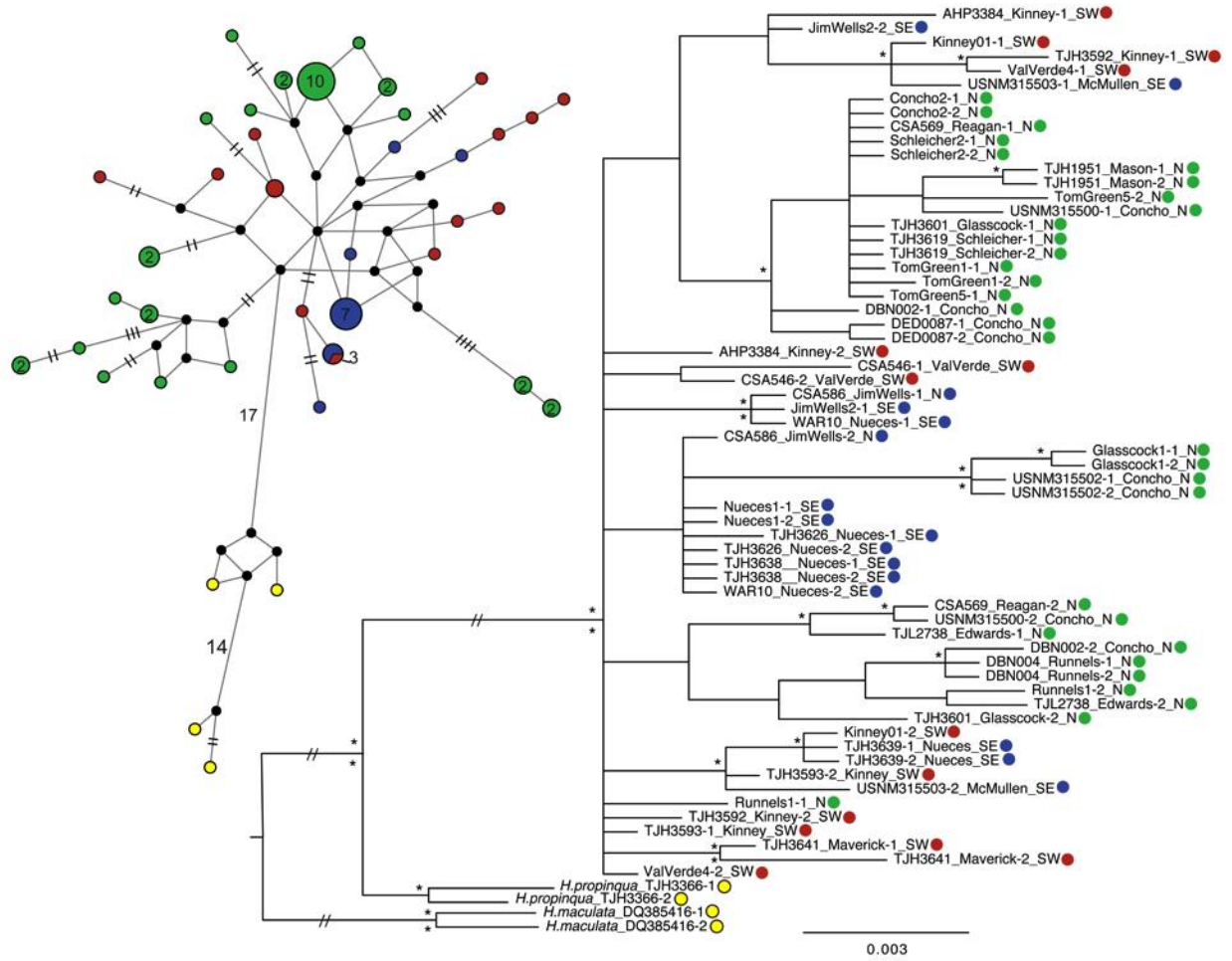
Figure 5.4. Median-joining network (left) of the observed 36 haplotypes for RAG-1 nuclear DNA gene of 66 individual spot-tailed earless lizards

Black circles indicate missing intermediates (unsampled). Cross-hatches represent mutational steps with all greater than four denoted by the number of steps. Bayesian analysis of the nuclear DNA RAG-1 gene (right). Numbers at the nodes are posterior probability values. Asterisks indicate values = 1.
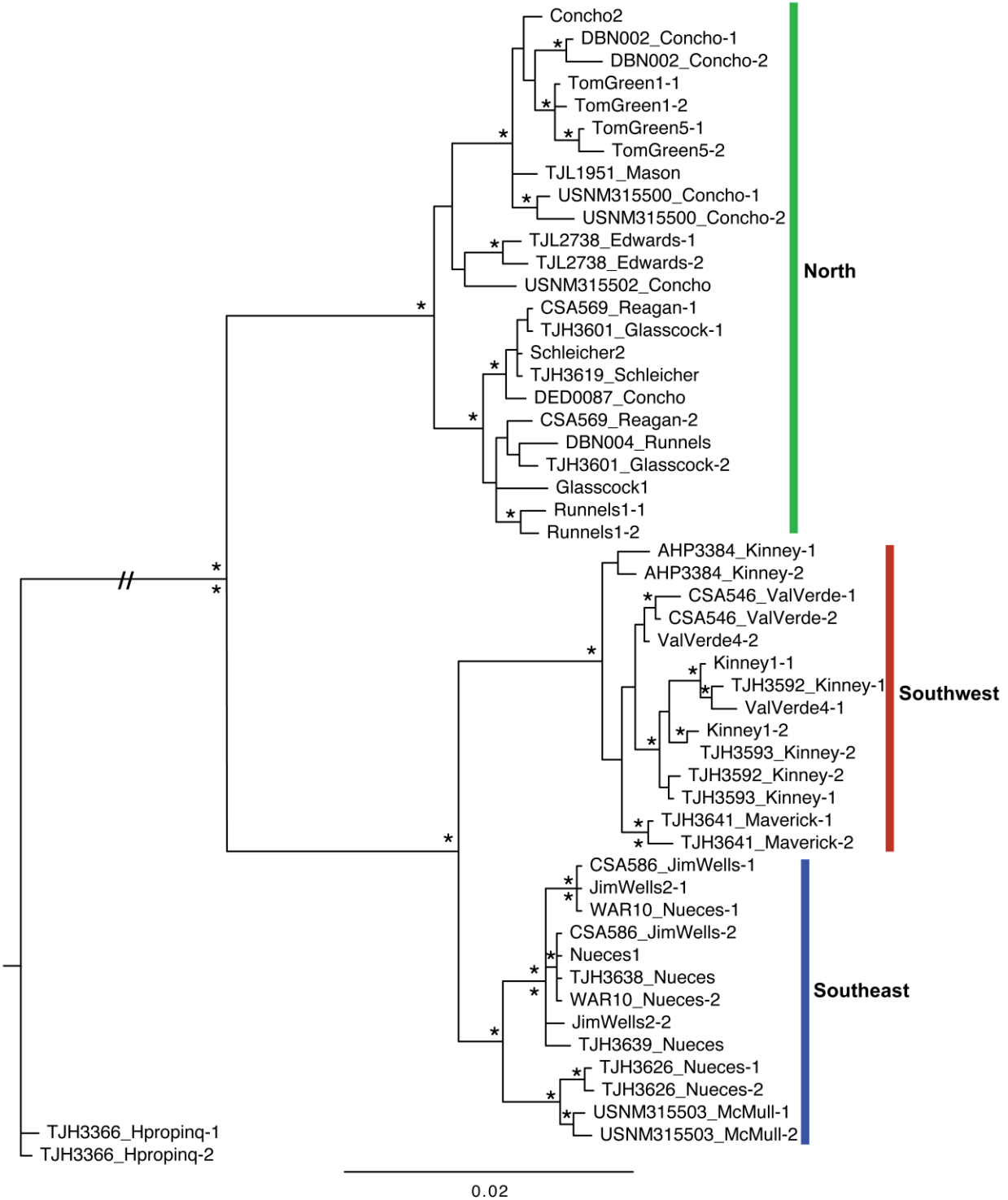
Figure 5.5. Concatenated Bayesian analysis of ND2 mtDNA and RAG-1 nuclear DNA genes Numbers at the nodes are posterior probability values. Asterisks indicate values = 1.

The Bayesian analysis for the concatenated gene trees under all models yielded identical topologies and similar support values at all nodes (Fig. 5.5). The topology resolved was consistent with our ND2 analysis resulting in two well-supported clades (posterior probability = 1.0 and bootstrap = 100), one comprised of *Holbrookia lacerata* individuals from north of the Balcones Escarpment and one comprised of individuals to the south. The southern clade is subdivided into the southwest and southeast individuals of *H. lacerata* (posterior probability $\geq$ 0.95 and bootstrap = $\leq$ 95; Fig. 5.5).

Morphology

We used 112 adult *H. l. lacerata* (northern) and 45 adult *H. l. subcaudalis* (southern) for our morphometric analysis. We found that the northern and southern *H. lacerata* were distinguishable in multivariate morphological space (MANOVA Wilks´ lambda = 0.4576, df_1 = 8, df_2 = 148, F = 21.92, p < 0.0001; visualized with PCA in Fig. 5.6). The first principle component was a gradient from lizards with more connected blotches to lizards with more femoral pores and leg spots. The second principle component was a gradient from lizards with fewer femoral pores to lizards with more connected blotches and leg spots (Table 1). Univariate t-tests showed (after Bonferroni correction) that northern and southern populations differed significantly in leg length (p < 0.0001), side spots (p < 0.0001), connected blotches (p = 0.0004), femoral pores (p < 0.0001) and leg spots (p < 0.0001). We also analyzed throat color on 42 male and 39 female northern *H. lacerata* and 26 male and 19 female southern *H. lacerata*. We found that 19% of male and 87% of female northern lizards had orange on their throat while no southern lizards of either sex had any orange throat coloration.
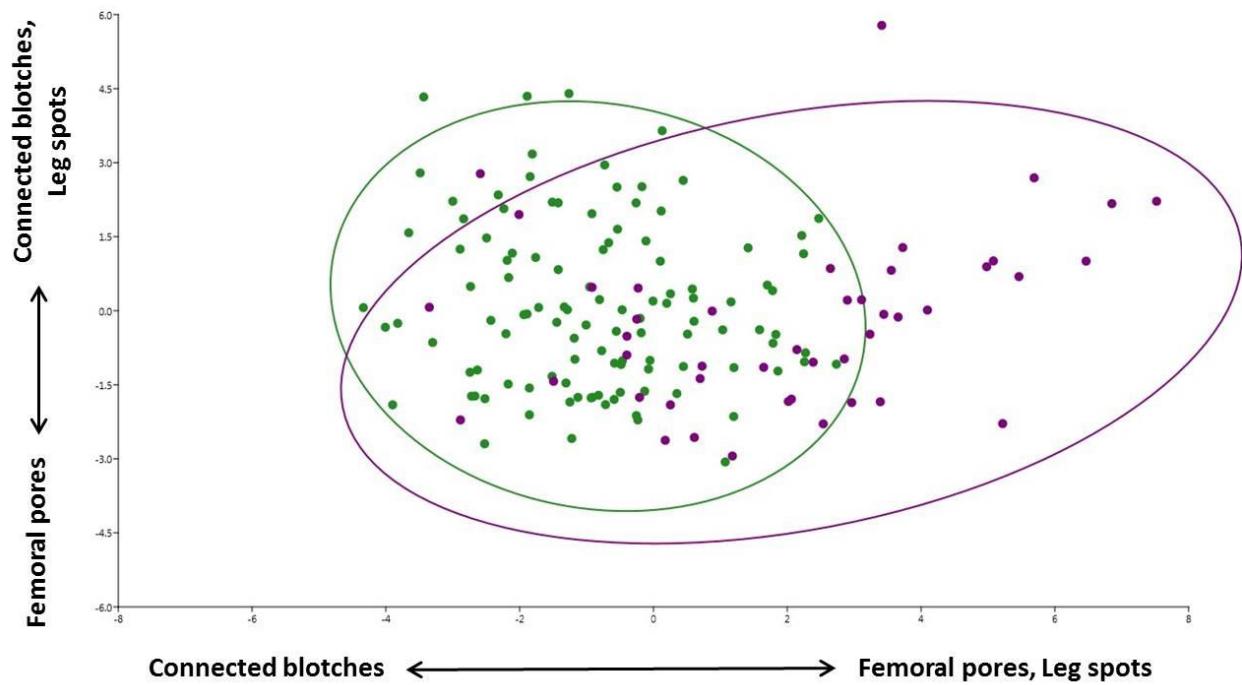
Figure 5.6. Principal components analysis depicting morphometric variables distinguishing northern subspecies, *H. l. lacerata* (green), from southern subspecies, *H. l. subcaudalis* (purple)

Table 1. Principle component analysis loadings and percent variance explained on the first four principle components

Character	PC1	PC2	PC3	PC4
Residual of femur	0.21394	-0.09816	0.044161	0.11725
Residual of humerus	0.028391	-0.00456	0.53391	0.105
Residual head length	-0.01932	0.084818	0.082944	-0.05065
Ventral spots	0.32219	0.086138	-0.11255	0.91769
Dorsal blotches	0.02751	0.022638	0.076205	0.01259
Connected blotches	-0.27386	0.74872	0.46545	0.03281
Left femoral pores	0.53315	-0.34184	0.45341	-0.20979
Leg spots	0.69946	0.54569	-0.26898	-0.29198
% variance explained	35.196	18.298	12.921	11.62

Ecological Niche Correlates

Holbrookia l. lacerata had a training AUC of 0.91 and a testing AUC of 0.81 and *H. l. subcaudalis* had a training AUC of 0.81 and a testing AUC of 0.79. These values indicate that the models are informative. The subspecies differ in the climate variables that contribute most to their ecological niche models and projected distributions (Table 5.2). Mean annual temperature is the most important variable to determine species occurrence for *H. l. lacerata* and precipitation seasonality is the most important variable for *H. l. subcaudalis* (both variables contribute more than 50% of the variation in their respective subspecies). Difference in variable importance contributes to differences in projected geographic distributions of each subspecies (Fig. 5.7).

Modeled niches were not equivalent (p <0.001), nor were they more similar than expected from background similarity (p = 0.23). Tests for niche equivalency showed that the two subspecies were not equivalent (i.e., niches were not identical) using both the D and I metrics for niche equivalency (Fig. 5.8A). Estimated niche overlap between subspecies was likely explained by regional differences in available habitat (Fig. 5.8B). The background similarity test was two-tailed, so the results indicate that the overlap was neither more similar than expected (niche conservatism) nor more divergent than expected (niche evolution) given the distribution of background climate variables.

Table 2. Variable contribution (%) and permutation importance for each variable to Maxent models for northern and southern populations

Variable	Variable Contribution		Permutation Importance	
	lacerata	*subcaudalis*	*lacerata*	*subcaudalis*
Mean Annual Temperature	53.99	21.19	55.30	21.17
Annual Precipitation	23.39	13.35	20.30	28.34
Isothermality	10.10	5.09	11.84	18.83
Precipitation Seasonality	6.67	54.01	6.16	28.94
Max Temperature Warmest Month	5.84	6.37	6.41	2.72
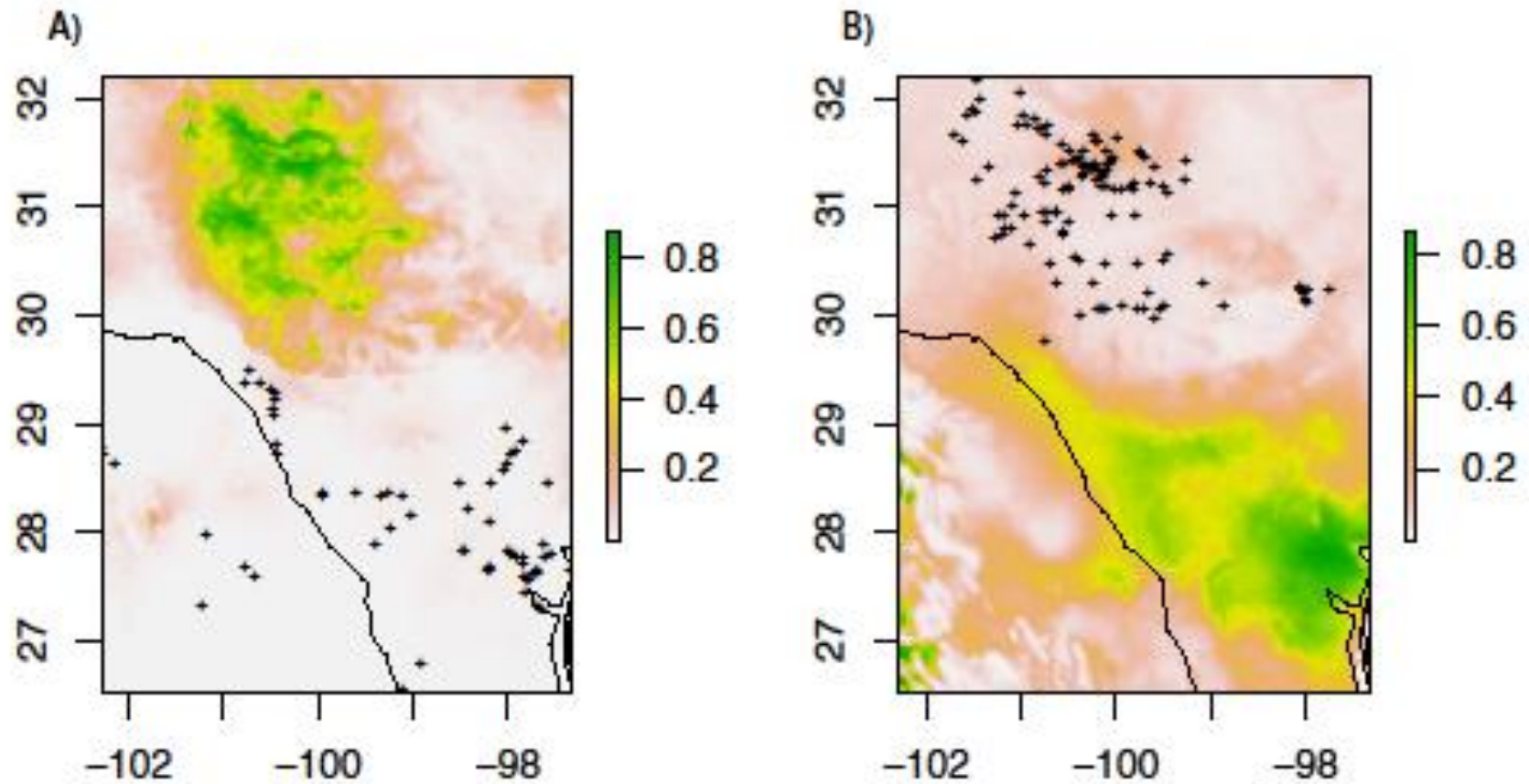
Figure 5.7. Projections for Maxent models into geographic space

The southwestern border between Texas and Mexico is shown as a black segmented line. The color gradient in each panel is identical, ranges from 0 to 0.8, and shows the raw Maxent values (higher values indicate higher suitability for each population). A) Projection of the Maxent model for *Holbrookia lacerata lacerata* shows there is no suitable habitat where *H. l. subcaudalis* occur. *Holbrookia l. subcaudalis* are indicated with the black plus sign. B) Projection of the Maxent model for the *H. l. subcaudalis* shows there is little suitable habitat where *H. l. lacerata* occur. *Holbrookia l. lacerata* are indicated with the black plus sign.
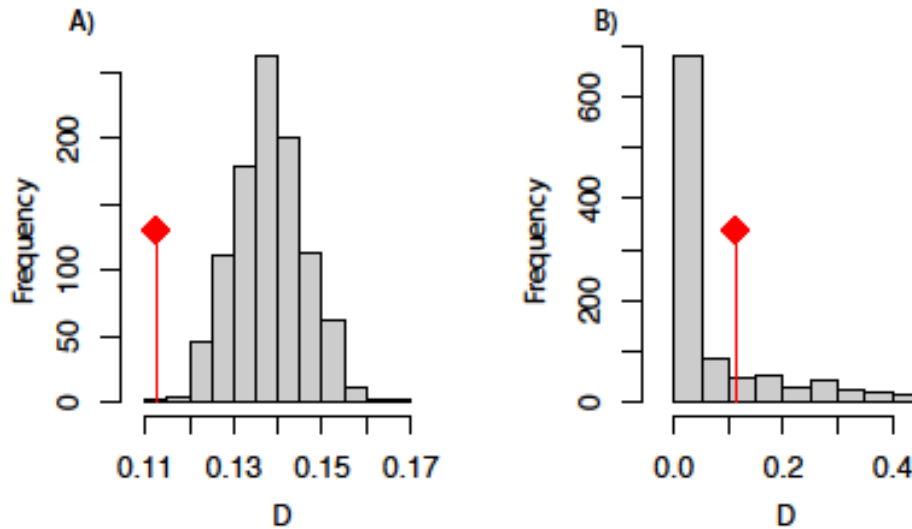
Figure 5.8. Histograms showing D statistic from randomization tests for niche equivalency (A) and background similarity (B)
Red diamond pointer shows D statistic position along x-axis.

Species accounts

Holbrookia lacerata **Cope 1880**
Plateau Spot-tailed Earless Lizard (Fig. 5.9)
Holbrookia maculata lacerata Stejneger 1890
Holbrookia lacerata lacerata Axtell 1956

Lectotype. U. S. National Museum (USNM 10160A); collected by G.W. Marnock in May 1879 within a 3 mile radius circle around Helotes, Bexar County, Texas, USA (29º 35' N; 98º 41' W).

Etymology. *Holbrookia* is derived from the last name of the American zoologist John Edwards Holbrook. *Lacerata* is derived from the latin word *lacerare,* which means to cut, destroy, or mangle. Cope (1880) described the posterior border of the transverse brown bars on the dorsum as serrate or digitate. This feature likely brought about the name *lacerata*.

Distribution: *Holbrookia lacerata* includes all populations north of the Balcones Escarpment in Texas. This distribution extends north to the Colorado River, east to the eastern edge of the Balcones Escarpment and west to the Pecos River and southern edge of the Llano Estacado.

Diagnosis. Morphological description adapted from Axtell (1968). This is a small, earless lizard usually with black spots on the underside of the tail. The average snout-vent length (SVL) is 55.1 mm, paravertebral and dorsolateral body blotches are usually fused forming two rows of transverse bands with the dorsal edges of the bands usually narrowing and extending anteriorly. The dark blotches on the hind legs usually form distinct bands. The sum of all femoral pores is less than 27. Females and some males develop a red-orange pattern on their throat and neck during the breeding season.

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Figure 5.9. Dorsal (top) and ventral (bottom) views of Plateau Spot-tailed Earless Lizard (*Holbrookia lacerata*)
Lectotype specimen collected by G.W. Marnock in May 1879 and housed at Smithsonian (USNM 10160)

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Holbrookia subcaudalis **(Axtell 1956)**
Tamaulipan Spot-tailed Earless Lizard (Fig. 5.10)
Holbrookia lacerata subcaudalis Axtell 1956
Holbrookia subcaudalis Hibbitts et al. 2018 (this study)

Holotype. Texas Natural History Collection, University of Texas (TNHC 20000); collected by Ralph W. Axtell on 6 June 1955 in plowed field 4.8 miles east northeast of Bishop, Nueces County, Texas, USA (27º 36' N; 97º 45' W) at an elevation of 75 feet.

Etymology. The name *subcaudalis* is derived from the latin word *sub* which means under or below and *cauda* which means tail. This refers to the dark spots on the underside of the tail in this species.

Distribution. *Holbrookia subcaudalis* is composed of all populations south of the Balcones Escarpment in Texas and west to the Sierra Madre Oriental in Coahuila, Nuevo Leon, and Tamaulipas, Mexico. They are absent from areas with sandy soils.

Diagnosis. Morphological description adapted from Axtell (1956). This is a small, earless lizard usually with black spots on the underside of the tail. Average SVL is 61 mm. The dorsal blotches form two longitudinal rows on each side of the midline and are usually fewer in number than in *H. lacerata*. The dark blotches on the rear legs are circular in shape and do not form into bands. The sum of all femoral pores is 28 or greater. The female body color is greenish yellow during the breeding season but they do not acquire orange on the throat in either sex.

Discussion

Systematics conclusions

Our genetic BI and ML analyses of the ND2 gene (Fig. 3) demonstrated that *Holbrookia lacerata* encompasses three strongly supported, reciprocally monophyletic lineages, each of which contained individuals from a single geographic region. Our concatenated ND2 and RAG-1 analysis reflected the same geographic lineages, with equally strong levels of support (Fig. 5). Our RAG-1 BI and ML analysis did not however show this same structuring (Fig. 4), which indicates that this gene has not fully sorted by lineage and geography. Despite not finding reciprocally monophyletic lineages by geographic region for RAG-1, there was clear sub-structuring in the phylogeny and haplotype network that suggest that haplotypes were virtually sorted by region. Indeed, we found just one haplotype that was shared between regions, being found in two individuals from Kinney County in the southwest and in two individuals from Nueces County in the southeast (Fig. 4). If the Balcones Escarpment indeed serves as a barrier to gene flow, which is suggested by the ND2 data and morphology, we would expect RAG-1 to sort by geography in the future.

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Figure 5.10. Dorsal (top) and ventral (bottom) views of Tamaulipan Spot-tailed Earless Lizard (*Holbrookia subcaudalis*)
Holotype specimen collected by Ralph W. Axtell on 6 June 1955 and housed at Texas Natural History Collection, The University of Texas at Austin (TNHC 20000).

Morphological conclusions

We found that the two species (formerly subspecies) of spot-tailed earless lizards differed significantly in several aspects of their patterns, leg lengths, and in breeding coloration. A MANCOVA also showed that the morphology of the two species differed significantly in multivariate space. In general, *H. subcaudalis* have longer hind limbs, more leg spots, more side spots, fewer connected dorsal blotches, and no orange throat coloration and the opposite is true in *H. lacerata*. Axtell (1956, 1968) observed similar morphological patterns; additionally, he found that *H. subcaudalis* had a larger maximum SVL and a proportionally longer tail than *H. lacerata*.

Ecological niche conclusions

Similar to our other bodies of evidence, the ecological niche of each species divides along the Balcones Escarpment. The most important variable describing *H. lacerata* localities north of this escarpment was mean annual temperature. South of the Balcones Escarpment precipitation seasonality determined the occurrence of *H. subcaudalis*. The Balcones Escarpment is also notable in that it divides two major ecoregions in Texas, the Edwards Plateau and the Southern Texas Plains (Griffith et al. 2004)

Taxonomic conclusions

The distinct genetic variation evident in *Holbrookia lacerata* corresponds with the subspecies boundaries (*subcaudalis* and *lacerata*) suggested by Axtell (1968), which were based on morphological differences in body size, pattern, and femoral pore number (Axtell 1956, 1968). The ranges of these subspecies do not overlap, and the southern edge of the Balcones Escarpment forms a zone of broken country that is not suitable habitat for either subspecies. The combined evidence from genetics, morphology and distribution is sufficient to consider these subspecies as distinct species (Wiens & Penkrot 2002) with the lizards north of the Balcones Escarpment retaining the name *Holbrookia lacerata*, while those south of the Balcones Escarpment should be called *Holbrookia subcaudalis*. We were not able to obtain tissue samples from any of the Mexican populations for our genetic analyses; however, based on morphological evidence, these Mexican populations should also be considered *Holbrookia subcaudalis* (Axtell 1968).

No obvious distributional barriers occur between the southeast and southwest populations of *Holbrookia subcaudalis* that can explain the phylogenetic structure observed. Additionally, the only obvious morphological feature that separates the two southern populations is maximum body size, with the largest individuals found in the southeast population (TJH, WAR pers. obs.). The intervening habitat is typical south Texas thornscrub and most of the 11 historical specimens found in the 200 km gap between the two populations were collected between 1950 and 1980. We did not find any additional specimens in this gap during our 2015 survey efforts. Invasive grasses, namely Buffelgrass (*Cenchrus ciliaris*) and King Ranch Bluestem (*Bothriochloa ischaemum var. songarica*), and brush encroachment have altered much of south Texas (Archer 1989). Both dense monoculture grasslands and dense south Texas thornscrub are habitats that could negatively affect lizard survival (Scott 1996). These species of grass are widespread in

South Texas, and continue to invade more sites since their introduction in the early 1900s (Gould 1975; Tix 2000). Therefore, they may play a role in the apparent reduction in the distribution of *H. subcaudalis*. Closed canopy brushlands are also inhospitable for *H. subcaudalis*, because there is less open space and sunlight available. These lizards are sit-and-wait predators that need open spaces with high visibility for foraging, as well as predator escape and thermoregulation (Hibbitts & Hibbitts 2015).

The Balcones Escarpment limits many other reptile species, notably *Crotaphytus collaris* (Say) (Eastern Collard Lizard) and *Diadophis punctatus* (Linnaeus) (Ring-necked Snake) whose distributions do not extend south of the Balcones Escarpment in Texas. In addition, the distributions of *Drymarchon melanurus* (Duméril, Bibron & Duméril) (Central American Indigo Snake)*, Gopherus berlandieri* (Agassiz) (Texas Tortoise)*,* and *Sceloporus variabilis* Wiegmann (Rose-bellied Lizard) do not extend north of the Balcones Escarpment (Smith & Buechner 1947; Dixon 2013). Like *H. lacerata* and *H. subcaudalis*, the sister species *Masticophis taeniatus* (Hallowell) (Striped Whipsnake) and *M. schotti* (Baird & Girard) (Schott's Whipsnake) also diverge at the Balcones Escarpment (Camper & Dixon 1994).

Conservation Implications

Spot-tailed Earless Lizards are currently under consideration for federal listing as one species (*Holbrookia lacerata*) with two subspecies (*H. l. lacerata* and *H. l. subcaudalis*). The FWS can make decisions on whether to consider the species as a whole or whether one of the two subspecies is in need of Endangered Species Act protection. The elevation of these two subspecies to species should require the FWS to consider them separately. The two species have threats that are unique to their regions. *Holbrookia lacerata* is currently thought to be absent from most of the eastern part of its range (Axtell 1998); however, recent observations in Blanco County, Texas may indicate that isolated pockets persist. The western distribution of *H. lacerata* is much more robust, with *H. lacerata* observed on most surveys in the region (pers. obs.). The situation with *H. subcaudalis* is much different with only two smaller patches of a once larger distribution currently occupied (Fig. 1). The status of the species in Mexico is unknown. The elevation of these taxa makes *H. lacerata* the first endemic lizard in Texas and further highlights the uniqueness of the Edwards Plateau ecoregion in Texas.

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CHAPTER 6. GENETIC VARIATION WITHIN AND AMONG *HOLBROOKIA LACERATA* AND *HOLBROOKIA SUBCAUDALIS* THE SPOT-TAILED EARLESS LIZARDS OF TEXAS.

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Abstract

We examined genetic relationships among individuals and populations of the species *Holbrookia lacerata*, the Spot-tailed Earless Lizard, using whole mitochondrial genomes and some elements of the nuclear genome. Lizards were collected from south, central, and west Texas. We found significant amounts of genetic structure among populations and evidence of two major reciprocally monophyletic groups of Spot-tailed Earless Lizards in Texas. *Holbrookia lacerata lacerata* occurs on the Edwards Plateau and adjacent regions of West Texas North of the Balcones Escarpment, while *Holbrookia lacerata subcaudalis* occurs in South Texas and adjacent Mexico South of the Balcones Escarpment. These two recognized subspecies correspond to the two clades we discovered. *H. l. lacerata* occupies much of its historic range at sometimes high population densities, while populations of *H. l. subcaudalis* appear to be highly fragmented based on recent observations compared to their historic range.

Introduction

Approaches to species delimitation have changed over time with the emergence of new methodologies to quantify and analyze biodiversity. Currently, DNA sequence data are commonplace to identify structure in lineages, and thus, have naturally been adopted to delimit species based on phylogenetic patterns of gene trees. Recently, the theoretical developments of the multispecies coalescent have provided opportunities to delimit species statistically based on DNA sequence data (Rannala and Yang 2003; Yang and Rannala 2010). Recent controversies have highlighted the limitations of coalescent-based species delimitation and thus the inclusion of additional data types (Sukumaran and Knowles 2017), an approach that has been termed

"integrative taxonomy" (Dayrat 2005; Padial et al. 2010). The inclusion of coalescent-based methods with more traditional taxonomic approaches has been advocated as a fruitful approach for species delimitation (Fujita et al. 2012). For this project, we take an integrative taxonomic approach to investigate the lineage independence of *Holbrookia lacerata lacerata* and *Holbrookia lacerata subcaudalis* by using while mitochondrial genomes, as well as previously published morphological data. The single species previously named the Spot-tailed Earless Lizard (*Holbrookia lacerata*), has two recognized subspecies: *Holbrookia lacerata lacerata* (Northern Spot-tailed Earless Lizard) and *Holbrookia lacerata subcaudalis* (Southern Spot-tailed Earless Lizard) (Axtell 1956, 1958). Axtell (1956, 1958) published extensively on morphological differences between the two subspecies. *H. l. lacerata* is smaller than *H. l. subcaudalis* (mean SVL of 52 and 62 mm, respectively), has fewer femoral pore counts (12.8 vs. 15.7 mm, respectively), and differs in meristic characters such as dorsal and leg blotch shape and orientations (Axtell 1956, 1958). *Holbrookia* contains five currently recognized species and along with the genus *Cophosaurus*, is diagnosed by the lack of a visible auditory meatus. The two genera are part of the "sand lizard" lineage within the family Phrynosomatidae (Weins et al. 2010). Morphologically, one fixed character difference exists among both sexes and all ontogenetic age classes of the two Spot-tailed Earless Lizard subspecies. *H. l. lacerata* can be distinguished by rectangular or square shaped blotches, fused into bands on the hindlimbs while *H. l. subcaudalis* possesses oval or ellipsoid shaped blotches. While not fixed character differences at all life stages or in all individuals, there are also differences in dorsal blotch shape: fused in *H. l. lacerata* and unfused in *H. l. subcaudalis*, femoral pore counts: approximately four fewer in *H. l. lacerata* vs. *H. l. subcaudalis*, and coloration: some female *H. l. lacerata* acquire orange coloration during the breeding season, whereas *H. l. subcaudalis* do not (Axtell 1956). The two subspecies occur in allopatry, despite occupying similar habitats within their respective ranges. *H. l. lacerata* occurs south and west of the Colorado River on the Edwards Plateau, while *H. l. subcaudalis* occurs across most of south Texas and adjacent Mexico (Figure 6.1., Axtell 1956).

Methods

To obtain lizard specimens for genetic and morphological examination, we surveyed the museum collection at the University of Texas at Arlington's Amphibian and Reptile Diversity Research Center and collected new specimens from the wild during 2015-2017. Lizards were located by one of two methods: driving roads and looking for live or road-killed individuals, and by walking areas of suitable habitat while visually searching for individuals. Lizards were captured by hand or with the aid of lizard nooses. Surveys were conducted during daylight hours, as *Holbrookia* are diurnal. Sampling effort was concentrated at the warmest time of the day (1100-1600 hrs.) during the months of March and April. During the warmer months of June-September, survey effort was concentrated in the midmornings (0800-1000 hrs.) and at dusk (1800-2000 hrs.) when lizards were most active. If a lizard was found dead, as was common on roads, we collected skeletal muscle, liver, and integumentary tissues and stored them in RNAlater. Live lizards were transported to the lab, where they were euthanized. Tissue samples were collected from skeletal muscle, liver, heart, blood, and integument and stored in RNAlater. Some previously collected tissues had been stored in ethanol, but that did not influence any laboratory protocols. Additional tissues for this study were obtained from the Biodiversity Research and teaching collections of Texas A&M University and The University of Texas

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(Appendix 6.2). We examined a small number of whole specimens of several species of *Holbrookia* (Appendix 6.1) and counted dorsal blotches, leg blotches, and femoral pores.

We extracted DNA from *Holbrookia* tissues stored in ethanol or RNAlater using a standard phenol-chloroform extraction protocol. DNA extractions were quantified on a Qubit 2.0 fluorometer, using the broad range assay kit (Invitrogen). We sequenced the whole mitochondrial genome for *H. l. lacerata* (n=34), *H. l. subcaudalis* (n=16), *H. maculata* (n=2), *H. propinqua* (n=3) using the mitochondrial sequencing method developed by the laboratory of Dr. Matthew Fujita. Briefly, this protocol first digests the linear nuclear genome using exonucleases, leaving only the circularized mitochondrial genome intact. We amplified the remaining mitochondrial genome using strand-displacement amplification with Φ29 DNA polymerase (NEB). We constructed Illumina libraries from amplified mitochondrial genomes, multiplexing individuals using both inline barcodes and Illumina indices for sequencing on the Illumina HiSeq4000 producing 150bp paired-end reads.

The Illumina data were processed and cleaned using Fastx-Toolkit v 0.0.13 (http://hannonlab.cshl.edu/fastx_toolkit/download.html) and custom Perl scripts. Our adapters included an 8bp "unique molecular identifier" (UMI), which is a random stretch of 8 nucleotides at the beginning of each sequenced read. We removed this UMI before demultiplexing individuals based on their unique 5bp inline barcode. Barcodes and the T-overhang were subsequently removed. We filtered out and discarded low quality reads if 90% of the nucleotides did not have a Phred score ≥20, and the remaining reads were trimmed from both ends if bases had a quality score of ≤20. Cleaned reads were assembled using the CLC genomics genome assembler on CLC work bench 7 (Qiagen), producing a ~16kb contig. The assembled whole mitochondrial genomes were annotated on the Mitos Web server to identify the protein-coding, rRNA, and tRNA genes (Bernt et al. 2013).

For the phylogenetic analysis, we first used PartitionFinder V1.1.1 (Lanfear et al. 2012) to identify the best supported data partitions (based on the Bayesian Information Criterion) of the 13 protein-coding genes, separated by codons, from the mitochondrial genome alignments. We found seven partitions with models including HKY (Hasegawa et al. 1985), TrN (Tamura and Nei 1993), and SYM (Zarkikh 1994), some with invariant sites (+I) and some with site variability (+G). We chose to use the HKY+G model in a Bayesian framework to estimate phylogenetic relationships among mitochondrial genomes rather than more complex models in order to facilitate convergence during the MCMC run as implemented in BEAST v1.8.4 (Drummond et al. 2012). We ran four independent runs, each with 100,000,000 generations, with a burnin of 10,000,000, all ESS values for each parameter was >>200 for all for runs. As each analysis converged to the same posterior we combined all four analyses into a single posterior to estimate the Maximum Clade Credibility (MCC) tree.

We used the time tree from the BEAST analysis as input for species delimitation using the single-threshold model of the General Mixed Yule Coalescent method (GMYC; Fujisawa and Barraclough 2013). This approach finds the transition between within-species coalescence to between-species (multispecies) coalescence and uses this demarcation as a threshold for delimiting species. The two models tested via GMYC in our dataset include whether the samples belong to one species (this includes *lacerata* and the outgroups) or more than one species. We included the outgroups in the GMYC analysis as recommended when focusing on just a few species (in our case, we have one focal taxon, *H. lacerata*; Talavera et al. 2013).

We estimated the maternal effective population sizes of *H. l. lacerata* and *H. l. subcaudalis* using the pairwise distance from whole mitochondrial genomes. This assumes that

each subspecies is panmictic, which may be an appropriate assumption for *H. l. lacerata* (which does not have obvious structure based on the phylogeny), but is likely violated for *H. l. subcaudalis* because of its disjunct (and therefore structured) distribution. To determine the effective population size, we equated the average pairwise distance within each subspecies to the population genetic parameter theta (Piganeau and Eyre-Walker 2009). For mitochondrial genomes, theta = 2 x mu x Ne, where mu is the mutation rate per generation. Based on out time-calibrated estimates of mitochondrial mutation rates (Fujita et al. in prep), we estimate the Phrynosomatid lizard substitution rate to be 0.00347x10-6 substitutions/site/year. Assuming the equality of mutation and substitution rate (and thus assuming neutral evolution), we set mu = 0.00347x10-6 mutation/site/year, or 0.00694 mutations/site/generation assuming a 2 year generation time. Using average pairwise distances of 0.019 for *H. l. lacerata* and 0.014 for *H. l. subcaudalis*, we can solve for Ne.

We used double-digest restriction site associated DNA sequencing (ddRADseq; Peterson et al. 2012 with modifications following Streicher et al. 2014) to collect the genetic data from 71 individuals representing *Holbrookia lacerata lacerata*, *H. l. subcaudalis*, *H. propinqua,* and *H. maculata*. We processed the data using Stacks v1.48 (Catchen et al. 2013), which provides alignments of thousands of orthologous loci across our sampling. RADseq is known to produce datasets with significant missing data, though we restricted our analyses to datasets that were 50-70% complete (missing 30-50% data).

Results

We collected thirty-one (31) individual *H. l. lacerata* and *H. l. subcaudalis* during our surveys (iNaturalist 2017). We also observed another forty-three (43) that could not be collected. These lizards were observed in eleven counties. We also collected eighteen (18) *H. propinqua* from three counties and sixteen (16) *H. maculata* from four counties. All localities for tissues samples used in this study are shown in Figure 1.

The Bayesian phylogenetic analysis of whole mitochondrial genomes yielded a strongly-supported topology where *H. l. lacerata* and *H. l. subcaudalis* are reciprocally monophyletic. Sister to the *lacerata+subcaudlis* clade is a clade that includes *H. maculata* and *H. propinqua*. The long branches separating each of these four species indicates significant genetic divergence that is a signature of prolonged isolation (Figure 6.2). Thus, the genetic data support the recognizing of *H. l. lacerata* and *H. l. subcaudalis* as distinct subspecies.

The GMYC analysis based on the time tree produced from BEAST identified four potential species in our sampling: provisionally, *H. propinqua*, *H. maculata*, *H. lacerata*, and *H. subcaudalis*. In our examinations of whole specimens, we noticed no differences in blotch counts or shapes (Figure 6.3) or femoral pore counts from those reported by Axtell (1956, 1958). These results are consistent with the interpretation that *H. l. lacerata* and *H. l. subcaudalis* are diagnosably distinct (Axtell 1956). When using the estimated mutation rate of 0.00694 mutations/site/generation and pairwise distances estimated from whole mitochondrial genomes, we calculated the maternal effective population size for *H. l. lacerata* to be 1,368,876 individuals and for *H. l. subcaudalis* to be 1,008,645 individuals (Tables 6.1 and 6.2). We used Admixture (2009) to identify the populations within our dataset. Our results show three clear genetic groups belonging to *Holbrookia lacerata lacerata*, *H. l. subcaudalis*, and a combined *H. propinqua*/*H. maculata* (Figure 6.1). Though some individuals look as if they have mixed ancestry, this changes between the different datasets, indicating that it is an artifact of missing data and the

models used in Admixture. Thus, we conclude that there is no evidence of gene flow between any of these species groups.

Stacks provides evidence of genetic diversity within species (theta). We used this value and the equation theta = Ne x 4μ to calculate the effective population size (Ne) based on the nuclear mutation rate. We used a mutation rate 1.6 E-9 (Allison et al. 2017), which is an average across vertebrates. This provided values of Ne of 578,000 for *lacerata* (theta = 0.0037) and 920,000 for *subcaudalis* (theta = 0.0059). These values closely align with mitochondrial effective population sizes estimated from Roelke et al. (2018), with a slight deviation for *lacerata*. Mitochondrially, *lacerata* has an Ne of approximately 1,368,876 individuals, much higher than the nuclear estimated in this study. This small discrepancy can have several explanations, including sex-biased dispersal. For instance, females may not move around to the same extent as males, thus creating population structure in the female population that can elevate mitochondrial Ne. Further studies are needed to explain the difference between mitochondrial and nuclear Ne. Nevertheless, the effective populations of both subspecies are quite high and indicate that there is substantial genetic diversity despite a lack of fine-scale population structure (Fig. 6.4).

Discussion

The GMYC analysis supports the recognition of two species of Spot-tailed Earless Lizard clades. Despite some hesitation that GMYC oversplits (Fujisawa and Barraclough 2013), our results suggest it is possible that *H. l. lacerata* and *H. l. subcaudalis* are distinct species. This method identifies the transition between within-species coalescence and between-species coalescence, and uses that threshold to delimit species. One concern with GMYC is that it uses only one locus, and in this case we used the mitochondrial genome that sorts faster and has a higher mutation rate than nuclear loci. Thus, while support for two species based on mitochondrial DNA is strong, that coalescent signal may be less definitive with nuclear markers. Additional data, including genome-wide SNPs that are now easier to collect for non-model organisms, analyzed using coalescent-based species delimitation tools (BFD*; Leaché et al. 2014) and demographic methods (such as gene flow estimates, e.g. Streicher et al. 2014; Portik et al. in press), can provide deeper insight into the divergence between these two subspecies. As of now, with the evidence provided herein, we do not consider the evidence sufficient to elevate both subspecies of Spot-tailed Earless Lizard to species.

Effective population sizes are important because they affect population and lineage divergence. We wanted to estimate the effective population sizes of the two subspecies in question to begin understanding their demographic history. While we need additional nuclear data to estimate accurate ancestral effective population sizes and potential gene flow between the two subspecies, our estimates of maternal Ne were quite high for both subspecies, perhaps indicating that the Ne of the ancestral populations was also high. If this is the case, it is likely that the populations of both *H. l. lacerata and H. l. subcaudalis* have been stable despite the deep divergence between the two. While we do not have the data to support this, the long internal branches in the mitochondrial tree indicate substantial divergence that could be habitat-mediated. With additional nuclear data, we should be able to distinguish between selection and nonadaptive forces in the divergence between *H. l. lacerata* and *H. l. subcaudalis*.

Despite the divergence between *H. l. lacerata* and *H. l. subcaudalis*, we did not find significant morphological differences beyond those already described by Axtell (1956). While a more comprehensive morphological assessment is required to identify diagnostic differences

between the two subspecies (and perhaps between the distinct mitochondrial genetic clusters within each subspecies), it appears that *H. lacerata* exhibits overall morphological conservatism. These results may support a scenario of divergence in allopatry and the slight morphological differences arose nonadaptively, which could have stemmed from the patchy nature of the lizard's distribution. Axtell (1958) did not believe the slight morphological differences that he used to designate subspecies of *H. lacerata* warranted description of both forms to full species, and thus their utility as additional evidence for species delimitation may not be satisfactory under an integrative taxonomy framework. Cryptic diversity is a difficult and grey area for species delimitation that relies largely on genetic data, though an integrative taxonomy can incorporate ecology, behavioral, and other organismal attributes. Unfortunately, little is known about these for *H. lacerata*, and until additional nuclear sequence data and organismal data become available, it is most prudent to consider the subspecies as a single species.

The taxonomic recognition of two diagnosable clades or evolutionary significant units of Spot-tailed Earless Lizards, currently classified as *H. lacerata*, will have profound effects on the conservation management of the two forms. Currently *H. lacerata* is being treated by the US Fish and Wildlife Service (USFWS) as one species with two subspecies. We believe that based on this paper, *H. l. lacerata* and *H. l. subcaudalis* are discrete entities that warrant consideration for listing by the USFWS under the Endangered Species Act as separate subspecies. Based on this assumption, several conclusions regarding the conservation status of the two subspecies can be made.

The Southern Spot-tailed Earless Lizard appears to have undergone substantial reduction in range wide occupancy, leading to two allopatric populations with no geographic intermediates (iNaturalist 2017). Though it remains locally abundant in a small number (< 5) of discrete localities, it is uncommon nearly everywhere else it can still be found within its range. Many recent (within five years) localities where multiple *H. l. subcaudalis* have been found in close geographic proximity are within or immediately adjacent to active grain agricultural fields (iNaturalist 2017).

The Northern Spot-tailed Earless Lizard occupies much of its historic range on the Edwards Plateau and Eastern West Texas based on recent records (iNaturalist 2017), though it appears to have disappeared from many historic localities on the Eastern Edwards Plateau. In some highly human impacted habitats, most notably fields used for intensive grain agriculture and overgrazed pastures, *H. l. lacerata* can be locally abundant. Sightings of more than ten individual lizards per hour of observer effort are not uncommon (pers. obs. CER). Unlike *H. l. subcaudalis*, *H. l. lacerata* can be found in many localities devoid of grain agriculture.

Both *H. l. lacerata* and *H. l. subcaudalis* can be abundant in agricultural fields, especially where there are significant proportions of bare soil lacking vegetation. We hypothesize that the tilled soil allows lizards to burrow or exploit burrows made by other animals, find abundant food in the form of insects, and the large proportions of bare soil and open canopy allow the lizards to easily thermoregulate, engage in social behavior, and forage. We hypothesize that historically, the abundance and range wide occupancy of available habitat could have been positively mediated by the presence of natural fire and grazing of large herbivores, such as American Bison (*Bison bison*). Disturbances from these two sources would likely have maintained the open canopy habitats and large areas of bare ground required by both subspecies of Spot-tailed Earless Lizards (Hibbitts and Hibbitts 2015). Assuming lizards can find adequate food and suitable refugia to retreat underground, we believe Spot-tailed Earless Lizards can persist at high population levels in highly human altered habitats. Historically, many areas in Texas, especially

Eastern South Texas, have been exposed to intensive agriculture. We expect this pattern to continue and this should allow at least some subpopulations of both subspecies of Spot-tailed Earless Lizard to maintain healthy population sizes.

Acknowledgements

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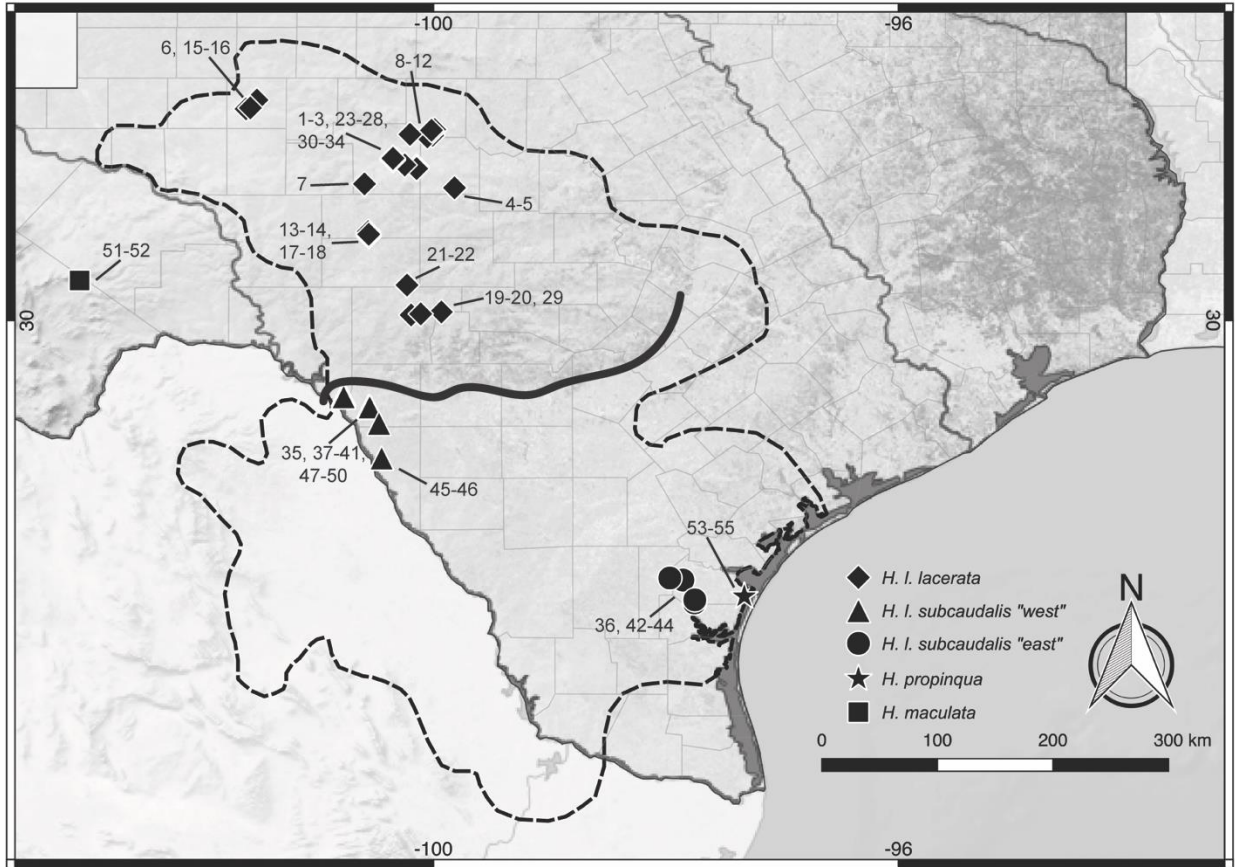
Figure 6.1. Sampling map of the focal taxa (*H. l. lacerata* and *H. l. subcaudalis*) and outgroup taxa (*H. maculata* and *H. propinqua*)

The sampling ranges for the nominal taxa are representative of their current distributions. The historical distribution of *H. lacerata* is represented by the dotted line, while the Balcones Fault/Escarpment, the natural biogeographic barrier between the two subspecies, is represented by the solid black line.
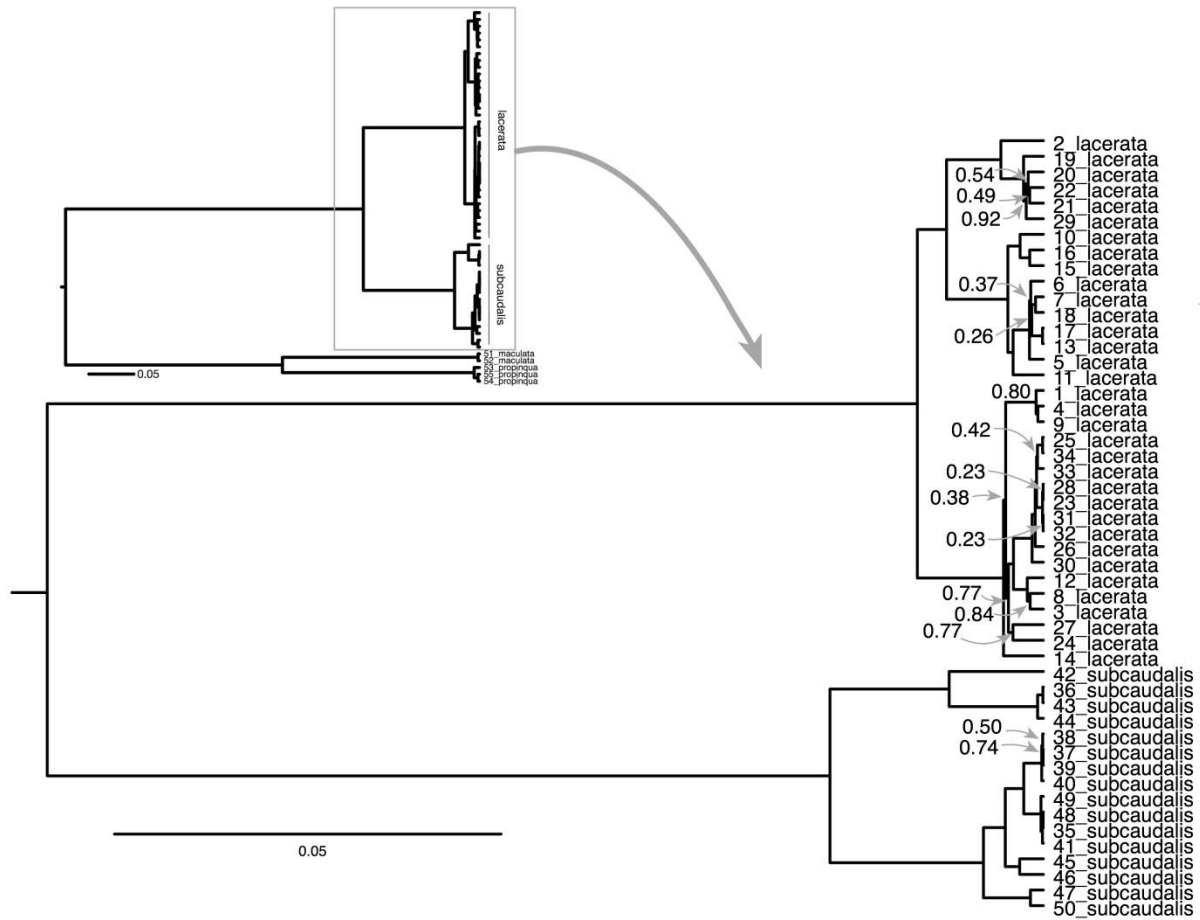
Figure 6.2. Bayesian phylogeny of whole mitochondrial genomes from *H. l. lacerata* and *H. l. subcaudalis*, with *H. maculata* and *H. propinqua* as outgroup taxa
Numerical values are Bayesian posterior probabilities; all other nodes represent values > 0.95. Scale bar represents percent genetic divergence.

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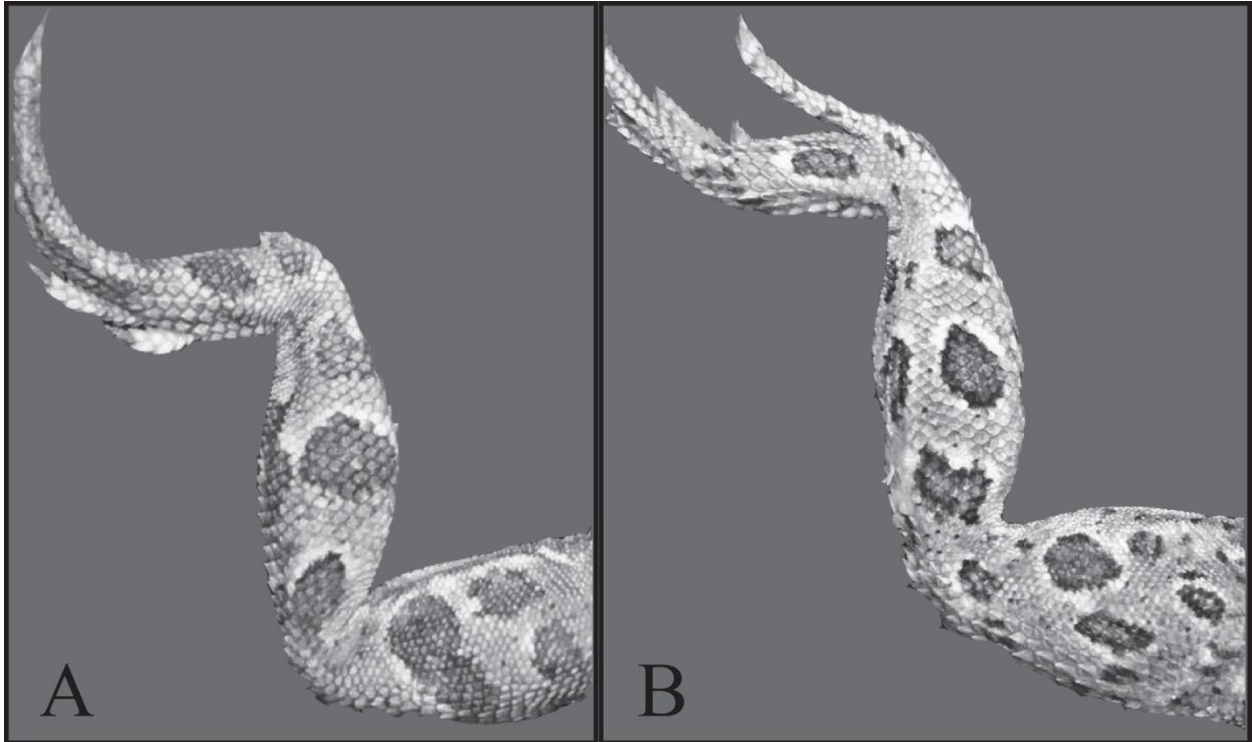
Figure 6.3. Hindlimb blotches of A) *Holbrookia l. lacerata* (UTA R 63333) and B) *H. l. subcaudalis* (UTA R 63303)

In *H. l. lacerata*, most blotches are oblong and fused into bands. In *H. l. subcaudalis*, blotches are ellipsoid.
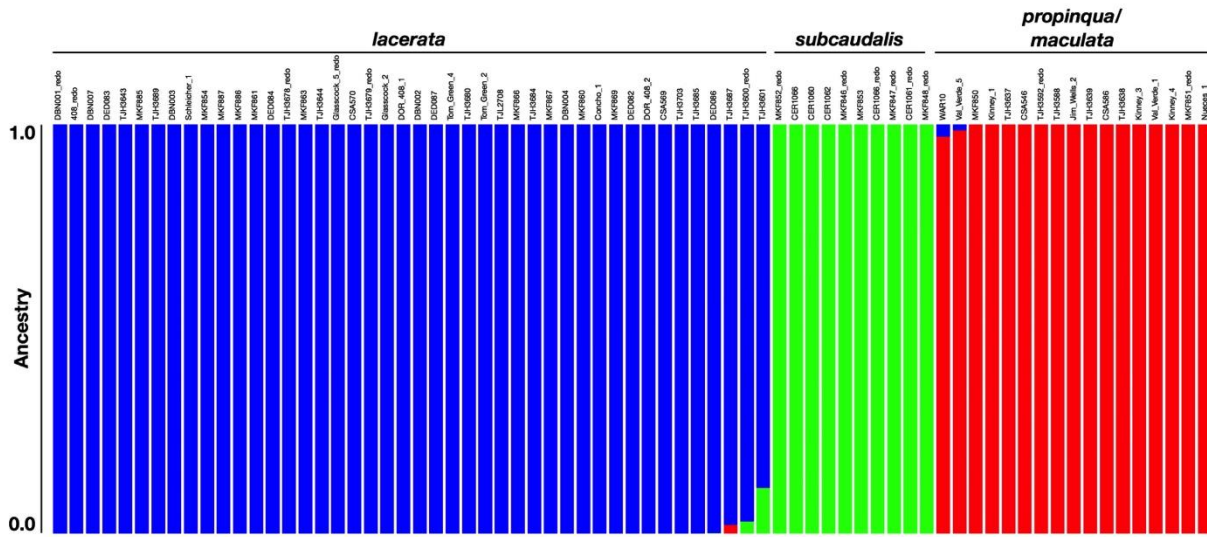
Figure 6.4. Structure plot showing potential gene flow among individuals of *H. l. lacerata* and *H. l. subcaudalis*

Group	Mean Within Group Distance	Ne (million)
North Unit	0.00847224	0.610391930835735
SW Unit	0.00123773	0.089173631123919
SE Unit	0.00648091	0.466924351585014

Table 6.1. Effective population sizes of *H. lacerata* based population unit, calculated from nuclear genome based RadSeq data

population	N	r70 pi	Ne (r70)
subcaudalis	17	0.0059	921875
subcaudalis_High	12	0.0058	906250
subcaudalis_Low	2	0.0051	796875
lacerata	44	0.0037	578125
lacerata_High	19	0.004	625000
lacerata_Low	3	0.0044	687500

Table 6.2. Effective population sizes of *H. l. lacerata* and *H. l. subcaudalis* based on habitat classes, calculated from nuclear genome based RadSeq data

Appendix 6.1 – Morphological specimens examined

Holbrookia elegans	UTA R 63329
Holbrookia lacerata lacerata	UTA R 32627
Holbrookia lacerata lacerata	UTA R 32641
Holbrookia lacerata lacerata	UTA R 32642
Holbrookia lacerata lacerata	UTA R 38588
Holbrookia lacerata lacerata	UTA R 44012
Holbrookia lacerata lacerata	UTA R 44013
Holbrookia lacerata lacerata	UTA R 55025
Holbrookia lacerata lacerata	UTA R 61067
Holbrookia lacerata lacerata	UTA R 63302
Holbrookia lacerata lacerata	UTA R 63323
Holbrookia lacerata lacerata	UTA R 63324
Holbrookia lacerata lacerata	UTA R 63327
Holbrookia lacerata lacerata	UTA R 63330
Holbrookia lacerata lacerata	UTA R 63331
Holbrookia lacerata lacerata	UTA R 63332
Holbrookia lacerata lacerata	UTA R 63333
Holbrookia lacerata lacerata	UTA R 63334
Holbrookia lacerata lacerata	UTA R 63335
Holbrookia lacerata lacerata	UTA R 63336
Holbrookia lacerata lacerata	UTA R 63337
Holbrookia lacerata lacerata	UTA R 63338
Holbrookia lacerata lacerata	UTA R 63339
Holbrookia lacerata lacerata	UTA R 63340
Holbrookia lacerata subcaudalis	UTA R 57756
Holbrookia lacerata subcaudalis	UTA R 63303
Holbrookia maculata	UTA R 63325
Holbrookia maculata	UTA R 63326
Holbrookia propinqua	CER 200
Holbrookia propinqua	CER 201
Holbrookia propinqua	CER 202
Holbrookia propinqua	CER 937
Holbrookia propinqua	CER 938
Holbrookia propinqua	CER 939
Holbrookia propinqua	CER 940
Holbrookia propinqua	UTA R 37822

Appendix 6.2 – Molecular samples

Field Number	Species	Phylogeny Number
DED082	*Holbrookia lacerata lacerata*	1_lacerata
DED083	*Holbrookia lacerata lacerata*	2_lacerata
DED084	*Holbrookia lacerata lacerata*	3_lacerata
DED086	*Holbrookia lacerata lacerata*	4_lacerata
DED087	*Holbrookia lacerata lacerata*	5_lacerata
Glasscock 5	*Holbrookia lacerata lacerata*	6_lacerata
MKF854	*Holbrookia lacerata lacerata*	7_lacerata
MKF861	*Holbrookia lacerata lacerata*	8_lacerata
MKF862	*Holbrookia lacerata lacerata*	9_lacerata
Runnels 1	*Holbrookia lacerata lacerata*	10_lacerata
Runnels 2	*Holbrookia lacerata lacerata*	11_lacerata
Runnels 3	*Holbrookia lacerata lacerata*	12_lacerata
Schleicher 1	*Holbrookia lacerata lacerata*	13_lacerata
Schleicher 2	*Holbrookia lacerata lacerata*	14_lacerata
TJH3600	*Holbrookia lacerata lacerata*	15_lacerata
TJH3601	*Holbrookia lacerata lacerata*	16_lacerata
TJH3619	*Holbrookia lacerata lacerata*	17_lacerata
TJH3620	*Holbrookia lacerata lacerata*	18_lacerata
TJH3643	*Holbrookia lacerata lacerata*	19_lacerata
TJH3644	*Holbrookia lacerata lacerata*	20_lacerata
TJH3678	*Holbrookia lacerata lacerata*	21_lacerata
TJH3679	*Holbrookia lacerata lacerata*	22_lacerata
TJH3685	*Holbrookia lacerata lacerata*	23_lacerata
TJH3686	*Holbrookia lacerata lacerata*	24_lacerata
TJH3687	*Holbrookia lacerata lacerata*	25_lacerata
TJH3689	*Holbrookia lacerata lacerata*	27_lacerata
TJH3703	*Holbrookia lacerata lacerata*	28_lacerata
TJL2738	*Holbrookia lacerata lacerata*	29_lacerata
Tom Green 2	*Holbrookia lacerata lacerata*	30_lacerata
Tom Green 4	*Holbrookia lacerata lacerata*	31_lacerata
Tom Green 6	*Holbrookia lacerata lacerata*	32_lacerata
Tom Green 7	*Holbrookia lacerata lacerata*	33_lacerata
Tom Green 8	*Holbrookia lacerata lacerata*	34_lacerata
CSA546	*Holbrookia lacerata subcaudalis*	35_subcaudalis
Jim Wells 2	*Holbrookia lacerata subcaudalis*	36_subcaudalis
Kinney 1	*Holbrookia lacerata subcaudalis*	37_subcaudalis
Kinney 2	*Holbrookia lacerata subcaudalis*	38_subcaudalis
Kinney 3	*Holbrookia lacerata subcaudalis*	39_subcaudalis
Kinney 4	*Holbrookia lacerata subcaudalis*	40_subcaudalis

TJH3588	*Holbrookia lacerata subcaudalis*	41_subcaudalis
TJH3626	*Holbrookia lacerata subcaudalis*	42_subcaudalis
TJH3637	*Holbrookia lacerata subcaudalis*	43_subcaudalis
TJH3638	*Holbrookia lacerata subcaudalis*	44_subcaudalis
TJH3640	*Holbrookia lacerata subcaudalis*	45_subcaudalis
TJH3641	*Holbrookia lacerata subcaudalis*	46_subcaudalis
Val Verde 2	*Holbrookia lacerata subcaudalis*	47_subcaudalis
Val Verde 3	*Holbrookia lacerata subcaudalis*	48_subcaudalis
Val Verde 4	*Holbrookia lacerata subcaudalis*	49_subcaudalis
Val Verde 5	*Holbrookia lacerata subcaudalis*	50_subcaudalis
MKF844	*Holbrookia maculata*	51_maculata
MKF848	*Holbrookia maculata*	52_maculata
CER1065	*Holbrookia propinqua*	53_propinqua
CER1066	*Holbrookia propinqua*	54_propinqua
CER1067	*Holbrookia propinqua*	55_propinqua

CHAPTER 7. HABITAT MODEL

Introduction

The goal of this study was to provide an evaluation of the geographic extent of potentially suitable habitat within the historic distribution of *Holbrookia lacerata* in Texas (Fig. 1). Thus, the project's scope did not include an evaluation of potential habitat in northeastern Mexico. As species distribution models (SDMs) evolved, we used them to direct biological surveys to portions of the species' historic range with the highest modeled probability of encountering an individual. We compiled a database of 302 occurrence points of *H. lacerata* historic specimen locations and results of recent surveys. Biologists at TAMU surveyed potentially suitable habitat for *H. lacerata* using walking and driving surveys. Surveys were conducted from April through September to capture the known seasonal activity period of the lizard. Where access to private lands was granted, we conducted walking surveys with 2–5 observers in areas of potentially suitable habitat. Where access to private land was not granted, we conducted driving surveys with 2–3 observers through potentially suitable habitats. Surveys were also conducted in potentially non-suitable habitat. We grouped specimen records for both subspecies together to assess the largest possible study area, though the final model was comprised of three separate runs, 1 for each unit. Using historic presence-only *H. lacerata* specimen location data and a suite of physiographic variables as predictor variables, we used Maxent to create a 30-arc-second resolution (1 km^2 at equator) modeled relative probability of occurrence map. Potential sample bias caused by clusters of *H. lacerata* localities near roadways was reduced by using a bias grid.

Evolution of the model

As the larger research program for *H. lacerata* evolved, several versions of the habitat model were done in response to changing needs of the project. In this report, we provide an explanation for the final model version. However, we include a written narrative of the evolution of the model. A short summary of the habitat model creation timeline follows.

Dec 2014–Feb 2015

We completed a preliminarily assessment of habitat that may potentially support *H. lacerata* using a species distribution model that incorporated various physiogeographic features thought to support suitable habitat for the target species.

March–May 2015

The preliminary species distribution model was corrected for sampling bias and spatial autocorrelation.

Mid-2015

We finalized an amended scope of work and amended our contract at the request of the Texas Comptroller of Public Accounts. This additional work incorporated stakeholder feedback by including the new task of identifying core conservation areas and population connectivity by refining the modeling approach. As of September–November 2015, work done to date included identifying and prioritizing focal areas based on habitat modeling and core-area fragmentation analyses indicating core habitats, suitable habitat, along with connection habitat.

December 2015–March 2016

Through a second contract amendment requested by the Texas Comptroller of Public Accounts, new personnel were brought into the project to provide additional support and expertise in habitat modeling. This included Cody Schank and Paul Holloway, two graduate students of Dr. Jennifer Miller of The University of Texas at Austin Department of Geography & the Environment. This support permitted greater scope and certainty in habitat modeling methodology. A modeling framework was developed to incorporate an improved sampling bias

correction, additional environmental covariates, methods for determining habitat classes, quantification of associated uncertainty, and use of samples collected during 2015 field surveys for *H. lacerata*. A third-party technical review of the new methods was conducted by Nathan Allan of the Austin, Texas Ecological Services Field Office of the U.S. Fish & Wildlife Service and David Smith of the Leetown Science Center of the U.S. Geological Survey.

March–May 2016

The new population-specific models were constructed for three *H. lacerata* study units ("North", "Southeast", and "Southwest") and were presented to the stakeholder group. The new models represented an updated analysis of *H. lacerata* relative probability of occurrence. The justification for separating the dataset into the three regions rather than a single dataset comprising the entire distribution of the species is that preliminary results of mitochondrial DNA analyses suggested that the Texas distribution of *H. lacerata* were grouped into three distinct units. In addition, we were inclined to treat them as distinct study units because FWS suggested this may be the approach they would use in their assessments.

December 2016

An external review of the new model was completed in late December by Dr. Matthew L. Niemiller, Dr. Mark A. Davis, and Dr. Michael J. Dreslik, who are modeling experts at the Prairie Research Institute of the Illinois Natural History Survey at the University of Illinois Urbana-Champaign.

January 2017

The final model we completed and present in this report was updated considering the external review and stakeholder meeting inputs including the 2016 survey data and additional environmental layers.

Modeling approach

The approach used to complete the final habitat model is explained here.

Framework

We used Maximum entropy (MaxEnt) as the statistical method to model the species-environment relationships. MaxEnt has been used extensively across the SDM discipline, and has been found to generate accurate predictions of species' distributions using presence-only data (Elith and Graham 2009). Other models do exist for presence-only data, but either they are not well validated because of less rigorous examination (e.g. Maxlike, Point Process Models) or have been determined to be inferior to MaxEnt (e.g. GARP, ENFA – Elith and Graham 2009).

Response data

To account for uncertainties in data collection methods, opportunistic sightings, and poor accuracy of observation localities, we only used survey data collected 2008–2016. These include data obtained during the 2015–2016 sampling season as well as data obtained by Axtell and Duran during 2008–2009 sampling, and can be considered the most reliable observations, which should lead to less uncertainty in the model output. Additionally, by only using current data, current landscape classification variables (e.g., urban, row crop, etc.) are more valid to use as covariates.

Bias data

We controlled for sampling bias by incorporating a bias grid (Stolar and Nielsen, 2014). If unaccounted for, any sampling bias violates the assumption of independency in the response data and could strongly influence results. A bias grid can be considered the equivalent of a sampling probability surface, where the cell values reflect sampling effort and provide a weight to the

pseudo-absence data used in modelling (Fourcade et al. 2014). The bias grid created for this modeling effort was based on distance to roads. In this bias grid, areas within approximately 300 meters of a road were assigned a value of 100, while all other areas were given a value of 1. Related to the response above about bias grids, there was no filtering of data performed before fitting the models (unless this refers to splitting the data into three subareas). An 80/20 (training/testing) split was used. There were 91 presence points in the Northern unit, 40 in the Southeast, and 75 in the Southwest.

Spatial autocorrelation

There are methods that can either 'neutralize' spatial autocorrelation in the data (SAR, CAR, GLMM, spatial eigenvector, etc.) and harness additional information in the spatial auto-correlated data (autologistic, the method in Crase et al. 2011). However, to our knowledge, they all require at least presence/absence data. We only had presence data available to us and therefore did not use approaches to address spatial autocorrelation.

Multicollinearity among predictor variables

We did not investigate multicollinearity because climate variables were not used. Additionally, multicollinearity interferes in determining the precise effect of each predictor, but does not affect the overall fit of the model or produce poor predictions. Because the primary goal of our modeling efforts was spatial prediction modeling (we did not perform ecological response modelling or projective distribution modeling), we did not anticipate results would be influenced by multicollinearity.

Environmental variables

Environmental variables included pedologic (sand percent in top 5 cm of soil), compound topographic index (CTI; includes slope and flow accumulation; Gessler et al. 1995), and land cover (EMS land cover; TPWD, 2014) features. EMS land cover classes were then reclassified into seven broader categories: barren, grass, forest, row crops, shrub, urban, and wet. A circular focal window was used to count the amount of each broad land cover type within 90 meters of each pixel (values range from 0 to 29). We also used the median Enhanced Vegetation Index (EVI) for 2015 downloaded from Landsat time series in Google Earth Engine. EVI was used instead of the more commonly used proxy for vegetation productivity Normalized Difference Vegetation Index (NDVI) because it is more responsive to canopy structure variations (and should parse out the influence of sparse vegetation on *H. lacerata* localities). We used only linear and quadratic terms in the algorithm settings to avoid overfitting the model. Climatic variables were not used due to coarse resolution and results of population surveys, which suggested that landcover would be the most important potential predictor.

Determination of habitat categories

Predicted surfaces from the model output were divided into three categories: not suitable, low suitability, and high suitability. The minimum training presence (MTP) and maximum training sensitivity plus specificity (MTSS) were used as thresholds to determine these classes. MTP represents the lowest probability associated with a record, while MTSS represents the modeled habitat that captures all survey locations and balances "presence" & "pseudo-absence". MTP would have a lower modeled probability of occurrence "cutoff" than MTSS. The MTSS+MTP habitat classification is based on methods for converting continuous probabilities into presence/absence (Jiménez-Valverde and Lobo, 2007; Blanco-Pastor et al., 2013). Using the defined intervals of Table 7.1, interval delineations were made using the species distribution model probability output (Figures 7.1, 7.2; Table 7.2).

Quantification of uncertainty

We replicated our training / testing split, model fit, and habitat classification 100 times. These maps were then stacked in an ensemble fashion, and the mode of the stack at each pixel was used as the final habitat classification.

Evaluation metrics

For model evaluation, we used the common SDM assessment metric Area Under the Curve (AUC). Model evaluation was performed during each model iteration and summarized across the ensemble. Further, density and prevalence estimates calculated from the field work will allow for improvement of habitat classification tiers (thresholding).

External review

An external review of the final model was completed in late December 2016. The habitat model was further updated using the latest survey data, including all 2016 survey data. The model also included two new environmental layers: CTI (compound topological index) and the 2016 Polaris Soil Data (to fill SSURGO soil data gaps). This model was presented in January 2017 at a stakeholder meeting organized by the Texas Comptroller of Public Accounts in Austin, Texas. Comments from the stakeholder group included a question as to why a species-level distributional model (at least for the Texas populations) was not developed. Our group discussed and presented justifications for the data sets used to create the model but agreed that revised models could/should be run to address these concerns (e.g., the species-wide model will likely be required by USFWS for their analysis). Funding for these revisions, however, is not within the current scope of the contract.

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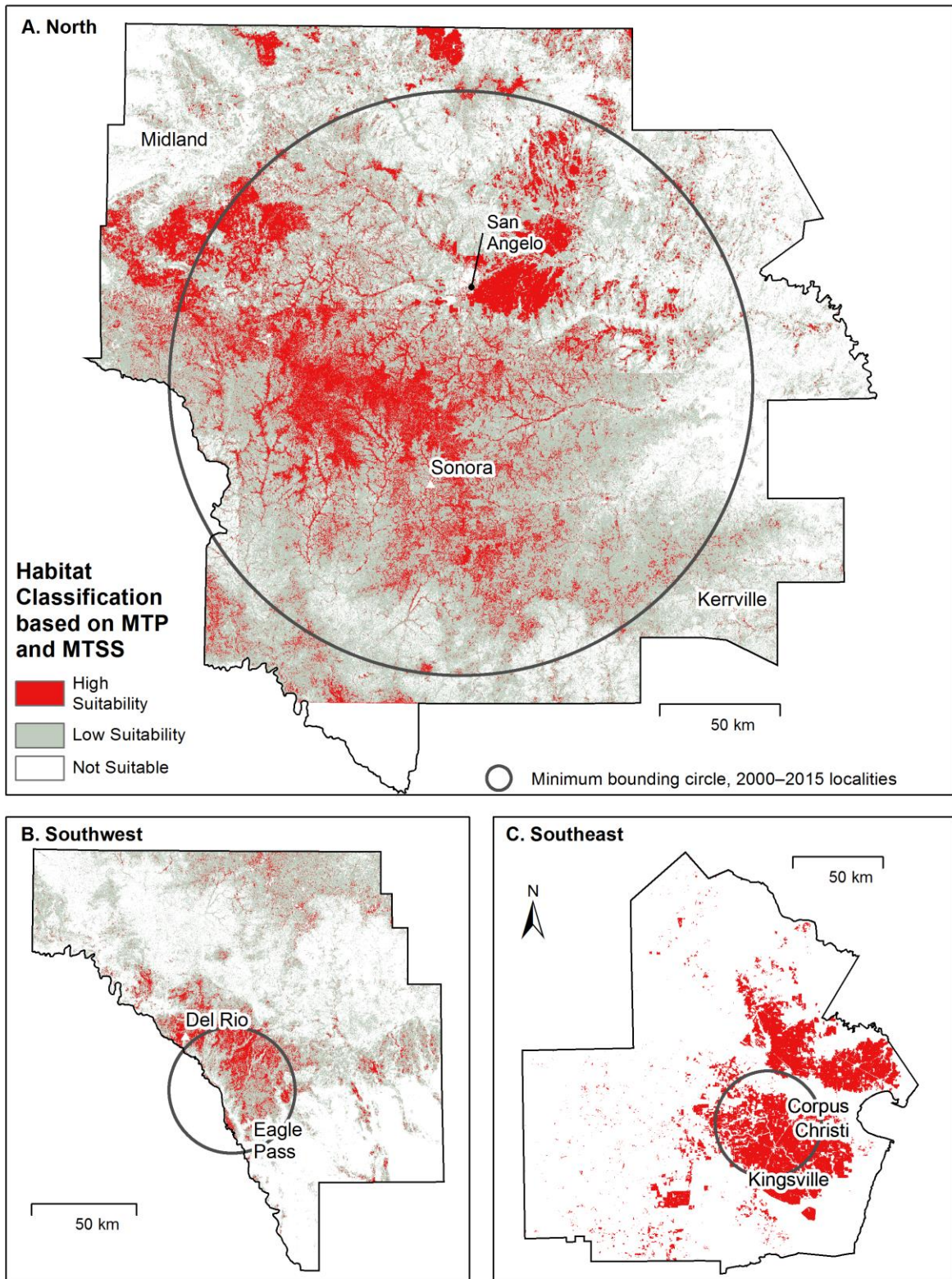
Figure 7.1. Habitat classifications for Spot-tailed Earless Lizard
Based on minimum training presence and maximum training sensitivity plus specificity.

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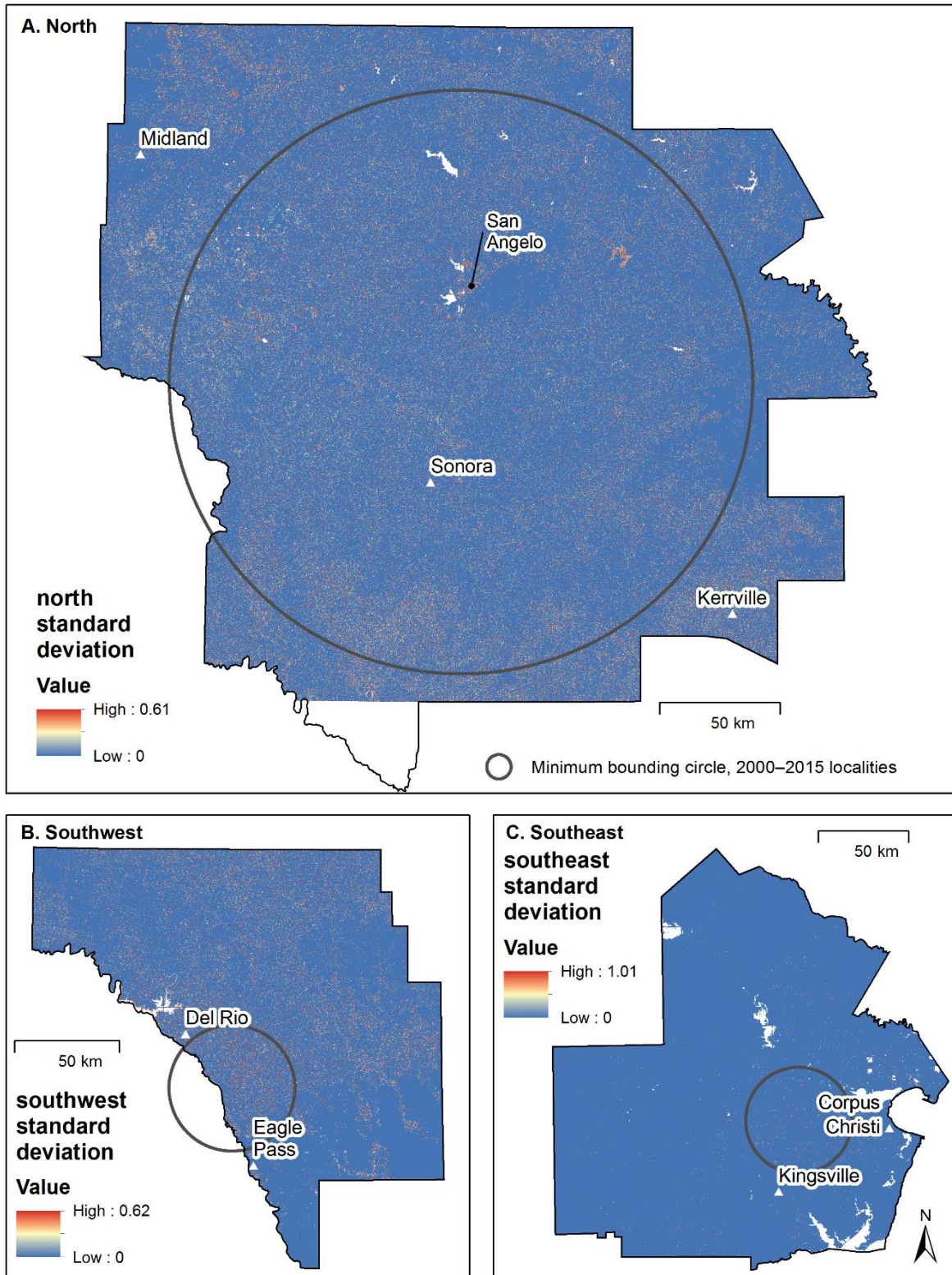
Figure 7.2. Standard deviation of habitat classifications for Spot-tailed Earless Lizard Based on minimum training presence and maximum training sensitivity plus specificity.

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Table 7.1. Habitat model thresholding results for three study units
Mean Minimum Training Presence (MTP) and Maximum Training Sensitivity + Specificity (MTSS) for Each Study Unit.

	Southwest	**Southeast**	**North**
MTSS	0.1346	0.2181	0.1491
MTP	0.0149	0.1653	0.0267

Table 7.2. Areal measurements (km²) for each classification type for each Study Unit
Area calculations were derived by projecting SDM results from geographic coordinate system North American 1983 to an Albers Equal Area Conical projection.

	Habitat Classification	**Method MTSS+MTP (km²)**
Southeast Unit	High Suitability	24,494
	Low Suitability	0
	Not Suitable	122,141
Southwest Unit	High Suitability	2,000
	Low Suitability	11,015
	Not Suitable	18,302
North Unit	High Suitability	127,709
	Low Suitability	399,154
	Not Suitable	236,907

CHAPTER 8. CONNECTIVITY ASSESSMENT: CONSERVATION ASSESSMENT AND POPULATION CONNECTIVITY

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We initially intended to perform a conservation assessment for *Holbrookia lacerata* that identifies key conservation areas based on field surveys and habitat modeling, important habitat for known populations, and habitat connectivity/expansion zones. The purpose of this task was to understand any potential corridors and pathways needed for genetic transfer. This information could be used by managers to guide where conservation action, surveys, and funding would be most effectively implemented. Hence, understanding where extant versus historical populations exist and connectivity within and among current populations to inform management plans was the objective.

Primary analyses for this task involved creation of study unit-specific models and designation of habitat tiers. The framework of these steps was completed as part of the habitat modeling described in Chapter 7. However, the evolution of the project, dictated by stakeholders and incoming data, changed some of the end goals of the project. We did not complete the connectivity assessment because three separate study units were defined (Figure 7.1); because the three separate study units are geographically separated by considerable distance, connectivity between the study units is not possible. The only apparent overlap (between North and Southwest study units) is caused by minimum bounding circles around the geographic distribution of individuals, which are separated by the Balcones Escarpment (Figure 1.1). In addition, genetic analyses by TAMU and The University of Texas at Arlington (Chapters 5, 6) strongly suggest that individuals in the North versus Southeast and Southwest study units are separate species. Additional work incorporating differences in morphology and habitat assessments were included in the work led by Texas A&M (Chapter 5) further supporting the recognition of *Holbrookia lacerata* in the north (N unit) and *Holbrookia subcaudalis* in the south (SW and SE units).

CHAPTER 9. ANTHROPOGENIC LANDSCAPE ALTERATION 2008–2012

Summary

This chapter presents a novel approach for evaluating land-use changes caused by energy development and other anthropogenic activities. We illustrate this technique by assessing the landscape footprint of energy development in the Eagle Ford Shale Play and Permian Basin of Texas, which saw rapid expansion in drilling during 2008–2012. We compare changes in land-use from oil and gas infrastructure construction during this time period with that of wind energy development in West Texas, urbanization in Central Texas, and extensive agricultural areas. Previous studies often use land-use proxies when comparing the footprint of energy infrastructure (e.g., 1-km^2 gridded well density or proposed wind project footprints) with other anthropogenic land-change. This chapter presents an improved technique because it compares high-resolution datasets of agricultural activity and urbanization with mapped—not surrogate—land-change from oil and gas and wind power infrastructure using high-resolution (1-m) aerial imagery. We found that changes in land-use caused by anthropogenic factors affected 1.06% (3,456 km^2) of the ~324,000 km^2 study area. Oil and gas development (well pads and pipelines) was ~48% of total changes in land-use (but did not account for access roads), changes in agriculture caused ~26%, and urbanization was ~24%. Construction of wind turbine pads and high voltage power transmission lines was less important (~1%). We illustrate this approach for a single species (i.e., Spot-tailed Earless Lizard, *Holbrookia lacerata*) in Texas. This study is part of an ongoing, multi-year research program generating science to inform the federal Endangered Species Act listing decision for *H. lacerata*. Additionally, this technique can facilitate effective management of a variety of biotic resources in other rapidly developing environments globally by identifying what anthropogenic activities are most important and where land-change is most intense so that on-the-ground conservation strategies can be implemented where they are needed most.

Introduction

Improvements in directional well drilling and hydraulic fracturing contributed to a rapid increase in oil and gas production from unconventional shale plays since 2008 in Texas and other hydrocarbon-producing states (Fig. 9.1; Allred et al. 2015). As a result, construction of oil and gas well pads, access roads, pipelines, and other surface infrastructure has increased and caused important changes in land-use (Abrahams et al. 2015; Brand et al. 2014; Drohan et al. 2012; Kiviat 2013). For example, oil and gas infrastructure constructed 2000–2012 in North America is estimated to have removed ~30,000 km^2 of vegetation from the continent's ecosystems (Allred et al. 2015). Texas led U.S. hydrocarbon production, accounting for ~44% of total U.S. crude oil output in November, 2016 (U.S. Energy Information Administration, EIA, 2017a). In addition to oil and gas development, the expansion of wind power generation across the U.S. has converted land for turbines, access roads, and high voltage power transmission lines (Kuvlesky et al. 2007; McDonald et al. 2009). For example, Texas now produces more wind energy than any other state in the U.S. (Shrimali et al. 2015). Texas also has five of the eleven fastest-growing cities in the United States and forecasts of population growth from 2020–2070 estimate a 70% increase in

future residents (Census 2016). Thus, it is important to understand the relative contribution to changes in land-use from these various anthropogenic activities.

Recent research has investigated how surface infrastructure associated with urbanization, roads, agriculture, wind power and oil and gas development has altered the landscape across North America—and has identified Texas as a critical area for continued research (Alig et al. 2004; Allred et al. 2015; Drohan et al. 2012; Entrekin et al. 2015; Jones et al. 2015; Liu et al. 2013; McGuire et al. 2016; Milt et al. 2016; Moran et al. 2017; Pierre et al. 2015; Pierre et al. 2017; Theobald et al. 2012; Wiggering 2014). "Energy sprawl"—the rapid expansion of the footprint of oil, gas, wind, and other industries—has been identified as an important anthropogenic process with implications for biotic resource management (Copeland et al. 2011; McDonald et al. 2009; Trainor et al. 2016). However, how land-use change caused by energy sprawl compared to that resulting from urbanization and agriculture is an important, but poorly understood question that is the focus of this study.

We demonstrate a novel approach to map and evaluate anthropogenic changes in land-use using the Spot-tailed Earless Lizard (*Holbrookia lacerata*) as an example of how results of this technique can be used to inform biotic resource management. This land-change mapping approach improves upon previous studies because it directly maps changes in land-use from oil and gas and wind power development, whereas many previous studies use lower-resolution proxies for land-change from energy sprawl (e.g., well density or proposed project footprints; Trainor et al. 2016; Copeland et al. 2009).

Historically, *H. lacerata* occupied much of Central and South Texas (Fig. 9.1), in open native grasslands with gentle slopes and soils with low sand content (Axtell 1956, Duran et al. 2011). Anthropogenic activities in the lizard's historic range includes the Eagle Ford and the Permian Basin hydrocarbon provinces, in addition to areas that were converted to agriculture or experienced extensive urbanization. After 1970, however, the species' populations appear to have declined sharply (Axtell 1968; Axtell 1998; Duran and Axtell 2010; Duran et al. 2011). Hypotheses for this decline in *H. lacerata* reflect trends affecting reptiles globally (Gibbons et al. 2000), including: (1) agricultural practices and pesticide use (Axtell 1998; Chapin et al. 2000; Duran et al. 2011; Flanders et al. 2006; Fulbright et al. 2013; Sparling et al. 2010), (2) introduced invasive species, (3) road construction (direct vehicle contact and habitat fragmentations; Andrews et al. 2008), (4) urbanization (McKinney 2008; Wolf et al. 2013), and (5) energy development. The decline is not necessarily tied to energy expansion, but is potentially exacerbated by urbanization and invasive vegetation and fauna, which may follow land-use changes associated with drilling. Thus, in light of the species' historic decline in population, *H. lacerata* awaits a decision by U.S. Fish and Wildlife Service (FWS) for possible protections under the Endangered Species Act.

This study presents a novel approach for comparing 2008–2012 land-use changes caused by a suite of anthropogenic activities within the historic range of *H. lacerata* in Texas. We selected this time period because it corresponds with the initial rapid expansion of oil and gas well drilling associated with directional drilling and hydraulic fracturing (Fig. 9.1) and enables the comparison of high-resolution mapping of "energy sprawl" with other major anthropogenic land uses. Specifically, this study addressed the following questions:

1. What changes in land-use occurred within the study area?
2. What are the implications of such land-use change for management of biotic resources?

This study is part of a larger research program developing science to inform management actions for *H. lacerata*. Thus, we illustrate this land-mapping approach for one widely-distributed species in Texas; however, the technique can be used to assess a variety of anthropogenic activities in other environments globally to inform a biotic resource management for a variety of species.

Material and methods

Study area

We mapped changes in land-use within the historic range of *H. lacerata* (Fig. 9.1; Axtell 1998), a study area which included ~47% of the land area of Texas (324,300 km^2). Annual precipitation ranged from 260–1,250 mm (west to east, respectively; PRISM 2016). Primary land cover included shrub/scrub (53%), herbaceous (13%), cultivated crops (9%), hay/pasture (7%), and evergreen forest (5%; Jin et al. 2013). The study area included Austin and San Antonio—two of the ten most rapidly urbanizing areas in the country (2010–2015; U.S. Census 2016)—in addition to the cities of Del Rio, Laredo, Midland, and San Angelo. Extensive wind power generation (~4,700 wind turbines; FAA 2016) occurs between Midland and San Angelo and east of Laredo (see Fig. 5 of Fischlein et al. 2013). Two important and rapidly expanding oil and gas producing regions, the Permian Basin and Eagle Ford Shale Play are also included in the study area (Fig. 9.1).

Mapping anthropogenic changes in land-use

Changes in land-use from unconventional shale oil and gas well pad development, hydrocarbon pipeline construction, wind power turbine and electrical transmission line installation were mapped using aerial imagery interpretation. Importantly, publicly available land-use databases, such as the National Land Cover Dataset (NLCD; Jin et al. 2013; USGS 2014), which were used to map agricultural activity and urbanization do not expressly map oil and gas pads and pipelines, wind generation turbine pads, and high voltage power transmission lines. Thus, we created these datasets following the workflow of Pierre et al. (2015, 2017), which is summarized in Fig. 9.2. The objective of our study is similar to that of Pierre et al. (2017); however, we evaluated a larger geographic area and also included wind energy, urbanization, and agriculture in our land-use change analysis.

We compiled datasets of anthropogenic activities within the study area during the 2008–2012 time period, which corresponded with the initial period of rapid development of unconventional oil and gas drilling in the Permian Basin and Eagle Ford Shale Play (Fig. 9.1). However, if a dataset did not fall exactly within this range, we used the closest year available. We defined "land-use change" as landscape converted from pre-existing vegetation to another use. While these changes in land-use may not necessarily have occurred simultaneously over time, we assume that cumulative effects were considered during the study period.

We used a semi-automatic approach to identify and quantify land cover changes attributed to high voltage power transmission lines, oil and gas development, and wind turbine pads, incorporating unsupervised image classification (ISO unsupervised classification in ArcGIS 10.2) and supervised image classification (maximum likelihood classification in ArcGIS 10.2; eCrews-Meyer et al. 2004). We compared our mapping of energy-related changes in land-use to existing databases of agricultural activity and urbanization (i.e., NLCD).

Oil and gas drilling pad infrastructure was mapped by first downloading all oil and gas wells permitted in the study area March 2001–December 2012 (i.e., production, injection, horizontal, vertical, abandoned, wildcat, etc.; IHS, 2016). We chose 2001 as our starting point to

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be sure that changes in land-use caused by the 50 wells permitted before 2008 that were classified as producing from the Eagle Ford Shale Play were mapped. We did not consider wells coded as recompleted, re-drilled, or deepened, which we assumed to be a reworked existing well. We used the permit date, not the date drilling began (i.e., spud date) because changes in land-use occur before a well is drilled when the well pad is constructed (e.g., Pierre et al. 2015). It is permissible to include permitted but undrilled wells because changes in land-use would not be mapped.

The footprint of oil and gas well pads was mapped using 1-m resolution National Agriculture Imagery Program (USDA, 2014) aerial images acquired in 2012. This imagery was the most recent available at start of the study. Iso cluster unsupervised image classification was executed in ArcGIS (version 10.2) to create 10 landscape classes (following the methods of Pierre et al. 2015). Classified imagery was resampled to 10-m resolution and converted to "bare-earth" polygons. We "cleaned" our mapped changes in land-use by removing areas less than 300 m^2, which we found—based on visual inspection of aerial imagery in active oil and gas areas— were generally too small to be associated with anthropogenic processes of interest. We assigned wells to mapped changes in land-use that occurred within 90-m of a bare earth polygon to represent land-use change from drilling pads. A 90-m distance was selected through an iterative manual process which optimized the area of resulting well pads based on of visual inspection of aerial imagery. We visually inspected areas of land-use change that were greater than three standard deviations of the mean and accepted only changes in land-use clearly associated with drilling activity.

Efforts have been made to map land-change resulting from well pad access road construction in unconventional oil and gas plays and wind power generation regions (e.g., Allred et al. 2015; Moran et al. 2015; Jordaan et al. 2017 manuscript and Supplementary Table 2). However, we did not include access roads in our analysis because a database containing private oilfield road locations—which is necessary to constrain the spatial extent of our alteration mapping—was not available. While the land-change mapping of Johnson et al. (2010) specifically reported alteration from (1) well pad construction and (2) other infrastructure (e.g., access roads, pipelines, water impoundments, we are not aware of a study that specifically presents land-use change resulting only from the construction of access roads. Reasons for this may be because semi-automated mapping approaches (e.g., Allred et al. 2015; Jordaan et al 2017; Pierre et al. 2017) have difficulty separating access roads and well pads from one contiguous bare earth polygon. Also, because access roads are constructed by the field operator and are not generally publicly-funded, they are not typically included in publicly available road databases (e.g., state highway databases or TIGER; Census 2017). Without mapped access road right-of-ways, the semi-automated mapping approaches we used could over-attribute land-use changes from access roads. Second, manually digitizing landscape alteration from aerial imagery by a GIS analyst (e.g., Johnson et al. 2010; Drohan et al. 2012) is not feasible for large regional studies such as this (324,300 km^2). Thus, this study does not map land-change from well pad access roads, which remains an important topic for future research.

We extracted the footprint of oil and gas pipelines, wind power turbine pads, and high-voltage electrical lines using the well pad mapping approach. We acquired hydrocarbon pipeline locations from the Railroad Commission of Texas (RRC 2014) and identified changes in land-use along pipelines using our imagery classification approach. Jordaan et al. (2009) estimated pipeline construction edge effects using a 100-m buffer; however, we found that a buffer of this width overestimated changes in land-use. Thus, we visually inspected aerial

imagery and applied a 30-m buffer to RRC pipelines using an iterative manual approach so that mapped bare earth was only associated with pipeline construction (following the approach of Pierre et al 2017).

We downloaded a database of wind turbine locations, which was based upon a Federal Aviation Administration (FAA) dataset (FWS 2015). Wind turbine pads were mapped in the same way as oil and gas well pads, except we used locations permitted by the FAA. Based on visual inspection of aerial imagery, we found 90-m to be a suitable distance to optimize classification of bare earth polygons resulting from wind turbine pad construction. For wind power transmission lines, we acquired mapping of the 2011 approved Competitive Renewable Energy Zone (CREZ) high voltage (345 kV) routes from Texas Parks and Wildlife Department (Wicker 2014). Because as-built plans are not publicly available, we manually digitized final line locations in Google Earth using the 2011 approved routes as a guide, resulting in ~4,800 km of lines. We applied a 30-m buffer to the edited high voltage transmission routes and extracted land-use change resulting from the construction of power lines, after the methods of Pierre et al (2017).

Changes in agricultural activity and urbanization were assessed using the NNLCD 2006 to 2011 from-to change index, which was the closest temporally available to our 2008–2012 study period. Classes 81 and 82 (pasture/hay and cultivated crops, respectively) were used to map changes in agriculture. Urban expansion was mapped using classes 21–31 (Devloped, Open Space–High Intensity and Barrend Land; Jin et al. 2013; USGS 2014). Finally, we compared changes in land-use caused by each anthropogenic activity during 2008–2012 (i.e., oil and gas, agriculture, urbanization, wind power).

Implications for biotic resource management

This study generated a dataset to support conservation efforts in Texas, and is also part an ongoing, multi-year research program filling data gaps to improve our understanding of *H. lacerata*. We guided the development of this research program by organizing our hypotheses regarding what factors *H. lacerata* needs for its survival in a structured framework. We constructed an influence diagram for *H. lacerata* using expert elicitation of knowledge pertaining to this and other phrynosomatine lizards of LaDuc, Ryberg, and Hibbitts (e.g., Failing et al. 2007, Usalito 2007, Kuhnert et al. 2010). An influence diagram is a form of a Bayesian belief network, which presents causal relationships of factors affecting a species (e.g., Marcot et al. 2001, O'Laughlin 2005) in terms of a suite of landscape-scale factors, called "sources". These affect habitat quality, and can be mapped and classified with a quantifiable metric, such as the land-change mapping of this study. We used the influence diagram to identify data gaps in the current understanding of *H. lacerata* to inform the development of additional scientific studies to elucidate how each source may ultimately affect the species. The proposed research program was then presented to FWS and interested stakeholders (i.e., state agencies, private industry, etc.) for feedback as part of a public, transparent stakeholder-driven process (e.g., Gulley 2015), facilitated by the Texas Comptroller of Public Accounts to assure that the right science was being developed to guide efforts to conserve the species and inform the federal Endangered Species Act listing decision.

Results

What anthropogenic activities were most important contributors to land-use change?

We found that construction of oil and gas infrastructure (i.e., well pads and pipelines) was the most important process during 2008–2012, which corresponds with the initial rapid development of the Eagle Ford Shale Play and drilling in the Permian Basin (Figs. 9.3, 9.4;

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Table 9.1; GIS files available at: http://hdl.handle.net/2152/62642). Land-use change from all anthropogenic factors affected 3,456 km^2, or 1.06% of the study area. Oil and gas pads caused 48% of total land-use change at 1,664 km^2, or 0.51% of the study area. As expected, changes in land-use for oil and gas activities was focused in the Permian Basin and throughout the Eagle Ford Shale Play towards the Gulf of Mexico. Between these two broad zones of energy alteration, the installation of hydrocarbon pipelines caused long, linear changes in land-use compared to the many point changes in land use caused by well pads (Fig. 9.4B). Changes in agricultural land use (907 km^2) and urbanization (837 km^2) were each responsible for around a quarter of the total changes in land-use each. Agricultural changes in land-use were focused along an approximately 400 km long and 100 km wide swath to the south of San Antonio and east of Austin. Interestingly, this zone of changes in agricultural land-use is adjacent to major areas of urbanization in and around the San Antonio and metropolitan areas. Changes in land-use from wind turbine pads and high voltage power transmission lines were relatively minor at 48 km^2, or 1% of total changes in land-use. The spatial distribution of the wind power land-use change footprint was limited to a few areas near the Permian Basin and in along three major transmission lines leading from generating zones in the west to San Antonio, Austin, and Dallas in the east. We also identified, for all anthropogenic activities, relatively unchanged areas of the landscape between the cities San Angelo, Austin, San Antonio, and Del Rio (Fig. 9.4A). Contiguous parcels of relatively unchanged landscape also remained east of Laredo, San Antonio, and Austin (Fig. 9.4B).

Implications for biotic resource management

The influence diagram for the *H. lacerata* (Fig. 9.5) revealed gaps in our understanding of the species' biological needs and how sources may affect habitat quality, habitat quantity, and food availability. Using this information, along with stakeholders, we designed additional ongoing research studies (Table 9.2), which included: (1) guiding the locations of ongoing surveys by biologists to assess the species' current range and how different land-use types may affect habitat quality and population size, (2) improving the understanding of ecological needs of species, such as evaluating gut-contents to determine what food sources are most important, (3) describing current habitat conditions and demographics and also explaining past and ongoing changes in abundance and distribution, (4) assessing morphology and genetic structure of populations to understand taxonomic boundaries, and (5) forecasting the species' response to probable future scenarios of environmental conditions—such as climate change—and conservation efforts. These include estimating future changes in land-use from forecasted urbanization and Eagle Ford Shale Play and Permian Basin drilling patterns. When complete in 1–2 years, the results of this research program will be used by the U.S. Fish and Wildlife Serve to inform their federal listing decision and by biologists to guide successful conservation strategies for the species.

Discussion

We developed an approach to map and quantify the relative contributions of different anthropogenic activities to changes in land-use, illustrating this technique for *H. lacerata* as a focal species in Texas. We found that 2008–2012 oil and gas infrastructure construction during this time period caused approximately the same area of land-use change (1,664 km^2) as both agriculture and urbanization combined (1,744 km^2; Fig. 9.3; Table 9.1) and that effects of wind power generation and transmission infrastructure construction was relatively minor (48 km^2 total land-use change). The high-resolution land-use dataset generated by this is important because oil

and gas and wind power are not directly included in current land cover databases such as the NLCD.

While drilling of unconventional shale oil and gas plays has slowed in recent years, energy resource development in Texas—as with many shale plays in North America—is expected to continue when oil prices rebound (West Texas Intermediate Crude was ~$53/barrel in March 2017, falling from >$100/barrel 2 years before; EIA 2015; EIA 2017b). For example, only 10% of expected wells have been drilled in the Eagle Ford Shale Play (Gong et al. 2013; Scanlon et al. 2014), and a detailed economic outlook model supports an expected future up-tick in Eagle Ford drilling under higher oil price scenarios (Ikonnikova et al. 2017; Wolaver et al. accepted). However, future drilling trends will also be influenced by a suite of socio-economic factors (e.g., future energy type demands, environmental protections, etc.) and actual drilling in the Eagle Ford and other plays may ultimately differ from forecasts of Ikonnikova et al. (2017).

Urbanization was also an important anthropogenic process, amounting to approximately one quarter of total changes in land-use. The urbanization trend is expected to continue in Texas, particularly between Dallas, Austin, San Antonio, and Houston (Census 2016). Our results also reveal different spatio-temporal trends in land-use change depending on the cause. For example, urbanization is focused around existing metropolitan areas (Fig. 9.4D), while the spatial pattern of oil and gas well pads and wind turbine pads is much more widely-distributed in many smaller areas (Figs. 9.4B, 9.4E). We also found that spatial patterns of oil and gas pipelines and electricity transmission lines were linear, resulting in the bisection of pre-existing land-cover (Figs. 9.4B, 9.4E).

Comparison of this approach with other land-use change mapping techniques

We applied a novel anthropogenic land-change mapping technique, which facilitates a high-resolution comparison of energy sprawl with other land uses. This approach mapped land-change resulting from well pads, pipelines, wind turbine pads, and transmission lines so that as-built footprints, instead of proxy datasets (e.g., well density per unit area or planned infrastructure) can be compared to other non-energy-related anthropogenic changes in land-use, such as croplands and growing cities. In contrast to our approach, Trainor et al. (2016) assessed the amount of land required to produce a unit energy (km^2/TWhr; termed "land use efficiency") from drilled energy resources (oil and gas), mined energy resources (coal, uranium), biofuel biomass, and renewable electricity (wind, solar, hydropower, geothermal, bioelectricity). Changes in land-use from drilled energy resources using were estimated using EIA 2012–2040 cumulative production forecasts, which were based on state well spacing requirements—not actual mapping of land-use. Land-use for wind power projects was evaluated using project plans presented in environmental impact statements (EIS), environmental assessments (EA), and other publicly available sources—not more correctly using as-built project maps. Of the ~55,000 km^2 they identified as recent energy sprawl, 7% was from oil and natural gas and 3% from renewables (including wind power and other sources, such as biofuels). For estimating continental-scale changes in land-use from energy sprawl, the approach of Trainor et al. is satisfactory; however, the higher-resolution approach presented by this study may be better suited for land-change mapping of individual unconventional resource plays.

Proxy datasets for land-change mapping were also used by Kiesecker et al. (2011) and Fargione et al. (2012). These studies used an "oil and gas fields" dataset compiled by Copeland et al. (2009) based on the same oil and gas wells dataset of the present study (i.e., IHS). However, resolution was degraded by creating a binary 1-km^2 grid classified as (1) "producing" if any oil and gas well was present in a particular grid cell or (2) "non-producing" if a cell lacked

wells. As a result, this technique could potentially over-estimate land-change if few wells are present in a given cell. In contrast, we assessed changes in land-use on a well-by-well basis, which was more spatially-explicit. If desired, the land-change dataset we present here could easily be converted to a 1-km^2 well presence/non-presence grid. But, in many cases, it may be more desirable to assess potential overlap of activities with a species' habitats using the actual well or turbine pad footprints. In this aspect, the approach we present markedly improves upon that of Copeland et al. (2009), Kiesecker et al. (2011), and Fargione et al. (2012).

Another study that evaluated the footprint of energy sprawl is Copeland et al. (2011), who forecasted the spatial distribution of a suite of energy sources (i.e., hydrocarbons, uranium, wind, solar, geothermal) in Western North America. The hydrocarbon footprint was mapped using oil and gas lease boundaries from the Bureau of Land Management National Integrated Lands System database. However, using lease boundaries would aggregate actual well pad and infrastructure locations. While this approach may be satisfactory for regional-scale studies in the Western U.S. where drilling primarily occurs on public lands, most development in Texas and other states in the Eastern U.S. occurs on private land, where mapping the footprint of drilling activity requires using locations of individual wells (typically IHS or state sources). Copeland et al. (2011) also mapped potential wind power areas using U.S. and Canadian industry trade association data and U.S. Department of Energy footprint estimates per megawatt, instead of the actual FAA-permitted turbine locations we used in this study. Copeland et al. (2011) found that wind power had highest "land use intensity" of energy types assessed. In contrast, using area of land-change, we found the wind power footprint in Texas to be quite small compared to that of oil and gas development.

Implications for biotic resource management

An important product of this study is a foundation dataset for conservation efforts in Texas. We developed these maps as part of larger research program for *H. lacerata* with the long-term goal of improving our understanding of what the species needs for its survival, what may threaten its long-term viability, and what management actions may result in its conservation (Table 9.2). Our research program results will be used by FWS to inform its listing decision whether the species warrants protection under the Endangered Species Act by developing a Species Status Assessment (SSA) for *H. lacerata* (SSA; FWS 2016, Earl et al. 2017; Smith et al. 2018). Specifically, the SSA framework—and our research program objectives—contributes towards improving our understanding of: (1) what the species needs, (2) what is the current condition of the species, and (3) what is the species' likely future condition (Fig. 9.5; Table 9.2). Thus, an SSA organizes all the biological information needed for all Endangered Species Act decisions for a particular species, which may include the listing decision, grant allocation, permitting, and recovery planning by supporting resource managers to design effective conservation strategies. To this end, our results may also inform pre-listing conservation efforts as part of a Candidate Conservation Agreement with Assurances (CCAA)—or a Habitat Conservation Plan (HCP), should the species ultimately receive federal protection under the Endangered Species Act.

Essential to designing and implementing effective on-the-ground conservation strategies for *H. lacerata* and other species is understanding how anthropogenic land use may actually affect a particular species. Rapid anthropogenic infrastructure development leading to habitat loss and degradation is considered the primary driver of wildlife extinctions in terrestrial ecosystems (Forman et al. 2003; Juffe-Bignoli et al. 2014; Torres et al. 2016). To this end, assessment of changes in land-use from anthropogenic development and estimation of its effects

on wildlife habitats and populations have been identified as conservation priorities of global importance (Brooks et al. 2002; Fahrig 2003; Fischer and Lindenmayer 2007; Hansen et al. 2013; Mildrexler et al. 2007). However, some reptiles favor an altered landscape, and we suspect *H. lacerata* to be an early successional species that may favor certain types of anthropogenic changes in land-use (Axtell 1968), except where urbanization has converted native vegetation. Because Texas has five of the eleven fastest-growing cities in the United States (forecasted 2020–2070 population growth of 70%; Census 2016), land-change—particularly of agricultural lands—is expected to continue around expanding urban areas within the historic range *H. lacerata* (Theobald et al. 2012, Anderson et al. 2014).

Towards improving our understanding of how anthropogenic changes in land-use actually may affect the focal species (*H. lacerata*), we used the land-change dataset generated by this study to direct biologists to specific locations affected and unaffected by different land-change processes across a variety of land-use types within the species' historic range. Biologists are currently conducting field-based surveys to improve our understanding of the causal relationships between changes and land-use and the species' behavior. The surveys seek to understand how different vegetation types (e.g., grassland or crops) and activities (e.g., oil and gas operations) may affect the species. When they are available in 1–2 years, findings from ongoing biological surveys should provide insight as to (1) whether a particular anthropogenic activity has positive, negative, or neutral effects on the species, (2) estimate population density, and (3) elucidate how long-term viability may be affected by land-change processes. This information could be used to facilitate an evaluation of conservation actions similar to those of Paukert et al. (2011), who assessed how anthropogenic activities may affect aquatic biota and Fargione et al. (2012), who cited wind power turbines in low-quality habitats with pre-existing land-change to minimize impacts to undisturbed temperate grasslands. While the habitat assessment and land alteration approach presented here is focused on *H. lacerata* in Texas, this methodology should be directly applicable to the conservation and management communities addressing species awaiting listing decisions by FWS or undergoing recovery actions.

Future research directions

In addition to ongoing biological surveys of *H. lacerata* elucidating how changes in land-use may affect the species, several other studies of the larger research program (Table 2) are also in progress. For example, we have assessed cumulative anthropogenic land-use changes for the same study area as the present work through 2014 (Pierre et al. 2018, accepted). That study included additional evaluations of the relative contribution of edge effects to overall land-change resulting from (1) point changes in land-use (i.e., well pads and wind turbine pads), (2) linear changes in land-use (i.e., pipelines and high voltage power transmission lines), and (3) expansion of existing large, contiguous areas of land-change (i.e., urban areas). We have also used an economic outlook model to forecast future Eagle Ford Shale Play drilling locations and vegetation conversion (Wolaver et al., accepted). A similar study is also being completed to forecast Permian Basin drilling trends. The goal of both works is to understand where within these unconventional hydrocarbon provinces new wells are likely to be drilled to understand what habitats for *H. lacerata* and other species in the study area may be affected.

Assumptions and limitations of this approach

This study generated a valuable dataset of land-use change in Texas; however, we acknowledge several limitations of the approach. For example, agriculture caused approximately one quarter of observed changes in land-use, but the remotely sensed land cover data we used to assess agricultural activity (i.e., NLCD) may have some shortcomings. For instance, farms

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fallow during the early part of the study may not necessarily indicate an expansion in agricultural acreage if farming were later resumed under more favorable commodity prices. In addition, an independent assessment of Texas agricultural land use trends using a suite of state and federal financial and crop production data (Anderson et al. 2014) revealed agricultural lands in Texas declined by ~400 km^2 through conversion to other uses—primarily urbanization—from 2007 to 2012. Thus, improving techniques to evaluate remote sensing of agricultural land conversion remains an important topic for future research. As with all anthropogenic changes in land-use mapped by this study, removal of pre-existing vegetation by transmission line construction may be short-term, with re-growth occurring under towers within a matter of years. However, as aridity increases towards the western portion of the study area, it is reasonable to expect vegetation recruitment to take longer—and possibly return as early successional or invasive plant species instead of pre-existing native vegetation. Despite possible changes in plant communities following anthropogenic activities, the approach mapped the type of land-use that was present at the time National Agricultural Imagery Program (NAIP) aerial imagery was acquired. Another important limitation is the time lag between NAIP aerial imagery acquisition and when it becomes available to the public. The sensors may be flown anytime between spring and early fall, to correspond with the growing season; however, acquisition for a particular state is not synoptic and it may take weeks or months to complete one state—particularly large states such as Texas. Then, inspection of imagery by NAIP analysts can last months and final aerial imagery may not be available for almost a year after the acquisition date for all states. To this end, satellite-derived imagery, may in some cases be preferable to NAIP (e.g., Allred et al. 2015; Jordaan et al. 2017). Finally, reporting of infrastructure locations may vary. For example, oil and gas well location data may not be readily available, in a difficult to use format for GIS analyses, or proprietary (such as the IHS database used in this study). Furthermore, locations of infrastructure may not be accurately reported. We have noted in our visual inspection of aerial imagery that well locations may be incorrectly placed by 10s or meters, particularly for wells drilled before global positioning system (GPS) surveying became widely used. This necessitated a "cleaning" of mapped land-change using procedures described in the Methods. Oil and gas pipelines and high-voltage power transmission lines may be even more poorly located, with the precise location intentionally degraded due to security concerns. Despite these limitations, the land-use change dataset generated using the approach is valuable, particularly at the regional scale of this study.

Conclusions

This study presents a new method for evaluation of changes in land-use from energy development and other anthropogenic activities. We illustrate the approach in a portion of Texas that saw rapid growth of energy development in the Eagle Ford Shale Play and Permian Basin (particularly during 2008–2012), expanding wind energy development in West Texas, urbanization in Central Texas, and regionally extensive agriculture (Fig. 9.1). Our illustration of this approach found that oil and gas well pad and pipeline construction between 2008 and 2012 contributed approximately half of the changes in land-use in the study area. Agricultural land-use change and urbanization each contributed to around one quarter of the changes in land-use we mapped; however, fallow fields returning to production may overestimate land-change. The construction of wind power generation turbines and associated power transmission lines contributed to around 1% of changes in land-use. Relatively continuous unchanged land parcels remained between San Angelo, Austin, San Antonio, and Del Rio, as well as parcels south of Austin and San Antonio. The results of this land-use change study are being integrated into a

larger, multi-year research project developing science for *H. lacerata*, which FWS will use to develop an SSA for the species and inform their decision whether the species warrants protection under the endangered species act. While we illustrate this approach for a single focal species (i.e., *Holbrookia lacerata*) in Texas, this novel approach can be used to compare changes in land-use for a suite of anthropogenic activities in other environments globally, with implications for management for a variety of biotic resources.
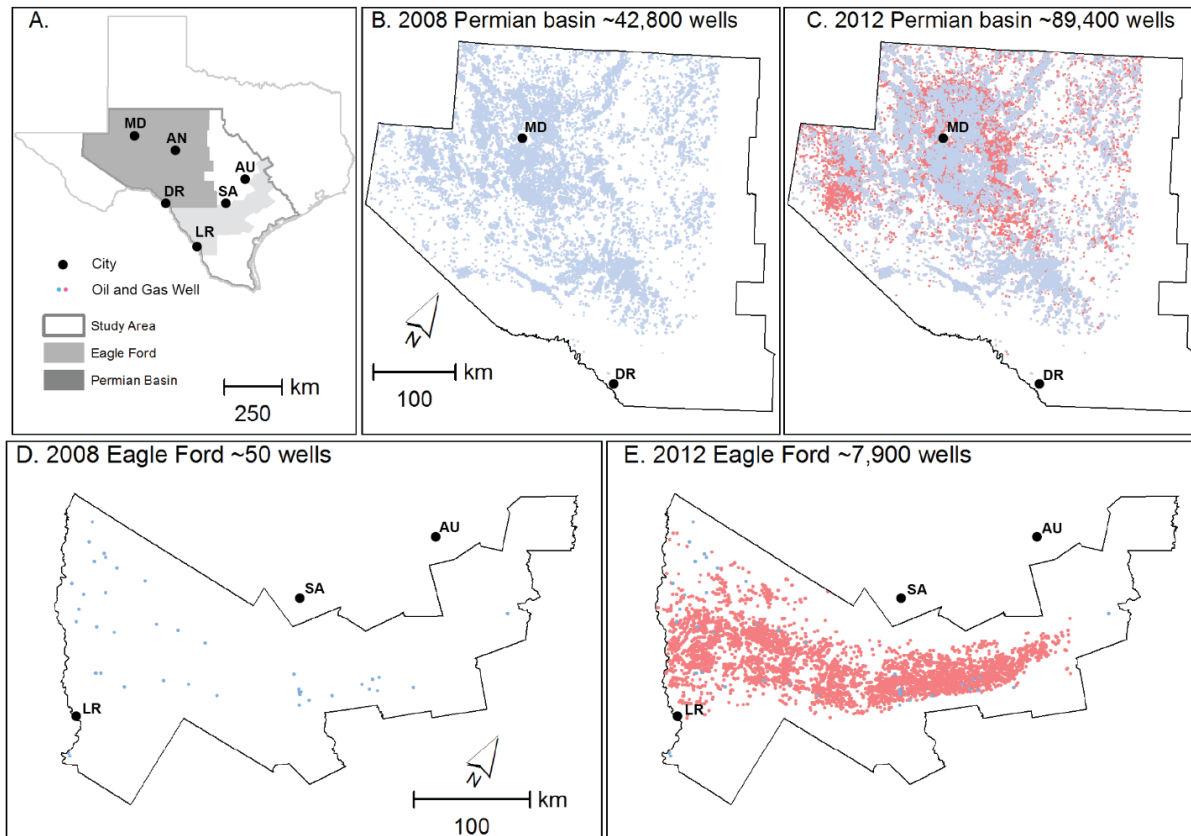
Figure 9.1. Study area and oil and gas wells

Study area (A) and oil and gas wells permitted in 2008 (blue) and 2009–2012 (red) in the Permian Basin (B, C) and Eagle Ford Shale Play (D, E; well locations from IHS 2014).

The historic distribution of *H. lacerata* (Axtell 1998) is included within the spatial extent of the Study Area (A). Cities: AN=San Angelo; AU=Austin; DR=Del Rio; LR=Laredo; MD=Midland; SA=San Antonio.

A. Well pads   **B. Pipelines**   **C. Wind turbines**   **D. Power lines**
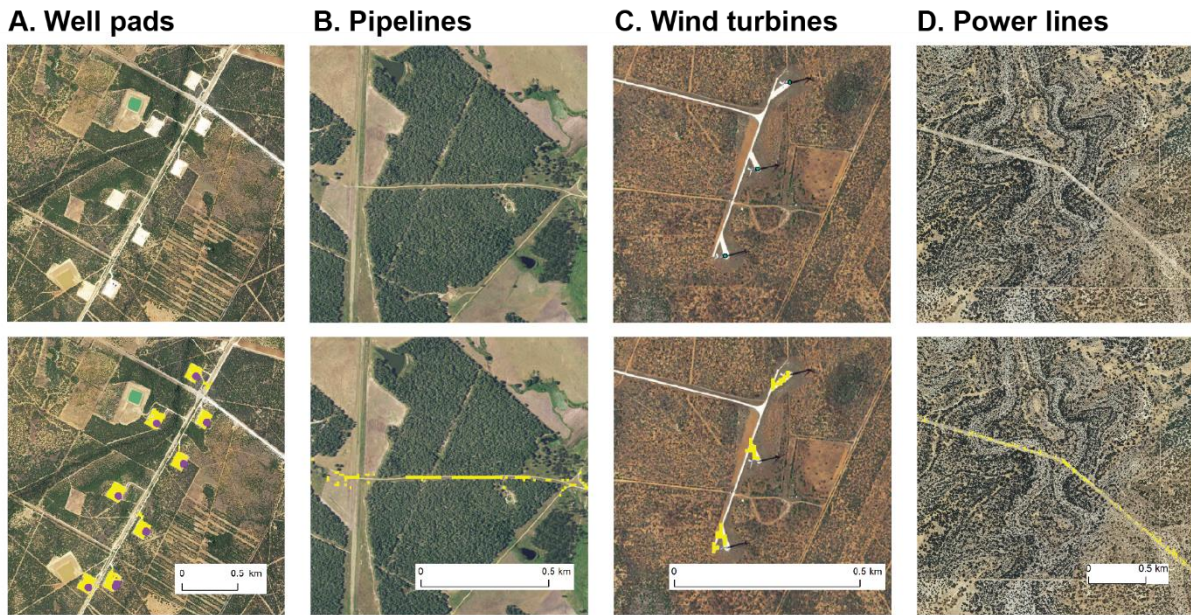
E. Land-use change evaluation approach
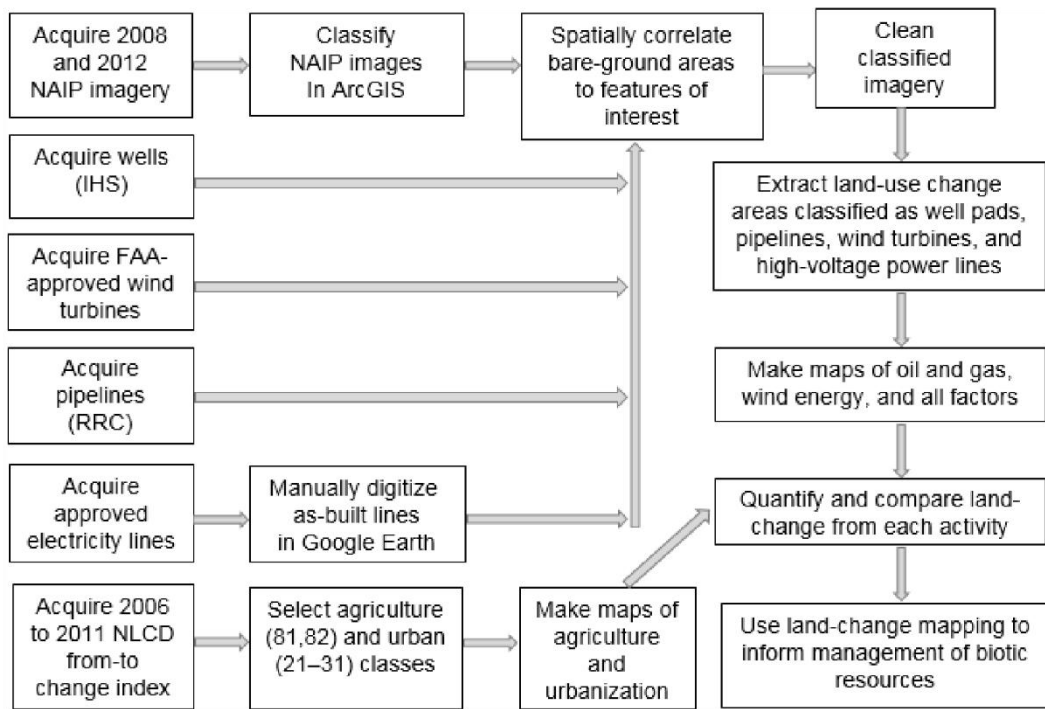
Figure 9.2. Land-use change evaluation approach for energy sprawl and other anthropogenic activities
(A–D) Representative energy-related oil and gas and wind power activities (top) resulting in changes in land-use mapped in this study (bottom) using the work flow of (E) which can be used to inform on-the-ground biotic resource management strategies. Refer to Methods section for complete data source citations.

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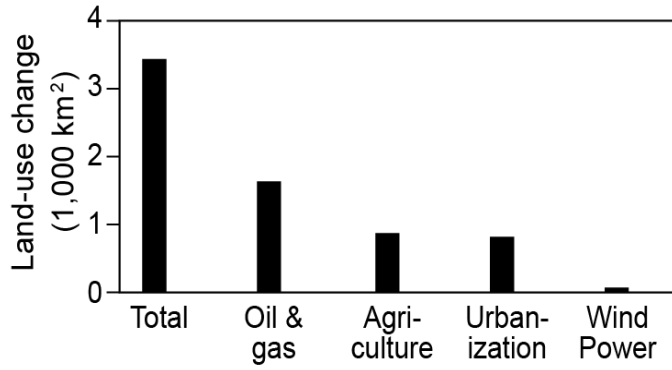
Figure 9.3. Changes in land-use from 2008–2012 anthropogenic activities
Oil & gas includes changes in land-use from construction well pads and pipelines (but not access roads), while wind power includes land-use changes from installation of wind turbine pads and power transmission lines (Table 1). Total is the sum of all changes in land-use resulting from anthropogenic activities.
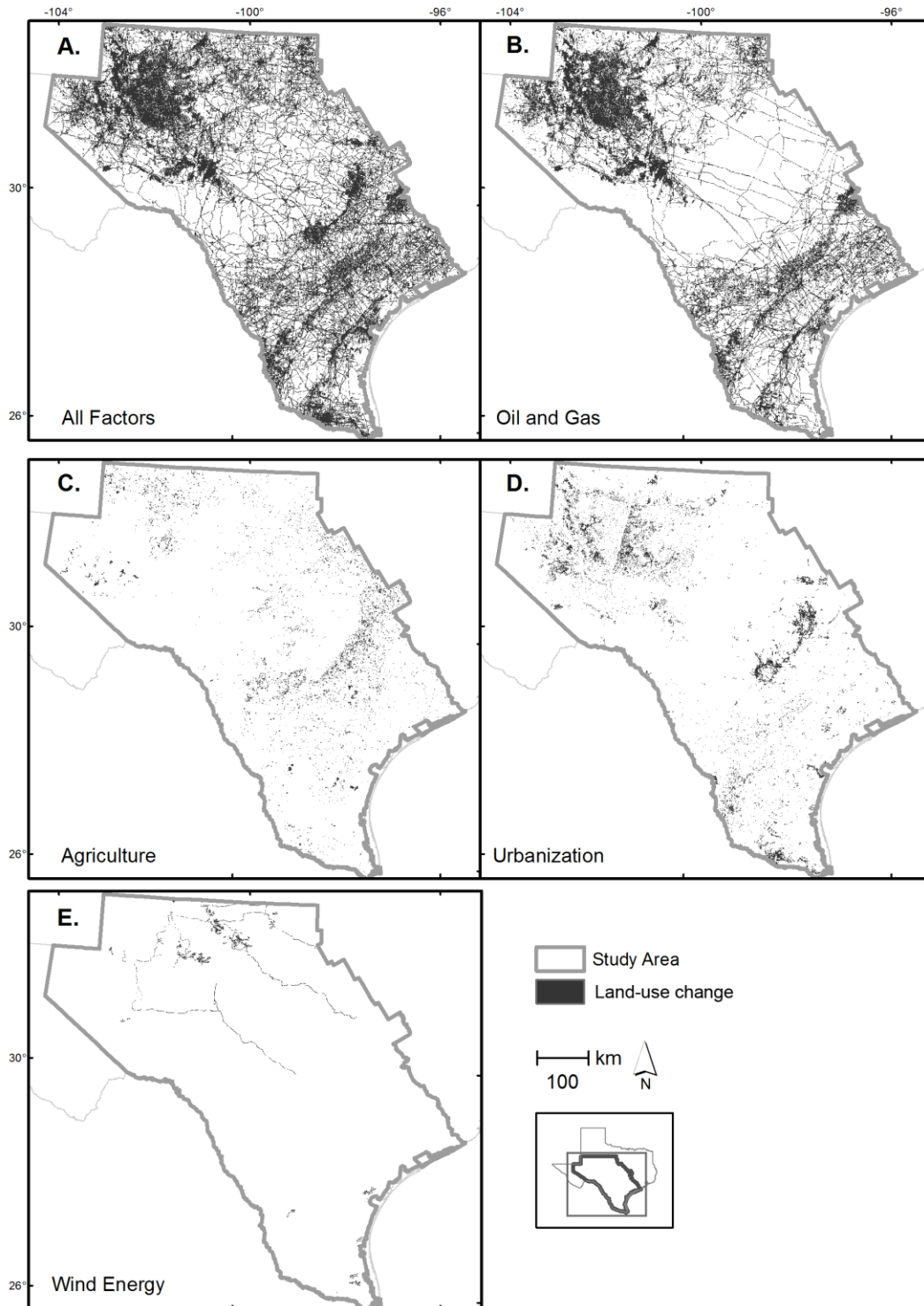
Figure 9.4. Changes in land-use from a suite of anthropogenic activities
Activities include: (A), oil and gas infrastructure (B), agriculture (C), urbanization (D), and wind turbines and high-voltage power lines (E)
Note: Black shading is used make changes in land-use apparent in regional maps.
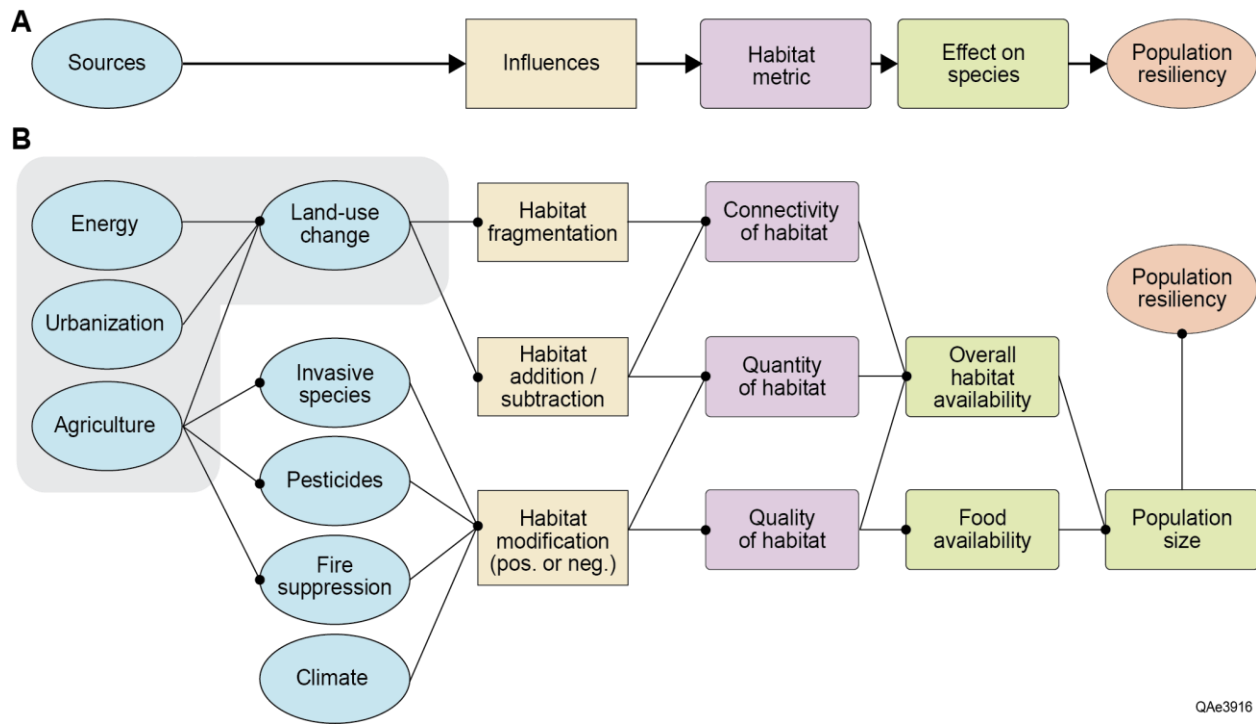
Figure 9.5. Influence diagram showing how changes in land-use and other factors may affect the focal species

An influence diagram is a form of a Bayesian belief network that outlines causal relationships, called "sources" which could act on the focal species in a positive, negative, or null manner. For *Holbrookia lacerata*, we used expert elicitation to identify sources, which included a suite of land use factors affecting the species' needs, current habitat, and future viability. The influence diagram shows (A) generic relationships of this Bayesian belief network. These linkages represent hypothesized pathways through which land-use (and other factors) may influence the species by causing increases or decreases in population size. The gray shaded box indicates factors considered by this study (B). Other components of this ongoing, multi-year research program for this species are generating the data needed to understand how sources actually affect the species (Table 2). The results of this research program will inform a Species Status Assessment (SSA; FWS 2016, Earl et al. 2017; Smith et al. 2018) to be prepared by FWS, which will be used to guide the Endangered Species Act listing decision for *H. lacerata*. The SSA could also be used by biologists to design on-the-ground conservation efforts, which may be included in a Candidate Conservation Agreement with Assurances (CCAA) prior to a possible federal listing, or a Habitat Conservation Plan (HCP) if the species were to receive federal protections under the Endangered Species Act.

Table 9.1. Changes in land-use between 2008 and 2012

	Total	Oil and Gas Pads and Pipelines	Agriculture	Urbanization	Wind Power Pads and Power Lines
Study area (km^2)	324,000				
Total land-use change (km^2)	3,456	1,664	907	837	48
Total land-use change as percent of study area	1.06	0.51	0.28	0.26	0.01
Percent of total land-use change [1]		48	26	24	1

[1]Sum does not equal 100 due to rounding.

Table 9.2. Implications for biotic management of focal species within Species Status Assessment framework

We illustrate this approach for *Holbrookia lacerata* in Texas. The objectives of the larger, multi-year research program include developing science to inform the U.S. Fish and Wildlife Service listing decision for possible protections under the Endangered Species Act. This research topic covered by the present study (indicated by gray shaded area in Figure 9.5) developed a novel mapping approach to assess 2008–2012 changes in land-use with the species' historic range. Other research program components are evaluating the species' needs, current conditions, and future viability (also shown on influence diagram of Figure 9.5).

Components of Species Status Assessment (SSA; FWS 2016)	**1. Species' Needs**	**2. Current Condition**	**3. Future Condition**
	Improve understanding of ecological needs of species	Describe current conditions of habitat and demographics and explain past and ongoing changes in abundance and distribution	Forecast species' response to probable future scenarios of environmental conditions and conservation efforts
Summary of how this research program is developing science to inform SSA	Assessing species' response to changes in land-use	Evaluating current land-use changes (and possible threats to species)	Forecasting future land-use changes (and possible threats to species)
	Evaluating habitat needs	Mapping current potential habitat	Mapping future potential habitat
	Analyzing diet	Assessing genetic structure of populations and using morphology to understand taxonomic boundaries	Quantifying range of potential climate effects on species
	Conducting distribution-wide surveys of species (i.e., mark-recapture, yielding estimates of density, vital rates)		
		Conducting conservation assessment and evaluating population connectivity	Using models to forecast species' extinction probability

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CHAPTER 10. ANTHROPOGENIC LANDSCAPE ALTERATION AS OF 2014

Land alteration: Agricultural production, roads, urbanization

The goal of this task was the evaluation of landscape alteration resulting from a suite of anthropogenic activities within the species' historic habitat. To this end, we have assessed cumulative landscape alteration through 2014 caused by agriculture, urbanization, roads, oil and gas pads and pipelines, and wind power turbine pads and electrical transmission lines. We found that landscape alteration from all factors affects ~23% of the study area (~76,000 km^2), led by agriculture (~16%; ~52,882 km^2). Oil and gas activities altered <1% of the study area (2,081 km^2), with 838 km^2 from pipelines and 1,242 km^2 from well pad construction—and that the median Eagle Ford well pad is 7.7 times larger than that in the Permian Basin (16,200 m^2 vs. 2,100 m^2). Wind energy occupied <0.01% (~24 km^2), with ~14 km^2 from turbine pads and ~10 km^2 from power transmission lines. These results are important in that they may be used as part of preparation of a Species Status Assessment to evaluate the species' current conditions. We submitted revisions to a paper on this topic to Environmental Management in September 2017.

Summary

Recent research has assessed how hydrocarbon and wind energy expansion has altered the North American landscape. Less understood, however, is how this energy development compares to other anthropogenic land use changes. Texas leads U.S. hydrocarbon production and wind power generation and has a rapidly expanding population. Thus, for ~47% of Texas (~324,000 km2), we mapped the 2014 footprint of energy activities (~665,000 oil and gas wells, ~5,700 wind turbines, ~237,000 km oil and gas pipelines, and ~2,000 km electrical transmission lines). We compared the footprint of energy development to non-energy-related activities (agriculture, roads, urbanization) and found direct landscape alteration from all factors affects ~23% of the study area (~76,000 km^2), led by agriculture (~16%; ~52,882 km2). Oil and gas activities altered <1% of the study area (2,081 km^2), with 838 km^2 from pipelines and 1,242 km^2 from well pad construction—and that the median Eagle Ford well pad is 7.7 times larger than that in the Permian Basin (16,200 m^2 vs. 2,100 m^2). Wind energy occupied <0.01% (~24 km^2), with ~14 km^2 from turbine pads and ~10 km^2 from power transmission lines. We found that edge effects of widely distributed energy infrastructure caused more indirect landscape alteration than larger, more concentrated urbanization and agriculture. This chapter presents a novel technique to quantify and compare anthropogenic activities causing both direct and indirect landscape alteration. We illustrate this landscape-mapping framework in Texas for the Spot-tailed Earless Lizard (*Holbrookia lacerata*); however, the approach can be applied to a range of species in developing regions globally.

Introduction

This study mapped direct anthropogenic landscape alteration in 47% of Texas (~324,000 km^2; Fig. 10.1) and compared alteration resulting from agriculture, urbanization, low-intensity development, and roads with alteration from oil and gas well pads, hydrocarbon pipelines, wind generation turbines, and high voltage transmission lines. While oil and gas infrastructure in

North America was recently mapped (Allred et al. 2015), the relative contribution of pads or pipelines was not assessed. In addition, the National Land Cover Database (NLCD; Homer et al. 2015) includes land use classes for agriculture and urbanization; however, it is difficult to map alteration from roads and right-of-ways without the corresponding roadway line maps (TXDOT 2016). Furthermore, it is impossible to assess the relative extent of direct landscape alteration from energy development activities that may be mapped as "developed" and "barren land" classes. Thus, this study fills an important need by mapping and comparing how much each non-energy and energy-related anthropogenic activity contributes to overall direct landscape alteration.

Understanding impacts from both direct and indirect anthropogenic landscape alteration is important because resulting changes in land cover threaten biodiversity globally (Fahrig 2003; McGarigal et al. 2005). Landscape alteration has also been identified as a main cause of wildlife extirpations and extinctions (Forman 2003; Juffe-Bignoli et al. 2014; Torres et al. 2016). Agriculture has been linked to habitat degradation and mortality (Gibbon et al. 2000; Sparling et al. 2010). Urbanization reduces habitat quantity and quality (Gibbon et al. 2000; McKinney 2008; Wolf et al. 2013). Road construction transforms and fragments habitat while directly causing mortality (Forman 2003; Andrews et al. 2008; Christie et al. 2015). Low-intensity development (such as rural development) and energy development has also been linked to habitat degradation (Finer et al. 2008; Brittingham et al. 2014; Christie et al. 2015), hydrologic alteration (King and Tennyson 1984; Trombulak and Frissell 2000; Pierre et al. 2015), habitat and vegetation fragmentation (Fahrig 2003; Hobbs et al. 2008; Drohan et al. 2012), and the spread of exotic species (Hansen and Clevenger 2005; Evangelista et al. 2011; Birdsall et al. 2012). In addition to effects to biodiversity, activities causing landscape alteration also may have effects to communities and water resources, but assessing these was outside of the scope of this study.

In North America, recent research has assessed anthropogenic landscape alteration from urbanization (Theobald 2003; Alig et al. 2004), road development (Pitman et al. 2005), and agricultural expansion (Huston 2005; Butsic and Brenner 2016). Other researchers have separately mapped landscape alteration resulting from energy development—such as wind power (Diffendorfer and Compton 2014; Evans and Kiesecker 2014) and oil and gas extraction (Drohan et al. 2012; Pierre et al. 2015; Slonecker and Milheim 2015; Milt et al. 2016). Energy infrastructure development for hydrocarbons and wind has recently increased nationwide (Drohan and Brittingham 2012; Kiviat 2013; Diffendorfer and Compton 2014; Brand et al. 2014; Shrimali et al. 2015; Abrahams et al. 2015; Pierre et al. 2015). The combination of horizontal drilling and hydraulic fracturing revolutionized the oil and gas industry circa 2008 (Driskill et al. 2012; U.S. Government Accountability Office 2012). Since then, the footprint of oil and gas in North America has increased exponentially (Allred et al. 2015), causing estimated changes in land use as large as approximately three Yellowstone National Parks (i.e., slightly smaller than the land area in Belgium) to accommodate this fossil fuel extraction infrastructure. Concurrently, wind energy expansion also rapidly converted land to meet human consumptive needs (Kuvlesky et al. 2007; McDonald et al. 2009; Diffendorfer and Compton 2014).

The effects of direct and indirect (e.g., edge effects) landscape alteration are species specific (Fischer and Lindenmayer 2007) and vary regionally (Jordaan et al. 2009). Some species may benefit from landscape modification while others may be adversely affected (Saunders et al. 1991). However, landscape alteration ultimately modifies the ecology of the surrounding landscape (Wilcove 1987; Saunders et al. 1991). Some species, such as those requiring interior habitat environments, lose habitats or their habitats are degraded. When landscape alteration

occurs, landscape matrices change and may become more heterogeneous, food webs change, landscape patterns and patch sizes change, hydrology may change, and ultimately habitat impacts are farther reaching than just the direct landscape alteration (Fahrig 2002; Sawyer et al. 2006; Fischer and Lindenmayer 2007; Hebblewhite 2011; Pierre et al. 2015). Therefore, understanding both direct and indirect alteration created from each disturbance regime is essential to developing an integrated approach to landscape conservation and management (Saunders et al. 1991; Ryberg et al. 2017). For example, linear disturbances, such as access roads and pipelines, bisect contiguous habitat, facilitate the spread of invasive species (Barlow et al. 2017), and disrupt soil water and nutrient flow (Nasen et al. 2011).

Texas has been identified as a critical area in need of continued research assessing how surface infrastructure associated with urbanization, roads, agriculture, wind power, and oil and gas development has altered the landscape (Drohan et al. 2012; Jones and Pejchar 2013; Moran et al. 2015; Slonecker and Milheim 2015). Texas has five of the eleven fastest-growing cities in the United States (U.S. Census 2016). Forecasts of population growth from 2020–2070 estimate a 70% increase in future Texas residents. Texas also has several important oil and gas producing regions, including the Permian Basin and Eagle Ford Shale Play. In fact, Texas leads all U.S. states in hydrocarbon (EIA 2017) and wind energy production (Shrimali et al. 2015).

Less understood, however, is how recent individual anthropogenic factors contribute to landscape alteration—with associated edge effects—across the United States and in Texas—the geographic focus of this study. These trends suggest that expansion of the anthropogenic footprint due to urbanization, road construction, wind power generation, oil and gas extraction, and other resource development in Texas will increase in the future. Also important is evaluating the extent to which different anthropogenic factors increase landscape alteration through edge effects. For example, some activities perforate landscapes (e.g., well or turbine pads) while others (e.g., linear pipelines and roads) effectively bisect the landscape (Fahrig et al. 2011; Battisti et al. 2016; Pierre et al. 2017). Thus, a map of recent direct landscape alteration is urgently needed from which to compare future alteration. Therefore, this study created a high-resolution map of land use in 47% of Texas—including the footprint of energy infrastructure—which is not readily available from datasets such as the National Land Cover Dataset (Homer et al. 2015) or the Ecological Mapping System of Texas (Elliot et al. 2009).

The objective of this study was to quantify and compare direct landscape alteration and edge effects resulting from oil and gas infrastructure and wind energy development to other anthropogenic factors. Specifically, we:

1. created a new dataset of the footprint of energy infrastructure as of 2014,
2. mapped the surface footprint of all oil and gas occurring in our study area—which includes wells in the Eagle Ford Shale Play (unconventional) and Permian Basin (conventional and an increasing number of unconventional), and
3. compared the relative impact of energy and non-energy-related development in the study area.

This study was motivated by conservation concerns regarding the Spot-tailed Earless Lizard (*Holbrookia lacerata*)—a lizard whose historic range included much of central and south Texas and has been petitioned for protection under the Endangered Species Act (Wild Earth Guardians 2010). Thus, the results of this study are being used to inform the U.S. Fish and Wildlife Service federal listing determination for the species—and can also be used to assess other environmental

questions in the study area. We chose 2014 as the time period for our study due to availability of high-resolution aerial photography, which was the latest available to us at the start of this project. This detailed knowledge of regional land use trends should be of great interest to stakeholders needing to plan and mitigate future development as well as establish a baseline for monitoring future changes on the landscape.

Materials and methods

Study area

We assessed direct landscape alteration for ~47% of Texas (~324,000 km^2) within the historic range of the Spot-tailed Earless Lizard in Texas (Fig. 10.1). The study area includes the metropolitan areas of Austin, San Antonio, and Midland and widely distributed agricultural activity. Also found in the study area are two major oil and gas regions—the Permian Basin and the expanding Eagle Ford Shale play (EIA 2017)— that recently experienced rapid growth as a result of increased use of hydraulic fracturing combined with directional drilling. Another expanding energy sector in the study area is wind energy development associated with the Competitive Renewable Energy Zone (Kuvlesky et al. 2007; Woodfin 2008).

Data used to assess landscape alteration.

We mapped direct landscape alteration resulting from a suite of anthropogenic factors using several datasets. The National Landcover Dataset (NLCD; Homer et al. 2015) was used to map alteration from agriculture and low-intensity development. The National Agricultural Imagery Program (NAIP) 1-m aerial photography (2014) was used to identify direct landscape alteration caused by oil and gas and wind power generation infrastructure. We downloaded all oil and gas wells (i.e., production, injection, horizontal, vertical, abandoned, wildcat, etc.) permitted within the study area as of October 24, 2014 from the IHS Enerdeq Database (IHS 2015). This date corresponded with the latest NAIP acquisition date in the study area. We acquired oil and gas pipeline networks from the Railroad Commission of Texas, the state oil and gas regulatory agency (RRC 2014). The locations of wind turbines installed as of December 31, 2014 were downloaded from the Federal Aviation Administration (FAA 2016). High voltage electrical transmission routes were plotted using approved 2011 Competitive Renewable Energy Zone lines. Roads and right-of-ways were assessed using the 2014 Texas Department of Transportation roadway inventory (TXDOT 2015) and 2015 TxDOT roadway lines (TXDOT 2016). Urban areas were plotted using the urbanized areas of Texas dataset (Texas Natural Resources Information System 2016). Non-energy-related landscape alteration was mapped directly using datasets, while energy-related development was mapped by creating derivative datasets—using the approaches described below. We assessed resulting alteration within Omernik Level III ecoregions (Omernik and Griffith 2014).

Mapping non-energy related development.

All non-energy related development was mapped by using datasets directly, either by resampling raster datasets or by rasterizing polygon datasets. We first mapped urban areas using a dataset of urbanized areas in Texas (Texas Natural Resources Information System 2016). The polygon shapefile was converted to a 10-m resolution raster. To map roadway development, we followed the methods of Pierre et al. (2017), whose methodology utilizes the 2014 TxDOT roadway inventory (TXDOT Texas Department of Transportation 2015) buffered by the right-of-way (ROW) width and the 2015 TxDOT roadway lines areas (Texas Natural Resources Information System 2016). All buffered roadways and polyline roadways were converted to a 10-m resolution raster. We identified agricultural development by resampling the 30 m 2011 National Land Cover Dataset (NLCD; Homer et al. 2015) to 10-m resolution. We combined

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NLCD values for cropland and pasture (Table 10.S1). Low-intensity development was mapped by combining the developed classifications from the resampled 10-m NLCD (Table 10.S2).

Mapping energy related development.

We created an entirely new land use/land change dataset, which mapped direct landscape alteration resulting from energy-related infrastructure development. The workflow we utilized to locate and map oil and gas drilling pad infrastructure is described in detail in Pierre et al. (2017); however, we provide a detailed summary of the approach here. We mapped direct landscape alteration using 1-m resolution National Agriculture Imagery Program (NAIP/USDA-NAIP 2014) aerial images acquired in 2014, which was the most recent available at start of the study. Iso cluster unsupervised image classification was executed in ArcGIS (version 10.2) to create 100 landscape classes (following the methods of Pierre et al. 2015 and Pierre et al. 2017), which were resampled to 10 m resolution and converted to polygons. Overlaps with roadways and urban areas were removed to create "bare-earth" polygons.

We mapped oil and gas drilling pad infrastructure by downloading all oil and gas wells permitted in the study area as of December 1, 2014 (i.e., production, injection, horizontal, vertical, abandoned, wildcat, etc.; IHS, 2016). Wells permitted after October 24, 2014 were eliminated to correspond with the latest NAIP acquisition date in the study area. We did not consider wells coded as recompleted, re-drilled, or deepened, which we assumed to be a reworked existing well. Bare-earth polygons within 90 m of one or more wells were converted to a 10-m landscape-alteration raster. Wells without mapped alteration representing a well pad were either moved to an altered-landscape cluster or removed from the dataset. When wells occurred in alteration clusters larger than 4.5 ha (likely fallow agricultural fields or other bare ground not associated with a well pad), we assumed that alteration from pad development was immediately adjacent to the well and not throughout the whole cluster. Therefore, we only classified cells in these large alteration clusters within a 30 m radius of a well as caused by oil and gas operations. When two or more wells were located within 100 m of each other, we classified them as multiple wells on a single pad.

We mapped direct landscape alteration from oil and gas pipelines following the methods of Pierre et al. (2017) and applying a 30-m buffer to mapped pipelines. To map wind energy turbine pads, we selected turbines built as of December 31, 2014 and followed the methods of Pierre et al. (2017), which was similar to the approach to map oil and gas alteration, except wind turbine locations permitted by the FAA were used in lieu of permitted well locations. We mapped high voltage electricity transmission lines by manually editing 2011 approved routes based on visual inspection of NAIP imagery because as-build locations are not publicly available for security reasons. We applied a 30-m buffer to the edited high voltage transmission routes and followed the methods of Pierre et al. (2017) to extract alteration from the construction of this infrastructure.

We did not map access roads to either O&G or wind pads as private access roads do not fall under the purview of TxDOT and these spatial data are not available. We recognize this as a limitation in our methodology and refer the reader to the "assumptions and limitations of landscape alteration assessment" section.

Hierarchical reclassification and summation of landscape alteration mapping

We used a hierarchical classification system to assign only one alteration type to pixels where several alteration factors overlapped following the schema in Table 10.S2. We also classified any developed areas from the NLCD not overlapping with the urbanized layer as low-intensity development. We created maps of the individual anthropogenic factors and of the

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cumulative direct landscape alteration of all past and present human actions since a baseline, pre-Columbian landscape by summing landscape alteration from each individual factor. We summarized these results at 1-km^2 resolution and mapped them as percent alteration of a 1-km^2 cell to facilitate display. We also present direct landscape alteration results for each ecoregion.

Landscape alteration metrics

We evaluated the extent to which edge effects may increase the overall landscape footprint alteration for each anthropogenic activity. Consistent with landscape ecology practices, we mapped edge areas by applying a 100-m buffer to each alteration cluster (Howell et al. 2006; Jordaan et al. 2009; Johnson 2010; Svobodová et al. 2011; Drohan et al. 2012). We calculated the ratio of the area of edge to the area of the alteration cluster surrounded by the 100-m buffer. Thus, we used the edge to alteration ratio as an informative metric to inform how the shape of landscape alteration cluster may increase the overall alteration area. For example, many small landscape alteration clusters, such as well pads, would have a higher edge to alteration ration than one, large altered area, such as an urban area.

Results

Cumulative alteration

We found that 23.4% (75,786 km^2) of the landscape in the study area has been altered (Figs. 10.2, 10.3; Tables 10.1, 10.2). Much of this direct landscape alteration occurs to the east and south of a line between Austin and San Antonio. Additional areas of focused direct landscape alteration occur within a ~300 km radius north of Midland. When we examined direct landscape alteration by ecoregions (Table 10.2), we found that the Western Gulf Coastal Plain had the highest cumulative direct landscape alteration area (22,061 km^2), followed by the East Central Texas Plains (10,533 km^2). However, by percentage, the Texas Blackland Prairies had the largest percentage of alteration (63%). In contrast, the Chihuahuan Deserts had the lowest total alteration (1,089 km^2, 3%).

Non-energy-related development

We found that agriculture dominated non-energy-related anthropogenic direct landscape alteration that occurred since a pre-Columbian baseline (Figs. 10.3, 10.4A; Tables 10.1, 10.2). Conversion of pre-existing vegetation to agriculture altered 16.4% of the study area (52,882 km^2) and accounted for 70% of total alteration (Fig. 10.3). Agricultural alteration dominates in the southeastern and northern portions of the study area (Fig. 10.4A). We assessed two types of development. First, we found that low-intensity development altered 3.2% of the study area (13.6% of total direct landscape alteration; 10,304 km^2; Figs. 10.3, 10.4B) and was distributed throughout the entire study area. The most affected ecoregion from low-intensity development is the Texas Blackland Prairies and the least are the Edwards Plateau and the Chihuahuan Deserts (Tables 10.1, 10.2). Second, urbanization caused 10.3% of total direct landscape alteration (7,817 km2, 2.4% of study area; Figs. 10.3, 10.4C; Tables 10.1, 10.2) and—apart from Austin and San Antonio—is dispersed in towns throughout the study area. A comparison of 1-km2 cells with at least one alteration pixel indicated that on average urbanization altered 64% of the cell and low-intensity development altered 5%. Roads altered 2,686 km2 of the landscape (0.8% of the study area; 4% of total alteration; Figs. 10.3, 10.4D; Tables 10.1, 10.2).

Energy-related development

Our mapped energy-related direct landscape alteration found that oil and gas extraction altered 2,081 km^2 (0.6% of study area; 2.7% of the total alteration; Figs. 10.3, 10.4E). Of this, direct landscape alteration from well pads was 1,243 km2 and hydrocarbon pipelines was 839 km^2. All the ecoregions in the study area had oil and gas development, however, ≤1% of any

given ecoregion was altered (Tables 10.1, 10.2). Other researchers have assessed the effects of oil and gas development to air, water quality, water demand, health, and social aspects (e.g., Nicot and Scanlon 2012; Vengosh et al. 2014); however, such assessments were outside the scope of this study. We also evaluated oil and gas pads in the study area (n=354,615) and calculated pad sizes and numbers of wells per pad (Table 10.3) for the Eagle Ford Shale Play, which is dominated by unconventional wells (i.e., horizontal, hydraulically fractured) and the Permian Basin, which is a mix of conventional wells (i.e., vertical), in addition to hydraulically fractured vertical wells and an increasing number of hydraulically-fractured horizontal wells.

Infrastructure development for wind power generation altered 24 km^2 (0.007%) of the study area and accounts for 0.03% of total alteration (Figs. 10.3, 10.4F). Of this, 14 km2 was turbine pads (median pad side =500 m^2) and 10 km^2 was from high voltage power transmission line infrastructure. The highest concentrations of alteration from wind were in the High Plains, Southwestern Tablelands, and the northern portion of the Edwards Plateau (Tables 10.1, 10.2). High concentrations of wind alteration also exist in the Western Gulf Plain region along the coast.

We also provide alteration data summarized at the county level in the Supplemental Results section to provide insight for practitioners involved with regional-scale planning and conservation efforts for the Spot-tailed Earless Lizard and other species of conservation concern. All data are available online for download at: https://doi.org/10.18738/T8/UDDPTE.

Landscape alteration metrics

We found that the edge to alteration ratio of non-energy factors (i.e., agriculture and urban areas) was lower than energy-related activities (i.e., wind power and oil and gas infrastructure; Table 10.1). For example, urbanization and agricultural development result in large, contiguous blocks of alteration with the lowest edge to alteration ratios, resulting in 0.1–0.6 km^2 of edge effect for every 1-km^2 of alteration (Table 10.1). Low-intensity development, which perforates landscapes, had a higher edge to alteration ratio (5.4). Roadway development, which bisects landscapes with relatively narrow corridors, had the highest non-energy edge to alteration ratio (13.0). We found alteration from energy-related activities generally affected smaller areas than non-energy factors; however, energy development had a consistently higher potential for creating edge effects. Linear alteration caused by construction of wind power transmission lines and oil and gas pipelines had the highest edge to alteration ratios (29.6 and 25.1, respectively). Pads for wind turbines had a higher edge to alteration ratio (25.0) than pads for oil and gas wells (13.7).

Discussion

Comparison of landscape alteration from non-energy and energy-related development

We created novel direct landscape alteration datasets for energy-related infrastructure development—not specifically included in publicly available land cover datasets—and found that agriculture, including crops and pasture, was the most important direct landscape alteration factor in our ~324,000 km2 study area (70% of total alteration; Figs. 10.3, 10.4). This was followed, in descending order, by low intensity development (14% of total alteration), urbanization (10%), and roads (4%). We found that less than 4% of total direct landscape alteration was attributed to energy infrastructure, with 3% caused by oil and gas operations and less than 1% from wind power generation. An interesting finding of this work is how anthropogenic alteration plays out in the landscape. For instance, low-intensity development and roads are widely dispersed across the study area and alter a relatively low percent of any 1-km2 cell we assessed (Figs. 10.4B, 10.4D). Agriculture, on the other hand, spans much of the Gulf Coast plains and High Plains and intensely alters the landscape where it occurs (Fig. 10.4A). Not

surprisingly, urbanization from major cities (i.e., Austin and San Antonio) is focused along transportation corridors and alters a high percent of the landscape where it occurs (Fig. 10.4C). Conversely, we found that oil and gas development is widely dispersed across large areas of the state—particularly in the Permian Basin and Eagle Ford Shale Play—and that this development, where it occurs, alters a relatively low percent of the landscape (Fig. 10.4E). The pattern of direct landscape alteration caused by wind power generation is similar to that of oil and gas in that wind turbines—like wells—are constructed on rectilinear pads. Furthermore, the installation of power transmission lines—like pipelines—result in long, narrow swaths of direct landscape alteration. We also found that wind turbines and associated power transmission lines affected a much smaller area than oil and gas infrastructure.

Our analysis of edge to alteration ratios for each anthropogenic factor elucidated important overall effects that simply evaluating direct landscape alteration area did not reveal. For example, we found that alteration from energy-related activities had a higher edge to alteration ratio than non-energy activities. Our assessment also revealed that linear infrastructure installed for energy conveyance—whether electricity or hydrocarbons—had the highest potential for edge creation. Finally, while wind turbine pads had higher edge to alteration ratios than well pads, the greater number of oil and gas wells (~665,000) compared to wind turbines (~5,700) highlights the overall importance of edge effects that resulted from drilling thousands of wells in the study area. One approach to mitigate the edge effects of well pad construction for oil and gas operators is to drill more multi-well pads.

Energy sprawl: Growth of oil and gas development and wind power generation

This study mapped anthropogenic activities and their impact on the landscape as of 2014. However, this footprint is not static and we expect the relative contribution of each alteration factor to change in the future. This trend is of particular interest for the energy sector, and has been labeled "energy sprawl" (Trainor et al. 2016). For example, oil and gas energy resource development in Texas—such as the Eagle Ford where the number of permitted wells has dropped from 5,613 in 2014 to 1,119 in 2016 (RRC 2017)—will continue expanding when oil prices rebound (West Texas Intermediate Crude was ~$53/barrel in March 2017, falling from >$100/barrel 2 years before; EIA, 2017). For example, development in the Eagle Ford is expected to continue, with only 10% of wells drilled to date (Gong et al. 2013; Scanlon et al. 2014). In addition, wind power generation has also expanded recently, and Texas now produces more wind energy than any other state in the U.S. (Shrimali et al. 2015). We found that the overall physical footprint of energy development on the landscape in Texas is relatively small; however, we did not assess how this development may affect broader biophysical processes or ecological/biological systems.

Comparison of well pads in the Eagle Ford Shale Play and the Permian Basin

Our analysis of direct landscape alteration resulting from oil and gas infrastructure revealed that pads for wells in the Eagle Ford Shale Play were more than four times the size of pads in the Permian Basin. This result is consistent with the findings of other researchers who assessed oil and gas infrastructure and found pads for unconventional wells to be larger than their conventional counterpart (Johnson 2010). We also found that drilling pads across the study area have on average of 1.2 wells per pad. Thus, future drilling operations could mitigate their impact by increasing the number of wells per pad and by sharing existing oilfield roads and pipelines (Drohan et al. 2012). To this end, our research group is currently generating 50-year forecasts of possible future well pad locations and resulting landscape alteration for the Eagle Ford Shale Play and Permian Basin in Texas. These forthcoming results could be used by operators to

optimize placement of oil and gas infrastructure that minimizes landscape alteration, and resulting potential impacts to species' habitat, erosion of soil, and degradation of watershed quality.

Implications for conservation of Spot-tailed Earless Lizard and other species with state and federal conservation interests

Anthropogenic activities cause land use changes, which threaten biodiversity globally (Fahrig 2003); however, responses to landscape alteration are species-specific and span a broad range. This study is a first step in understanding what landscape alteration is occurring within habitats of species in our study area. Essential to biodiversity conservation—for the Spot-tailed Earless Lizard and other species—is identifying potential threats and developing mitigation strategies. The Texas Conservation Action Plan (TCAP; TPWD 2012) identifies species of conservation interest, threats to habitats, and proposes conservation strategies for dozens of terrestrial and aquatic species of state and federal interest. The TCAP specifically calls out population growth (i.e., urbanization), agricultural land management, and energy production and transmission (oil, gas, and wind) as priority issues potentially affecting species conservation at a state and ecoregion level. Thus, the landscape alteration analysis we completed for this study can be applied by other researchers working on conservation of dozens of species listed in the TCAP and found within our study area. One such species—which is the motivation for this study—is the Spot-tailed Earless Lizard. We suspect the Spot-tailed Earless Lizard to be an early successional species that may favor certain types of landscape alteration. However, invasive vegetation and fauna following changes in land-use may also adversely affect the species (Axtell 1998). As part of a larger research program for the Spot-tailed Earless Lizard, ongoing studies, including the use of radio telemetry, seek to improve our understanding of how the species responds to landscape alteration. Once these data become available, our mapping of landscape alteration could be used to inform conservation strategies. Additionally, the landscape alteration mapping of this study will be used directly by the U.S. Fish and Wildlife Service to help determine whether protection for the Spot-tailed Earless Lizard under the Endangered Species Act is warranted. Should pre-listing conservation efforts such as a Candidate Conservation Agreement with Assurances (CCAA) be implemented, the results of this study will also inform these management actions. Thus, while we focused on the historical range of the Spot-tailed earless lizard, our results can be used to improve conservation outcomes for dozens of species of state and federal interest within this study area.

The goal of this study was to map and compare direct alteration from different landscape conversion regimes. However, it is important that land managers and planners also consider indirect impacts to the landscape as well. For instance, we have shown that patterns of direct landscape alteration from energy development results in a diffuse alteration of the landscape, whereas direct alteration from urban and agricultural expansion is larger and aggregated. We show these alteration types have different indirect edge impacts. In addition, the Texas Conservation Action Plans (Texas Parks and Wildlife Department 2012a-j) highlight the potential threats of different alteration regimes within each ecoregion on habitats of species of interest and call for different mitigation strategies. For example, the widely-distributed linear features associated with access roads and transmission lines for wind and O&G development may create edge effects through interior habitats opening up predator corridors and pathways for invasive species. Additionally, Texas does not require operators to reclaim these areas with native seeds. In contrast, conversion to agricultural production not only creates habitat loss but also creates additional concerns with pesticide and fertilizer, which may impact native fauna or

adjacent water sources. Therefore, different mitigation strategies are suggested for each type of alteration. Examples may include incentivizing private landowners to reclaim lands altered by energy development with native plants and working with the energy industry to find creative ways to avoid, minimize, and mitigate impacts to listed and candidate species (Texas Parks and Wildlife Department 2012a-j). These types of mitigation measures can be achieved by avoiding of intact landscapes, minimizing the creation of new access roads, the use of multi-well pads, controlled site access, and reclamation with native plant species. Similarly, agricultural and urban expansion can be limited by the creation of conservation easements or creating incentives when possible to prevent further conversion of the landscape.

Future research directions

This study assessed the cumulative impact of all past and present anthropogenic landscape conversions and mapped how they altered the landscape in our study area. As part of a larger research program investigating the Spot-tailed Earless Lizard, the results of this study will feed into ongoing studies that seek to (1) improve our understanding of how landscape alteration affects the species and (2) understand potential future threats to the species. First, to understand the species' response to its environment, we are currently conducting radio telemetry studies at several sites within the range of the Spot-tailed Earless Lizard. The results of the telemetry studies will be used to test potential hypotheses of how land development, invasive species, fire suppression, and other factors may potentially affect the species throughout its potential modern range. Second, while we now understand present direct landscape alteration and will soon understand how this information can be used to develop on-the-ground conservation strategies, successful conservation of the species depends upon understanding its potential future threats. To this end, as part of the larger research program, we are currently forecasting the footprint of agriculture, urbanization, wind power development, oil and gas infrastructure, and other anthropogenic factors.

Assumptions and limitations of landscape alteration assessment

Our analysis used the best available data to map landscape alteration resulting from a suite of anthropogenic factors in 47% of Texas as of 2014. Despite several limitations in the approach we used, the results provide a useful tool to identify and compare the relative importance of contributors to landscape alteration at a regional scale. One potential limitation is a result of the large size of our study area. Other researchers conducting studies in smaller areas have manually digitized the footprint of oil and gas (Drohan et al. 2012). The geographic scope of our study necessitated using a semi-automated landscape classification approach following the methods of Pierre et al. (2017), which may not be as accurate as manually digitizing well pads and pipeline routes. Nevertheless, it was not practical for us to digitize the 354,615 oil and gas pads in the study area. Also, locations of wells drilled before the advent of surveys using GPS in the 1990s (IHS 2016) occasionally did not plot on a well pad apparent from visual inspection of aerial imagery. However, the approach of Pierre et al. (2017) corrected for these inaccuracies and associated each well with its correct well pad. In addition, we manually corrected the location of proposed high voltage electrical transmission routes so that our final routes matched aerial photo interpretation. We used a hierarchical approach in classifying direct landscape alteration that first assigned alteration to previously mapped urban and road areas when these alterations were co-located with newly mapped energy development, potentially underestimating some of the mapped energy infrastructure.

Because spatial databases of private access roads in oilfields and wind farms do not exist for private lands in Texas, we did not map these important causes of landscape alteration. While

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other studies that were constrained to a smaller study area have mapped (Johnson 2010) or estimated access roads (Jordaan et al. 2017), we chose to accept the limitation of not mapping access roads for multiple reasons. First, semi-automated-mapping approaches (e.g., Allred et al. 2015; Jordaan et al 2017; Pierre et al. 2017) do not effectively distinguish energy infrastructure access roads from contiguous mapped landscape alteration. Second, the manual digitization of landscape alteration from aerial imagery by a GIS analyst (e.g., Johnson 2010; Drohan et al. 2012; Pierre 2015) is not a tractable approach to be used for studies such as this with a large regional spatial extent ($\sim$324,300 km^2). Thus, this study does not present landscape alteration caused by access roads to well pads or wind turbines. However, a study done in the Marcellus Shale (Drohan and Brittingham 2012) found the median of total disturbed area (pads, roads, compressor stations, etc.) to be 1.2 times larger than the median pad size. This suggests, at least for the Marcellus, the inclusion of roads (and other infrastructure) would double the direct landscape alteration caused by oil and gas well pad construction. Additionally, we would expect that indirect edge effects from oil and gas access roads to be similar to oil and gas pipelines and electrical transmission lines because they are also linear in nature. Another study that analyzed wind development found a high degree of variation in landscape alteration due to geographic variables (Diffendorfer and Compton 2014). Thus, mapping privately-constructed access roads remains an important topic for future research. However, despite these limitations, our results provide an important, previously unavailable regional-scale mapping and comparison of energy infrastructure and non-energy related anthropogenic activities for almost half of Texas, which can be used as a foundational dataset to understand potential effects on species' habitats.

Conclusions

1. Agricultural is the most important direct landscape alteration factor (70% of total alteration) and is spread throughout the study area, with the exception of the Edwards Plateau and Chihuahuan Deserts ecoregions.

2. Construction of energy infrastructure for oil and gas development (not including access roads) altered 1% of the study area and caused less than 4% of total alteration; however, forecasting future energy sprawl from potential infrastructure construction in the Eagle Ford Shale Play and Permian Basin is an important topic of ongoing research. We also found that well pads associated with drilling of unconventional wells (horizontal drilling using hydraulic fracturing) altered approximately four times the land area compared to drilling of conventional wells.

3. Construction of wind turbines and power transmission lines contributed to less than 1% of total alteration; thus, despite recent wind generation expansion, the wind power footprint remains a minor, but growing landscape alteration factor.

4. Energy development has a higher potential for edge effects than non-energy activities because pads for wells and turbines perforate and energy conveyance infrastructure bisects the landscape, compared to urbanization and agriculture, which have large, contiguous areas of alteration with relatively smaller edge areas.

This study presents a new approach to map and compare landscape alteration caused by energy- and non-energy related anthropogenic activities. We illustrate this landscape-assessment technique in Texas for the Spot-tailed Earless Lizard (*Holbrookia lacerata*). However, the approach should be of great interest to land planners, energy operators, wildlife biologists, and others evaluating and mitigating the relative impacts of a suite of anthropogenic factors for a range of species in developing regions globally.

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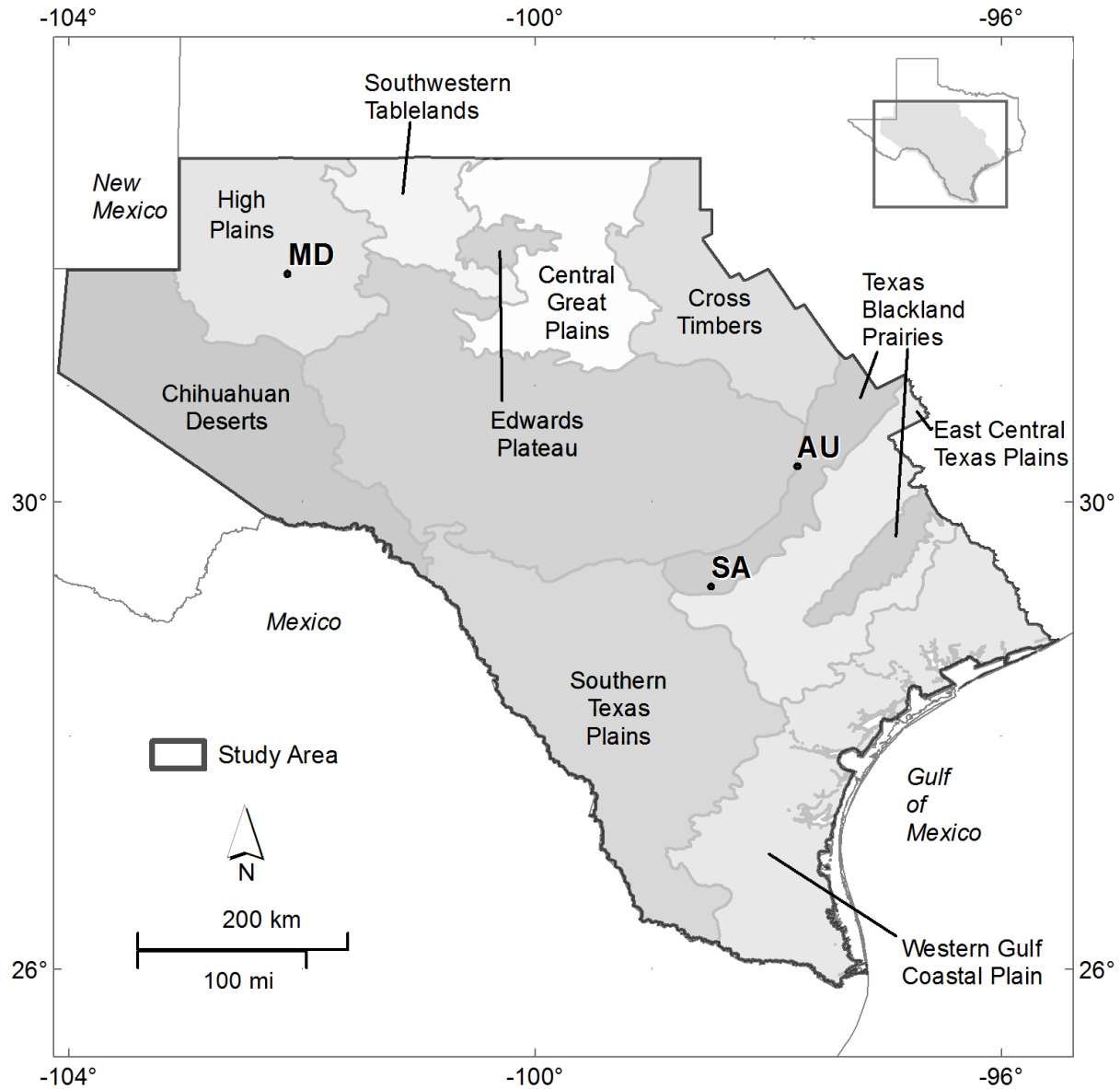
Figure 10.1. Study area, including ecoregions (Omernik and Griffith 2014)
The study area was selected to include the historic range of the Spot-tailed Earless Lizard (*Holbrookia lacerata*) in Texas. AU=Austin, MD=Midland, SA=San Antonio.
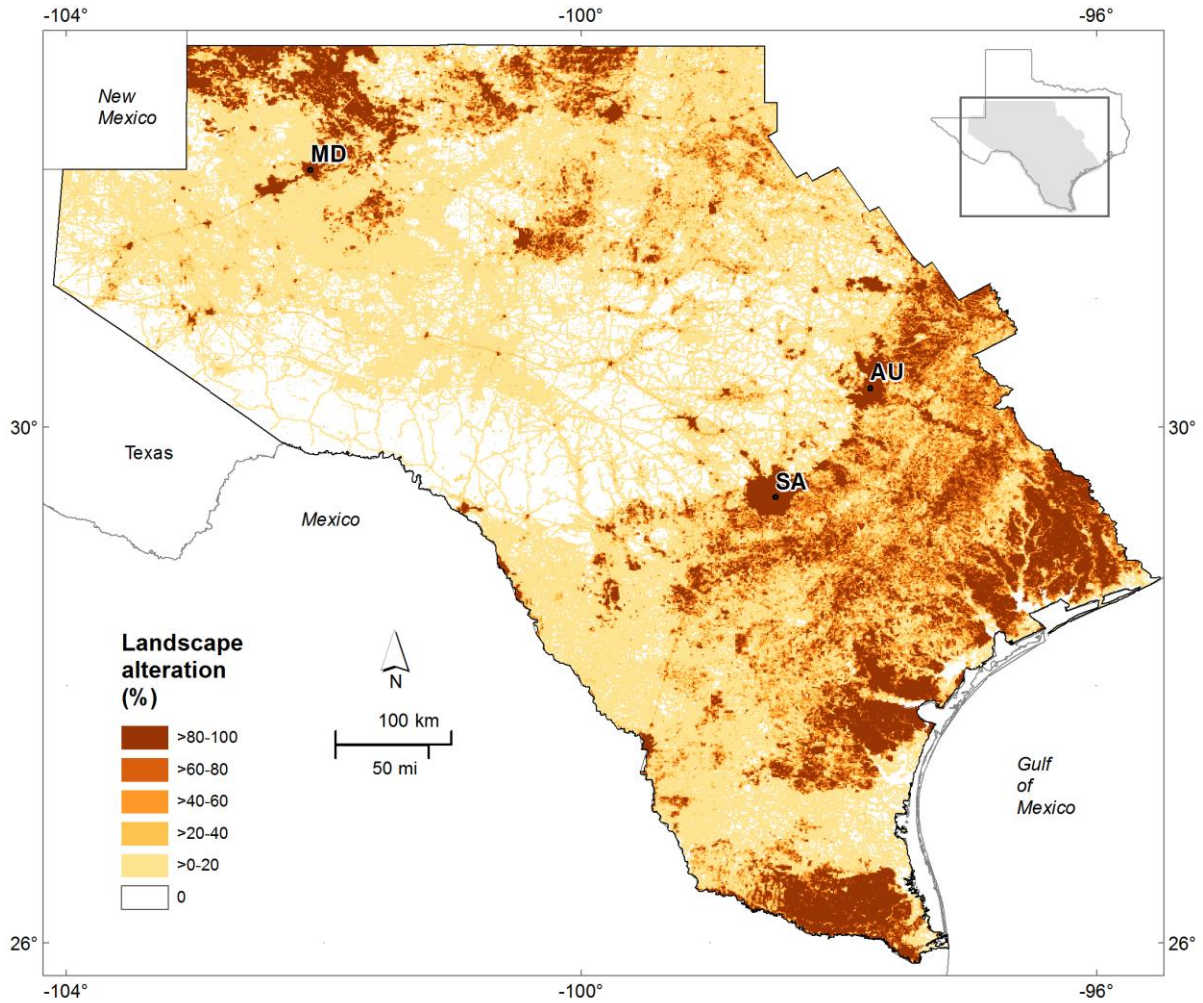
Figure 10.2. Cumulative landscape alteration
Shown as the sum of energy and non-energy factors, expressed as percent alteration of a 1 km^2 cell.
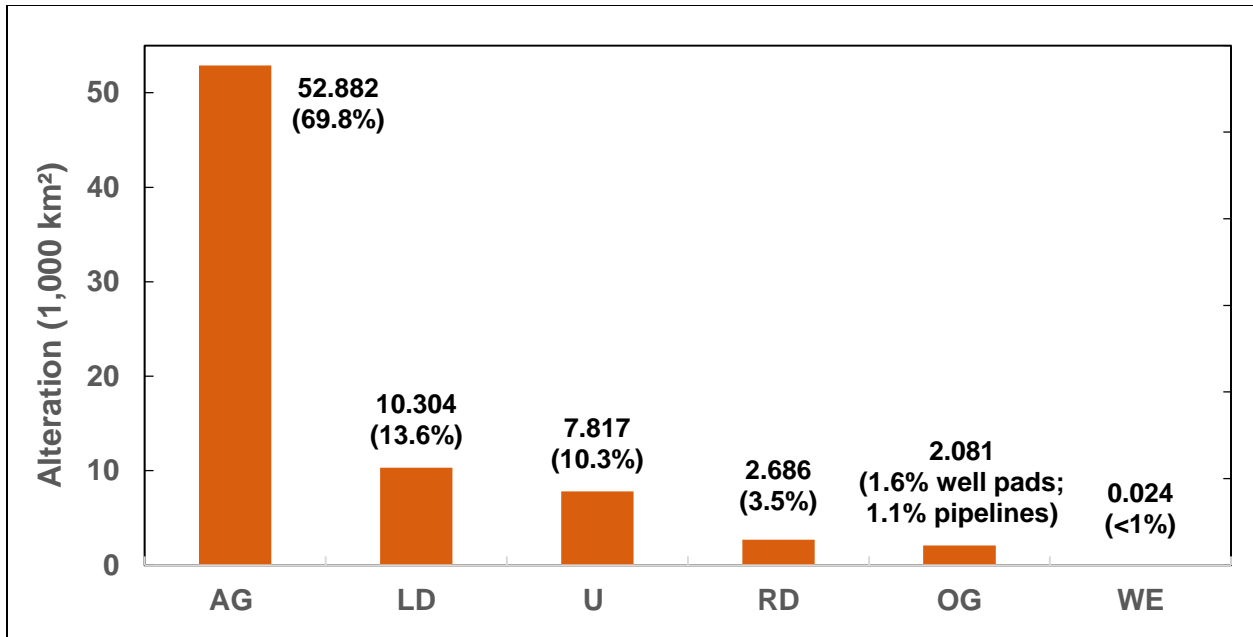
Figure 10.3. Landscape alteration resulting from each anthropogenic factor
Landscape alteration values on figures are reported in square kilometers and, in parentheses, percentage of total landscape alteration resulting from each anthropogenic factor (due to rounding percentages do not add up to 100%).
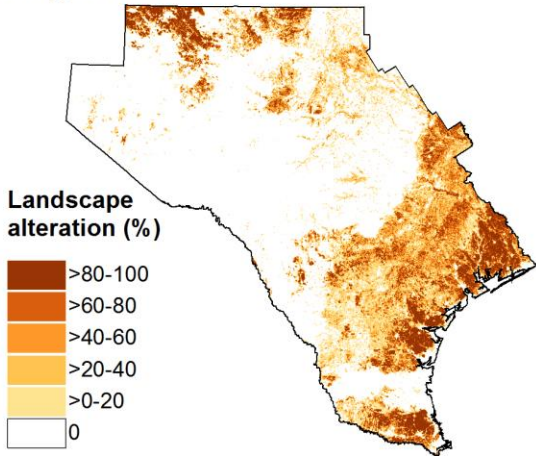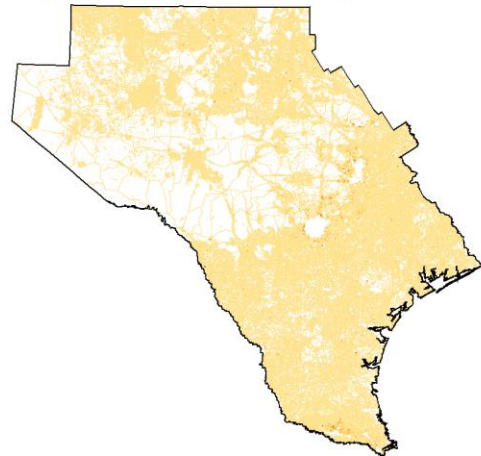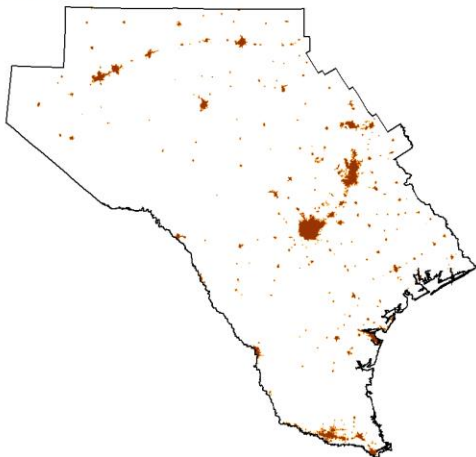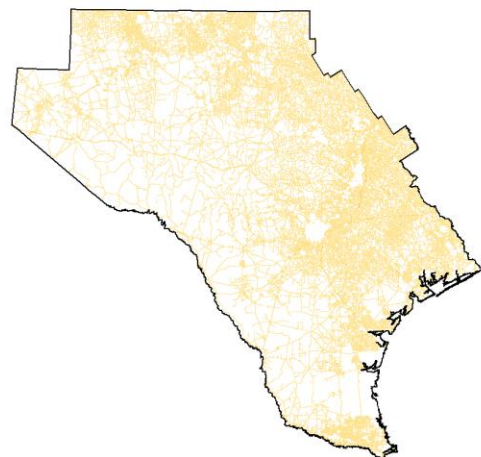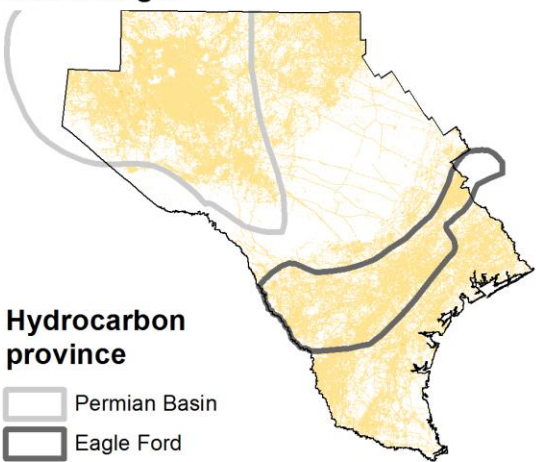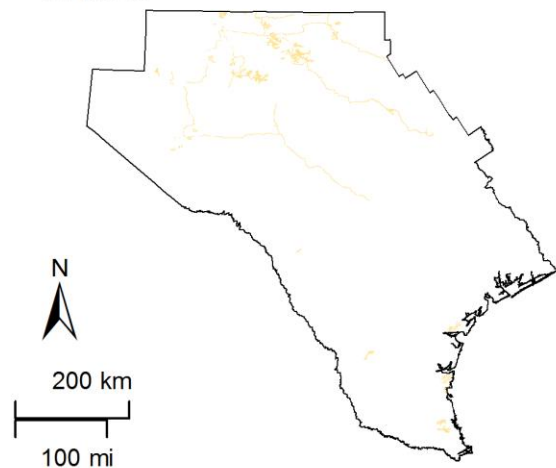
Figure 10.4. Landscape alteration, expressed as percent alteration of a 1 km^2 cell
Resulting from (A) agriculture, (B) low–intensity development, and (C) urbanized areas, (D)
TxDOT roads, (E) oil and gas, and (F) wind energy.

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Table 10.1. Landscape alteration within each ecoregion resulting from each anthropogenic factor
UA=unaltered area, A=agriculture, LD=Low-intensity development, U=urbanized areas, RD=roads, OG pads=oil and gas drilling pads, OG pipelines=oil and gas pipelines, Wind pads=wind turbine pads, Wind transmission=high voltage wind energy transmission lines.

| | Alteration by factor (km²) | | | | | | | | | Total alteration in ecoregion | Total ecoregion area |
| | non-energy | | | | | energy | | | | | |
Ecoregion	UA	A	LD	U	RD	OG pads	OG pipelines	Wind pads	Wind transmission		
Western Gulf Coastal Plain	18,484.2	18,142.6	1,584.9	1,725.4	400.2	99.1	106.4	2.3	-	22,060.8	40,545.0
East Central Texas Plains	13,425.4	8,711.3	1,048.8	284.7	312.7	100.1	75.1	0.0	-	10,532.6	23,958.1
Southern Texas Plains	43,359.5	6,723.1	2,048.8	527.9	297.5	226.8	201.2	0.6	-	10,025.8	53,385.3
Texas Blackland Prairies	5,471.1	5,902.8	826.4	2,092.6	278.0	34.5	18.2	-	-	9,152.5	14,623.5
High Plains	17,589.9	6,010.5	674.3	646.3	207.7	341.2	112.9	0.9	0.5	7,994.3	25,584.2
Central Great Plains	16,292.4	3,909.8	1,069.0	568.9	236.0	46.2	21.0	0.8	1.9	5,853.7	22,146.1
Edwards Plateau	70,936.4	424.1	1,599.3	1,250.2	451.1	165.9	126.8	6.0	4.1	4,027.4	74,963.8
Cross Timbers	18,399.6	1,588.1	899.5	513.1	235.8	33.6	26.7	0.5	2.4	3,299.7	21,699.3
Southwestern Tablelands	8,895.4	1,222.9	309.4	84.5	86.6	31.3	13.0	2.2	0.7	1,750.7	10,646.1
Chihuahuan Deserts	34,478.6	243.5	241.9	121.0	180.2	164.0	137.1	0.4	0.7	1,088.9	35,567.5
Total	247,332.4	52,878.6	10,302.4	7,814.6	2,685.9	1,242.7	838.4	13.5	10.4	75,786.4	
Edge to alteration ratio (km²/km²)	-	0.6	5.4	0.1	13.0	13.7	25.1	25.0	29.6	-	-

Table 10.2. Percent of ecoregion altered by each anthropogenic factor
UA=unaltered area, A=agriculture, LD=Low-intensity development, U=urbanized areas, RD=Roads, OG pads=oil and gas drilling pads, OG pipelines= oil and gas pipelines, Wind pads=wind turbine pads, Wind transmission=high voltage wind energy transmission lines.

| | Percent of ecoregion altered by each factor | | | | | | | | |
| | non-energy | | | | energy | | | | |
Ecoregion	A	MD	U	TD	OG pads	OG pipelines	Wind pads	Wind transmission	Total ecoregion alteration
Texas Blackland Prairies	40.4	5.7	14.3	1.9	0.2	0.1	-	-	62.6
Western Gulf Coastal Plain	44.7	3.9	4.3	1.0	0.2	0.3	-	-	54.4
East Central Texas Plains	36.4	4.4	1.2	1.3	0.4	0.3	-	-	44.0
High Plains	23.5	2.6	2.5	0.8	1.3	0.4	-	-	31.1
Central Great Plains	17.7	4.8	2.6	1.1	0.2	0.1	-	-	26.5
Southern Texas Plains	12.6	3.8	1.0	0.6	0.4	0.4	-	-	18.8
Southwestern Tablelands	11.5	2.9	0.8	0.8	0.3	0.1	-	-	16.4
Cross Timbers	7.3	4.1	2.4	1.1	0.2	0.1	-	-	15.2
Edwards Plateau	0.6	2.1	1.7	0.6	0.2	0.2	-	-	5.4
Chihuahuan Deserts	0.7	0.7	0.3	0.5	0.5	0.4	-	-	3.1

Table 10.3. Well pad size and number of wells per pad in Permian Basin and Eagle Ford

Region	Number of Well pads	Well pad size (m^2)		Wells per pad	
		Mean	Median	Mean	Median
Study Area	354,615	3,619	1,500	1.21	1
Permian	195,713	3,760	2,100	1.15	1
Eagle Ford	7,076	16,970	16,200	2.02	2
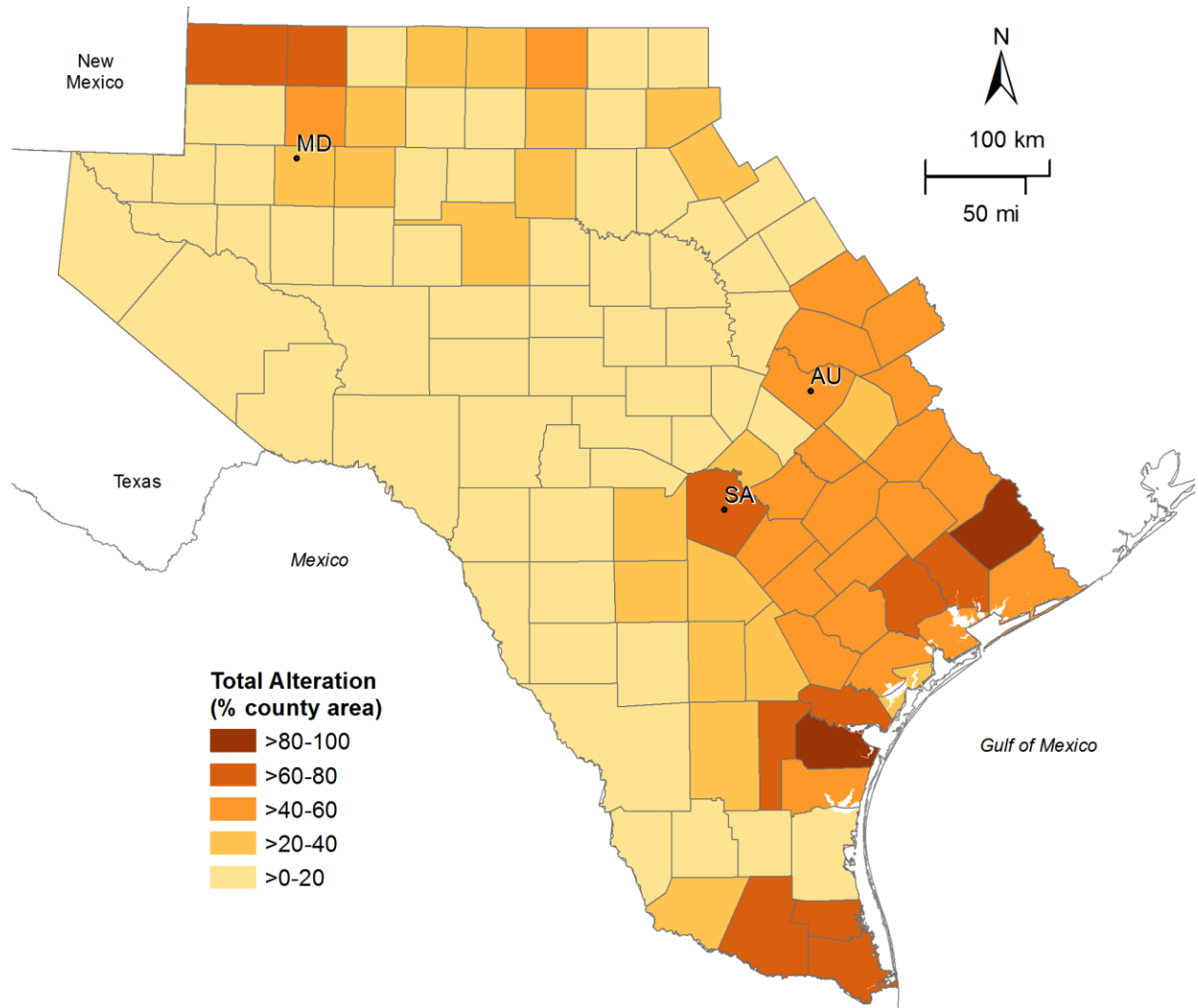
Figure 10.S1. Total landscape alteration aggregated by percent of county area
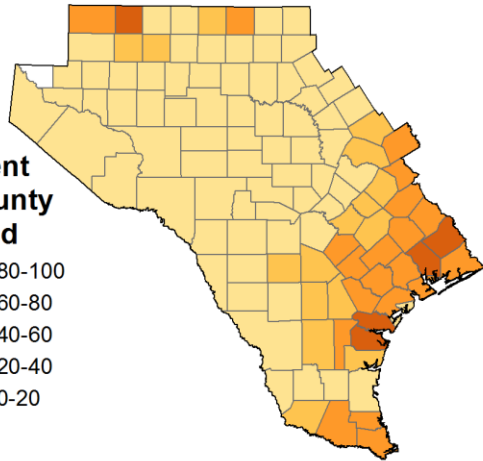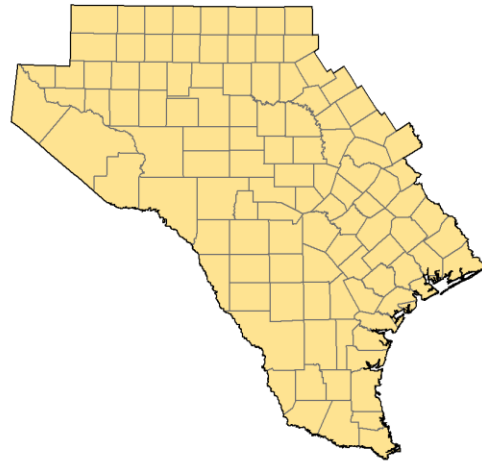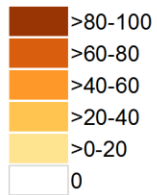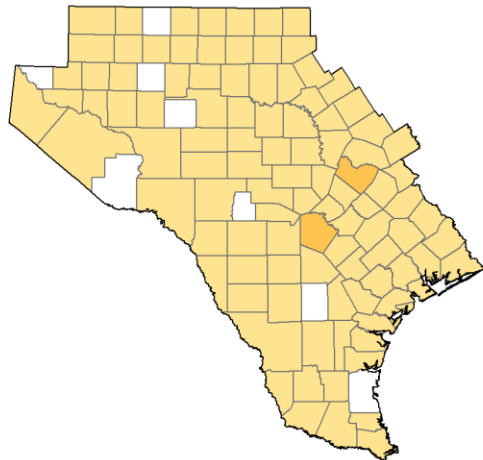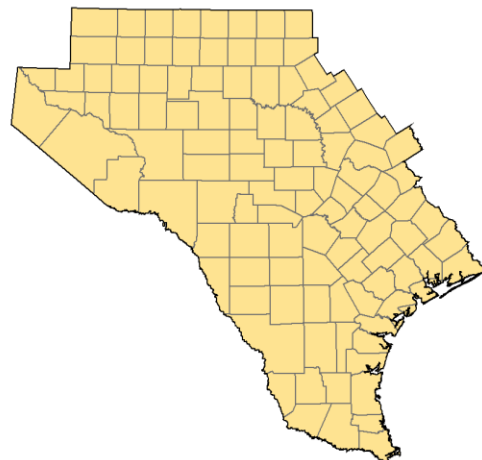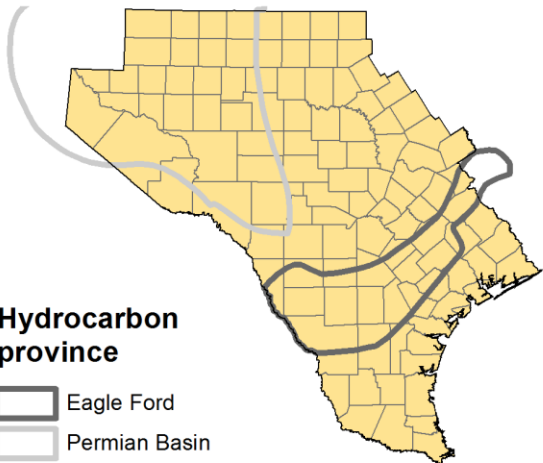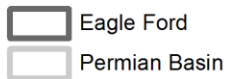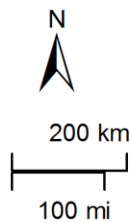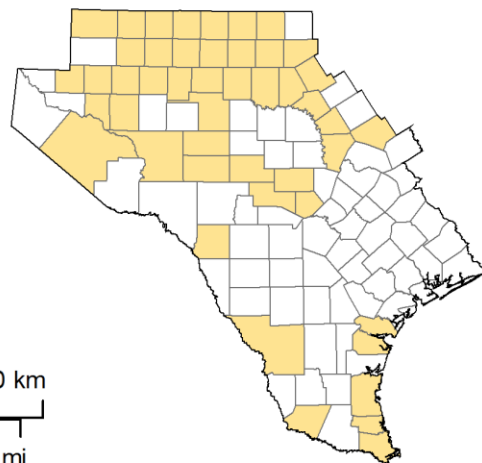
Figure 10.S2. Percentage of total landscape alteration area aggregated at the county level for each factor

Note that larger county areas may inherently have larger values. These maps do not necessarily reflect density (or intensity) of alteration

A. Agricultural

(km²)
- 1,395 - 2,125
- 774 - 1,394
- 399 - 773
- 111 - 398
- 0 - 110

B. Low–intensity development

(km²)
- 214 - 317
- 126 - 213
- 88 - 125
- 51 - 87
- 1.7 - 50

C. Urban

(km²)
- 558 - 1,319
- 223 - 557
- 88 - 222
- 30 - 87
- 0 - 29

D. Roads

(km²)
- 42 - 67
- 31 - 41
- 22 - 30
- 14 - 21
- 2.7 - 13

E. Oil and gas

(km²)
- 58 - 118
- 25 - 57
- 13 - 24
- 6 - 12
- 0 - 5

F. Wind energy

(km²)
- 1.3 - 2.8
- 0.34 - 1.2
- 0 - 0.3

N

200 km

100 mi
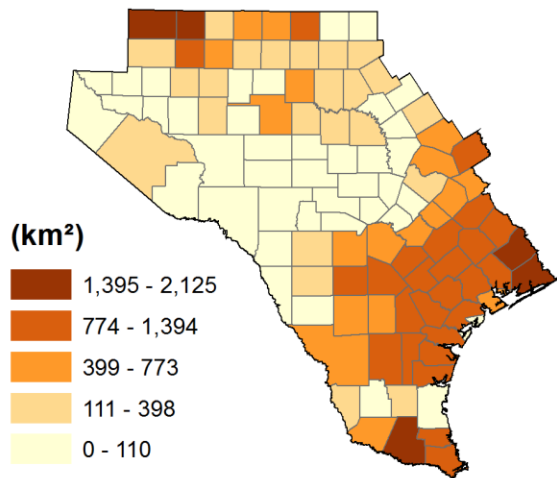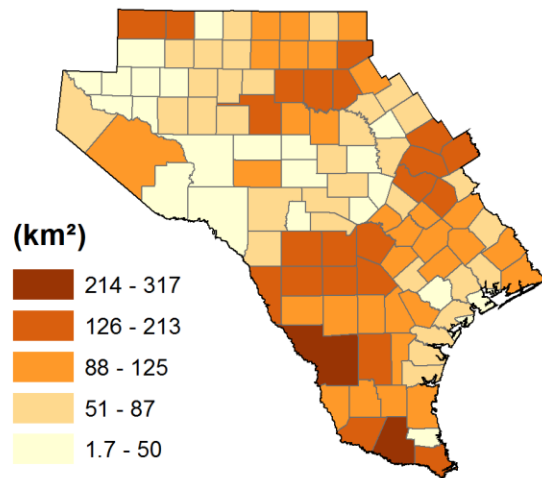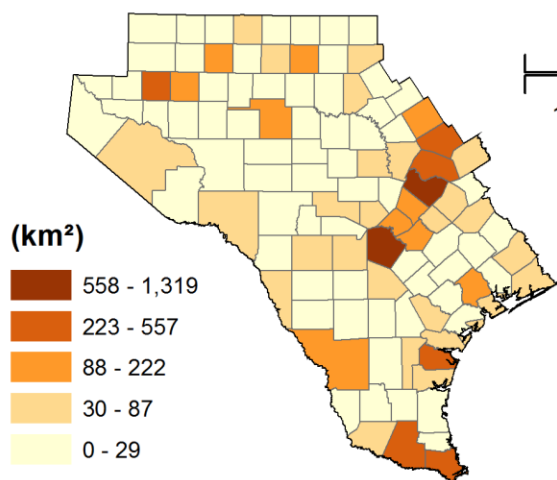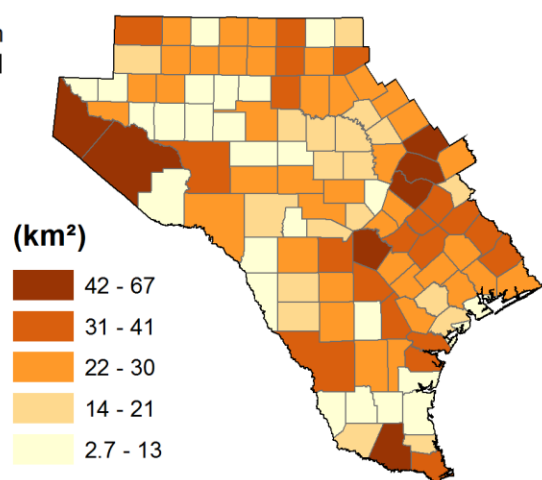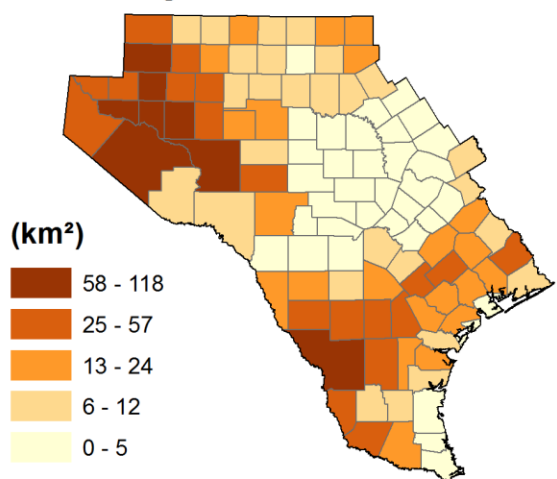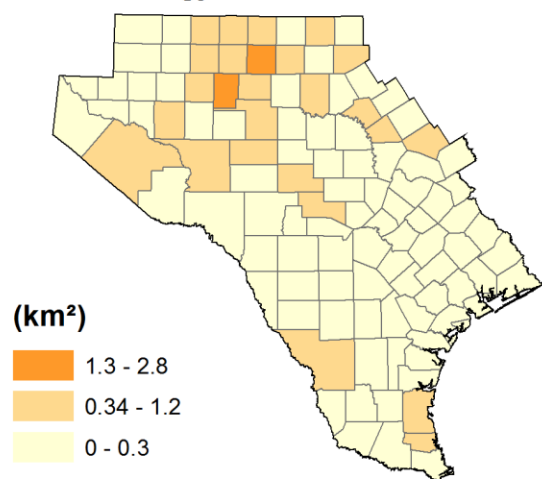
Figure 10.S3. Landscape alteration area aggregated at the county level for each factor
Note that larger counties may inherently have larger values. These maps do not necessarily reflect density (or intensity) of alteration

Table 10.S1. Reclassification of National Land Cover Database (NLCD) values

NLCD Value	NLCD Classification	Reclassification of NLCD values
21	Developed, Open Space	Low intensity development
22	Developed, Low Intensity	Low intensity development
23	Developed, Medium Intensity	Low intensity development
24	Developed, High Intensity	Low intensity development
81	Pasture/Hay	Agriculture
82	Cultivated Crops	Agriculture

Table 10.S2. Hierarchical reclassification of overlapping alteration layers
When landscape alteration resulting from two or more factors overlapped, the lowest value
(i.e., highest priority) was selected to represent landscape alteration.

Overlapping alteration layers	Reclassification hierarchy
Urban areas	1
Roads	2
Oil and gas pads	3
Oil and gas pipelines	4
Wind turbine pads	5
High voltage transmission	6
Agricultural areas	7
Low intensity development	8

CHAPTER 11. ANTHROPOGENIC LANDSCAPE ALTERATION FROM FUTURE EAGLE FORD DEVELOPMENT, PERMIAN BASIN DEVELOPMENT, AND OTHER FACTORS

CHAPTER 11.1. EFFECTS OF FUTURE EAGLE FORD SHALE PLAY DEVELOPMENT ON LANDSCAPE

This task assesses the spatial extent of landscape alteration resulting from future well pad construction in the Eagle Ford Shale Play through 2045. To this end, we applied an energy production outlook model, which used geologic and economic data from thousands of wells and three oil price scenarios, to map future drilling patterns and evaluate the spatial distribution of vegetation conversion and potential habitat impacts. This spatially-explicit approach forecasted where future well pad construction may be most intense and found important vegetation conversion in grassland and cropland habitats.

Summary

Directional well drilling and hydraulic fracturing has enabled energy production from previously inaccessible resources, but caused vegetation conversion and landscape fragmentation, often in relatively undisturbed habitats. We improve forecasts of future ecological impacts from unconventional oil and gas play developments using a new, more spatially-explicit approach. We applied an energy production outlook model, which used geologic and economic data from thousands of wells and three oil price scenarios, to map future drilling patterns and evaluate the spatial distribution of vegetation conversion and habitat impacts. We forecast where future well pad construction may be most intense illustrating with an example from the Eagle Ford Shale Play of Texas. We also illustrate the ecological utility of this approach using the Spot-tailed Earless Lizard (*Holbrookia lacerata*) as the focal species, which historically occupied much of the Eagle Ford and awaits a federal decision for possible Endangered Species Act protection. We found that ~17,000–45,500 wells would be drilled 2017–2045 resulting in vegetation conversion of ~26,485–70,623 ha (0.73–1.96% of pre-development vegetation), depending on price scenario ($40–$80/barrel). Grasslands and row crop habitats were most affected (2.30 and 2.82% areal vegetation reduction). Our approach improves forecasts of where and to what extent future energy development in unconventional plays may change land-use and ecosystem services, enabling natural resource managers to anticipate and direct on-the-ground conservation actions to places where they will most effectively mitigate ecological impacts of well pads and associated infrastructure.

Introduction

To support both domestic and international energy demands, total energy production in the United States (US) is predicted to rise 20% by 2040 (EIA 2017a). Meeting these energy demands will almost certainly increase the land-use footprint of energy development (Trainor et al. 2016) with implications for biodiversity and ecosystem services (e.g., McDonald et al. 2009).

In particular, while energy markets are subject to uncertainty (i.e., technological improvements, demographic and economic trends, and resource availability are difficult to

forecast), energy production from unconventional shale oil and gas plays may double by 2040 due to recent technological advances (i.e., directional drilling and hydraulic fracturing; EIA 2017a). This highlights the importance of mapping and quantifying changes in vegetation and habitat fragmentation that resulted from new well pads, pipelines, and other oil and gas production infrastructure (Allred et al. 2015; Drohan et al. 2012; Entrekin et al. 2015; Jones et al. 2015; Moran et al. 2015; Moran et al. 2017; Pierre et al. 2015; Pierre et al. 2017; Slonecker et al. 2014). Equally important as retrospective studies assessing how energy development affected the landscape is the development of techniques to forecast the extent of land use change and ecological impacts which may result from future drilling.

Recent improvements have been made in oil and gas production outlook models, which use rich geological and hydrocarbon production databases with economic modeling to predict future drilling patterns in terms of location and number of wells. Such approaches have been applied in the Barnett, Fayetteville, Haynesville, and Eagle Ford plays (Browning et al. 2013; Gülen et al. 2015; Gülen et al. 2014; Ikonnikova et al. 2014). However, these drilling forecasts have not considered how forecasted energy development may alter the landscape and potentially impact ecosystems. To this end, advances have been made in predicting ecological impacts which may result from future drilling and well pad construction. For example, forecasts of cumulative ecosystem service losses were estimated for development of several major US unconventional plays through 2040 (Moran et al. 2017).

We recognize that all parts of a play do not develop similarly (Pierre et al., 2017) and that the distribution of drilling across the landscape is fundamentally controlled by the underlying geology and well economics. Thus, we present an approach to forecast ecological impacts that may be expected from future drilling in unconventional oil and gas plays by (1) incorporating geologic and economic data which control expected drilling and (2) adding a spatial component to drilling forecasts and associated vegetation and habitat effects. We illustrate this approach with the rapidly expanding Eagle Ford Shale Play of Texas; however, the improved methods we present can be used to forecast ecological effects of future drilling in unconventional plays globally. The number of drilling permits in the Eagle Ford peaked in 2014 (5,613), reached a low in 2015 (1,119), and increased through November 2017 (the most recent data available) to nearly 2,000 as oil price recovered from a low in 2016 (Figure 1a; RRC 2018); thus, the play continues to be an important hydrocarbon source. We also illustrate the ecological utility of this approach using the Spot-tailed Earless Lizard (*Holbrookia lacerata*) as the focal species, which historically occupied much of the Eagle Ford (Axtell 1998) and awaits a federal decision for possible Endangered Species Act protection because of a historic decline in the past 70 years. The decline is not necessarily tied to energy expansion, but is potentially exacerbated by anthropogenic habitat alterations such as invasive vegetation and fauna and urbanization, which may follow land-use changes associated with drilling. To our knowledge, this is one of the first or few spatially-explicit forecasts of unconventional play development to integrate geologic and economic insights to more realistically assess where drilling may occur and estimate the ecological impacts such energy infrastructure development.

The Eagle Ford is an unconventional play where drilling and associated land-use changes expanded rapidly. Drilling took off in 2010 and continued until a precipitous oil price decline in 2014 (Figure 1; Figure S1). Prices remained under $50 per barrel and drilling since 2015 has been modest. However, the play remains economically important and produced ~15% of U.S. oil in March 2017 (EIA 2017b). While technological innovations enabled development in the Eagle Ford, energy price now limits drilling. We used a recent study, which modeled the probability of

drilling and resulting drilling density for new Eagle Ford wells drilled through 2045 for three oil price scenarios (Ikonnikova et al. 2017). This approach used a unique geologic dataset of ~11,000 existing wells to evaluate the play's productivity and a spatially-explicit economic model to map the geography of expected drilling. Using this forecast of likely drilling patterns, we distributed future well pads throughout the play and assessed vegetation conversion and habitat impacts resulting from well pad construction. Impacts to major ecoregions in the Eagle Ford were assessed by classifying vegetation types of affected habitats (Figure S1). We illustrate this approach for a single species in a specific unconventional play (i.e., *H. lacerata* in the Eagle Ford Shale Play); however, this novel method can be applied to analyze future drilling and resulting vegetation and habitat alteration in unconventional oil and gas plays occupying other environments globally with implications for a variety of taxa and communities.

Methods and materials

Future drilling patterns

We used for our study a mapping of projected drilling patterns in the Eagle Ford through 2045 generated by a comprehensive production outlook model (Ikonnikova et al. 2017). This model assigned for the entire play a probability of drilling and resulting drilling density based on (1) productivity expectations using comprehensive geologic and petrophysical analyses from existing wells and (2) economic assumptions, including oil and natural gas prices and cost projections. Profitability and corresponding probability of drilling were mapped for the entire play using an estimate of the total number of wells already drilled per unit area (1 mi^2, ~259 ha), distance to existing infrastructure, historical oil and natural gas decline data, projected well spacing, and expected energy prices (after Gherabati et al. 2016; Gülen et al. 2014; Ikonnikova et al. 2014; Male et al. 2016). As energy price is the primary factor affecting well drilling (Weijermars 2014), drilling development uncertainty was captured by assessing three energy price scenarios: \$40, \$50, and \$80/barrel, which represent the lowest observed price (on an annual basis), current price, and the most likely future high price from the U.S. Energy Administration's energy outlook (Ikonnikova et al. 2017). Natural gas prices also affect well economics and therefor drilling dynamics; however, the amount of natural gas produced even in more natural gas rich parts of the Eagle Ford is insufficient to affect drilling dynamics appreciably. For example, modeling by Ikonnikova et al. (2017) revealed that a change in natural gas price of \$1/MMBtu would change a wells' net cash flow by less than 7%. Thus, it is acceptable to forecast projected regional-scale drilling patterns in the Eagle Ford using potential future oil prices.

The production outlook model used a geologic input dataset compiled from 335 well logs, of which 120 had associated petrophysical analyses. These data were used to create maps of Eagle Ford net and gross thickness, porosity, water saturation, and pressure (Hammes et al. 2016). Based on historical oil and natural gas production, hydrocarbon quality (i.e., specific gravity), and directional surveys from ~11,000 wells drilled 2009–2016, a map was developed for areas of similar well productivity (Gherabati et al. 2016; Male et al. 2016) and divided into "tiers" of similar well productivity (following the approach of Gülen et al. 2013). Wells were analyzed for drilling depth and well lateral length. Future well production and profitability was predicted using a cash flow model incorporating each well's production, drilling and operating costs, taxes and royalties, and other factors for the three energy price scenarios (following Gülen et al. 2013; Ikonnikova et al. 2014). We assumed a static price over time, but recognize energy prices and resulting drilling fluctuates and moves around geographically to where drilling is profitable. Operators economically drill wells over the widest geographic area when energy

prices are high. When energy prices decline, drilling moves to high-Btu parts of unconventional plays, which produce oil instead of lower-price natural gas (Gülen et al. 2013).

Vegetation conversion from new well pads

We forecasted the extent and type of vegetation conversion from new well pads. Based on historical prices and observed drilling, estimates were made by Ikonnikova et al. (2017) of the total number of wells that would be drilled for each oil price scenario. Potential drilling locations were identified by mapping wells drilled by the end of 2015 and the outlook model was calibrated using observed 2016 drilling. We buffered horizontal laterals by 250 m and urban areas, roads, rivers and water bodies, state protected areas, cemeteries, and airports were further excluded from potential drilling locations. The number of wells to fill undrilled space for each price scenario was calculated under the assumption that future wells are similar to those drilled 2014–2016 from Information Handling Services (IHS) U.S. Well Database (i.e., well laterals length: ~1,675 m, average lateral spacing: ~150 m). We then assigned likely future drilling locations—and associated well pads—using spatially-balanced random points in ArcGIS. New wells within 90 m of 2014 well pads were assigned to existing well pads. Operator practices vary throughout the play. Thus, we mapped 2014 pads following Pierre et al. (2017) and for each productivity tier calculated the mean pad size and mean number of wells drilled per pad. Vegetation conversion resulting from new pad construction was estimated for each price scenario for major vegetation types (e.g., grassland, row crops, shrubs) using a field-verified database of modeled vegetation (TPWD 2017). We assumed operators would construct future well pads using 2014 well pad attributes and that pre-existing vegetation in a pad's footprint would be completely converted to drilling infrastructure. Because Texas does not require operators to restore drilling sites to pre-existing conditions and considering the play's semi-arid climate, we assumed nominal revegetation of well pads.

Habitat impacts

The Texas Conservation Action Plan (TCAP; TPWD 2012) describes conservation challenges affecting habitats for dozens of species of state and federal interest and guides local and regional natural resource management, conservation, and mitigation strategies. For the three ecoregions overlapping the Eagle Ford (South Texas Plains, East Central Texas Plains, Texas Blackland Prairies; Figure S1), the plan identified energy production and transmission as a priority anthropogenic impact. We quantified total vegetation conversion, identified which vegetation types would be most affected by construction of new well pads for each ecoregion and assessed, and assessed potential ecological implications of this forecasted landscape alteration.

Results

We estimated ~32,000–83,000 wells would be drilled from 2017 to 2045 ($40–$80 per barrel; Table S1). Our assessment of existing well pads found a mean of 1.3–2.9 wells per pad, depending on expected well productivity (Figure S2). The number of potential well pads was reduced to ~17,000–45,500 by assuming operators continue using multi-well pads and by placing wells within 90 m of an existing pad onto that pad. The mean size of well pads constructed through 2014 was 1.5–1.9 ha (Table S1), which we assumed would continue.

Vegetation conversion totaled ~26,485–70,623 ha, or 0.73–1.96% of pre-development vegetation, depending on price scenario (Table 1, Table S2). Heat maps revealed the spatial extent of well pad construction with energy price (Figure 2; GIS files available at: https://doi.org/10.18738/T8/1LLQCM). At $40 per barrel, drilling was constrained to the most productive parts of the play, including wet gas in the northeast. As price increased to $50 per barrel, drilling expanded in wet gas and oil. At $80 per barrel, operators could profitably drill

wells throughout the oil and wet gas parts of the play; however, dry gas was generally too deep to be profitable.

Habitats most likely affected by future drilling included cold deciduous shrubs, grasslands, and cold deciduous forests (up to 28,407, 26,209, and 8,752 ha, respectively; Table 1), which included native bushland/brush, native grassland/savannah, non-native pasture, forests/timberlands, bottomland/riparian, and wetlands (Supporting Documents of Elliott et al. 2014). Grasslands and row crops were the two most affected habitats in terms of percent reduction (up to 2.30 and 2.82%, respectively, depending on ecoregion; Table S2). Habitats of the South Texas Plains ecoregion were most affected in terms of total area, followed by East Central Texas Plains and Texas Blackland Prairies (Figure 3, Table 1). The Texas Blackland Prairies has the highest percent vegetation reduction (1.3–2.2%), while East Central Texas Plains has the highest rate of change in percent vegetation conversion as energy price increased (0.8–2.2%).

Discussion

Estimating current and future impacts of energy infrastructure on land-use is a critical component of future conservation and natural resource management strategies. Forecasting where future development is likely to occur is a poorly understood, but essential question to answer for successful conservation of species' habitats in unconventional plays. Natural resource managers on public and private lands need more accurate maps of expected drilling patterns to effectively plan for and mitigate effects of associated vegetation conversion on biodiversity. To this end—illustrating for the Eagle Ford—our study revealed that up to ~83,000 wells would be drilled in the through 2045 on as many as ~45,500 well pads, causing vegetation conversion of ~26,485–70,623 ha (Table 1; Table S1). While we forecasted probable well pad locations, we did not map potential future locations of associated infrastructure (e.g., surface water impoundments, compressor stations, etc.) or access roads and pipelines that would connect to drilling pads. Also, this study also did not calculate habitat fragmentation because population surveys to assess the current distribution of *H. lacerata* are ongoing. However, similar land-change analyses studies in unconventional oil and gas play have revealed that effects of land-use change extend beyond well pads (Johnson 2010; Drohan and Brittingham 2012; Pierre et al. 2015). For example, Drohan and Brittingham (2012) found that for the Marcellus Shale Play, the median area of land-change (which accounted for ancillary infrastructure, access roads, and pipelines) to be approximately twice the size of the well pad alone. Thus, doubling land-change results of this study (Table 1) would result in a reasonable estimate of overall footprint of all hydrocarbon extractive infrastructure (following the approach of Pierre et al. accepted). In addition, while this study did not formally evaluate fragmentation, the spatial representation of the anthropogenic activity causing changes in land-use would affect fragmentation. For example, well pad construction would cause many point changes in land-use. Conversely, the installation of hydrocarbon pipelines and well pad access roads (which were not directly assessed by this study) would cause long, linear changes in vegetation. Thus, both point and linear changes in land-use would be associated with edge effects which would act to increase the overall impact of land-change.

Grasslands and row crops had the two highest percent reductions from pre-development vegetation (>2% in all ecoregions) for the $80 per barrel scenario, which resulted in essentially all undrilled parts of the play being developed. Most affected, in terms of area, were habitats of cold deciduous shrubs, grasslands, and cold deciduous forests. Percent vegetation reduction was similar for the three ecoregions (~1.8–2.2% for $80 per barrel scenario). Our results are

consistent with findings from other studies. Allred et al. (2015) assessed ecosystem services lost to North American oil and gas infrastructure construction and found that ~70% of total "land degradation" from 2000 to 2012 affected rangelands and croplands. Moran et al. (2017) found disproportionately high ecosystem service losses from unconventional plays to grassland and deciduous forest habitats—and also to agricultural lands, which occupy a relatively small area overall but are economically important. For example, Moran et al. (2017) identified that 7.9% of the area of the eight major U.S. shale plays are "agricultural lands". In the Eagle Ford, agricultural lands comprise a much higher percent of land cover: 32.0% of pre-development vegetation is classified as grasslands (i.e., potentially pasture) and 2.3% as row crops. Thus, understanding potential impacts to the economically important agricultural sector *and* to species utilizing farms and ranches for habitats remains an important research topic in the Eagle Ford and unconventional plays.

We illustrated our approach for the first play-specific evaluation of vegetation and habitat impacts from future well pads in a semi-arid unconventional play—and the only one we are aware of to generate spatially-explicit forecasts of the ecological impacts of drilling in the Eagle Ford. While we recognize that any model forecasting future drilling patterns is uncertain, we found that the spatial extent of drilling that would occur under $80 per barrel would essentially fill all remaining undrilled portions of the play. Thus, this value makes sense as the highest price to model, and, because we assessed a range of reasonable future energy prices, we are confident that we accurately estimated how future Eagle Ford drilling could be expected to impact vegetation and habitats.

We understand that changes in land-use from anthropogenic activities threaten biodiversity globally (Fahrig 2003); however, species-specific responses span a broad range. For example, wildlife-vehicle collisions—such as from increased oilfield traffic—are a primary cause of some species' mortality but may have a nominal effects for other species (Forman et al. 2003). In the case of our focal species, *Holbrookia lacerata*, we suspect the lizard to be an early successional species that may favor certain types of vegetation conversion. However, invasive vegetation and fauna following changes in land-use may adversely affect the species (Axtell 1998). To understand potential threats to the species, we found that drilling would occur in much of the species' historic range within the Eagle Ford at high oil prices. However, the species' habitat does not include forests/timberlands, bottomland/riparian, or wetlands and the effects of drilling in these areas could be nominal. In contrast, future drilling at $80 per barrel in native bushland/brush, native grassland/savannah, and non-native pasture of grasslands and row crops has direct relevance to the species because recent surveys indicate continued persistence at sites with these vegetation types. Conversely, at $40 per barrel, drilling is concentrated in the northeast of the play and potentially affects the species much less. Importantly, if currently low prices were to continue, resource managers would have more time to plan conservation actions before price recovery and drilling expansion to larger portion of the species' historic range.

Identifying potential threats to species' habitat and developing mitigation strategies is essential to biodiversity conservation in expanding unconventional oil and gas plays globally. Our illustration of the approach for *H. lacerata* is relevant to other species in the Eagle Ford. For example, these may include those species identified in the Texas Conservation Action Plan (TPWD 2012), which outlines species of conservation interest, threats to habitats, and proposes conservation strategies. The plan identified effects of oil and gas development in the three ecoregions overlapping the Eagle Ford as potentially causing habitat loss and fragmentation, particularly in drier areas that may not revegetate quickly. In addition, the results of this study

may inform recovery efforts of species currently listed as federally endangered or threatened under the Endangered Species Act (Figure 4; Table 2). Our results reveal where Eagle Ford well pad construction and associated vegetation conversion may be most intense and what portions of species' habitats may require site-specific management actions necessary to achieve recovery of the species.

For species not currently protected by under the Endangered Species Act (such as *H. lacerata*), our future vegetation conversion estimates could inform pre-listing conservation strategies (e.g., Donlan 2014) for these candidate species (Figure 4; Table 2). These could include development of a Candidate Conservation Agreement with Assurances (CCAA), which would outline voluntary strategies to remove or reduce threats to the species. If a species found in the Eagle Ford were federally listed, our study results could also inform a Habitat Conservation Plan (HCP), which would show how impacts to a species would be minimized and mitigated. In the Eagle Ford, mitigation strategies for a CCAA or HCP may include (1) concentrating wells and along pre-existing development corridors, (2) using multi-well pads (Figure S3), (3) focusing development in the play to the least sensitive habitats, and (4) revegetating well pads to native vegetation once operations cease (Jones et al. 2015; Thompson et al. 2015; TPWD 2012). Thus, our forecasts of spatial trends in Eagle Ford drilling could minimize risks to biodiversity *and* potentially save operators money by enabling them to apply mitigation strategies only to where they are needed most.

Conclusions

We present a novel approach to forecast ecological impacts of expected drilling patterns in unconventional shale oil and gas plays. Using an energy production outlook model, which incorporated geologic and economic data from thousands of wells and three oil price scenarios to forecast drilling patterns, we mapped the location of future well pads. This technique improved estimates of future vegetation conversion and habitat impacts by adding a spatial component to forecasts of ecological impacts in developing unconventional oil and gas plays. Illustrating this approach in the Eagle Ford for *H. lacerata*, we found that future drilling and associated well pad construction may cause important reductions in grasslands, row crops, and cold deciduous forests and shrubs. The potential effects of development increased in spatial extent and magnitude as oil price increased from $40 to $80 per barrel. Natural resource managers can use these results to proactively identify where future vegetation conversion and habitat impacts may be greatest so that on-the-ground conservation actions may be optimized to mitigate potential effects of drilling. We illustrated this approach in the Eagle Ford Shale Play of Texas for the Spot-tailed Earless Lizard; however, this novel method can be applied to improve conservation outcomes for a wide range of taxa and communities in other rapidly developing unconventional plays in the U.S. and globally.

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Figure 11.1. Eagle Ford drilling and oil price history

Price history (a) and resulting landscape alteration from December 2008 (b) through December 2016 (c) for a representative portion of the play northeast of Cotulla, TX (southwest corner of

images). Infrastructure construction includes roads, well pads, surface impoundments, storage facilities and railway transport terminal. Note: * indicates well permitted by Texas Railroad Commission for Q1 and Q2 of 2017 (RRC 2018). Imagery: Landsat/Google Earth Pro. Oil price from EIA (2018c).
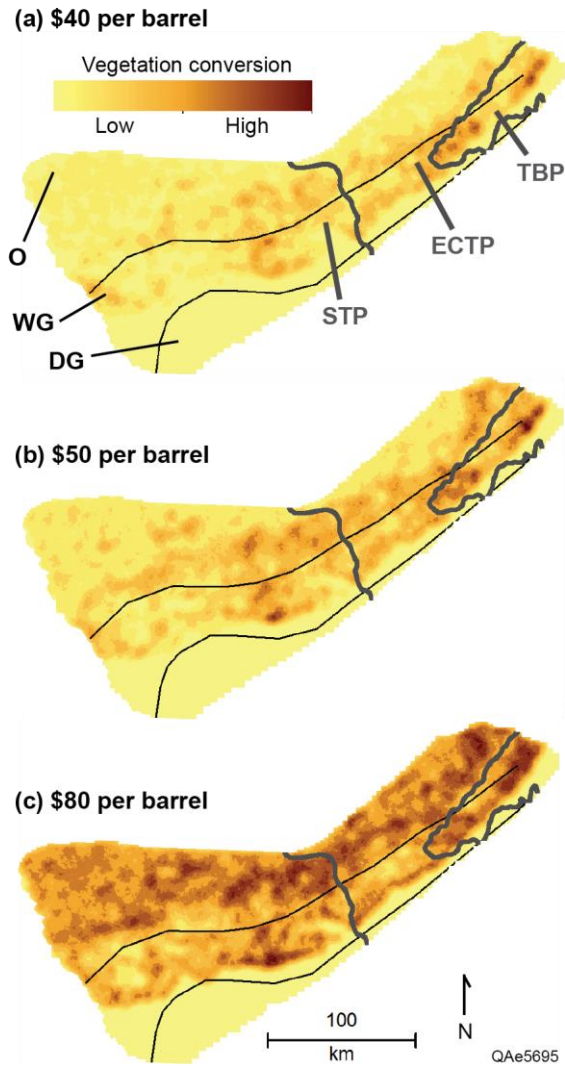
Figure 11.2. Heat map of vegetation conversion from estimated drilling through 2045
For three scenario: low, $40/barrel (a) medium, $50/barrel (b), and high, $80/barrel (c).
Hydrocarbon type: O=oil, WG=wet gas, DG=dry gas (thin black line; U.S. Energy Information
Administration 2014 Updates to the Eagle Ford Play Maps). Ecoregions: STP=South Texas
Plains, ECTP=East Central Texas Plains, TBP=Texas Blackland Prairies (thick dark gray line;
TPWD 2012).
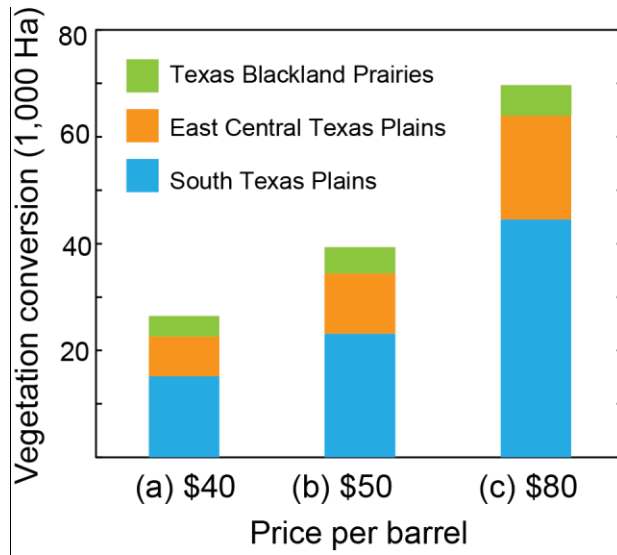
Figure 11.3. Estimated vegetation conversion by ecoregion
Vegetation conversion is resulting from well pad construction through 2045 for each energy price scenario
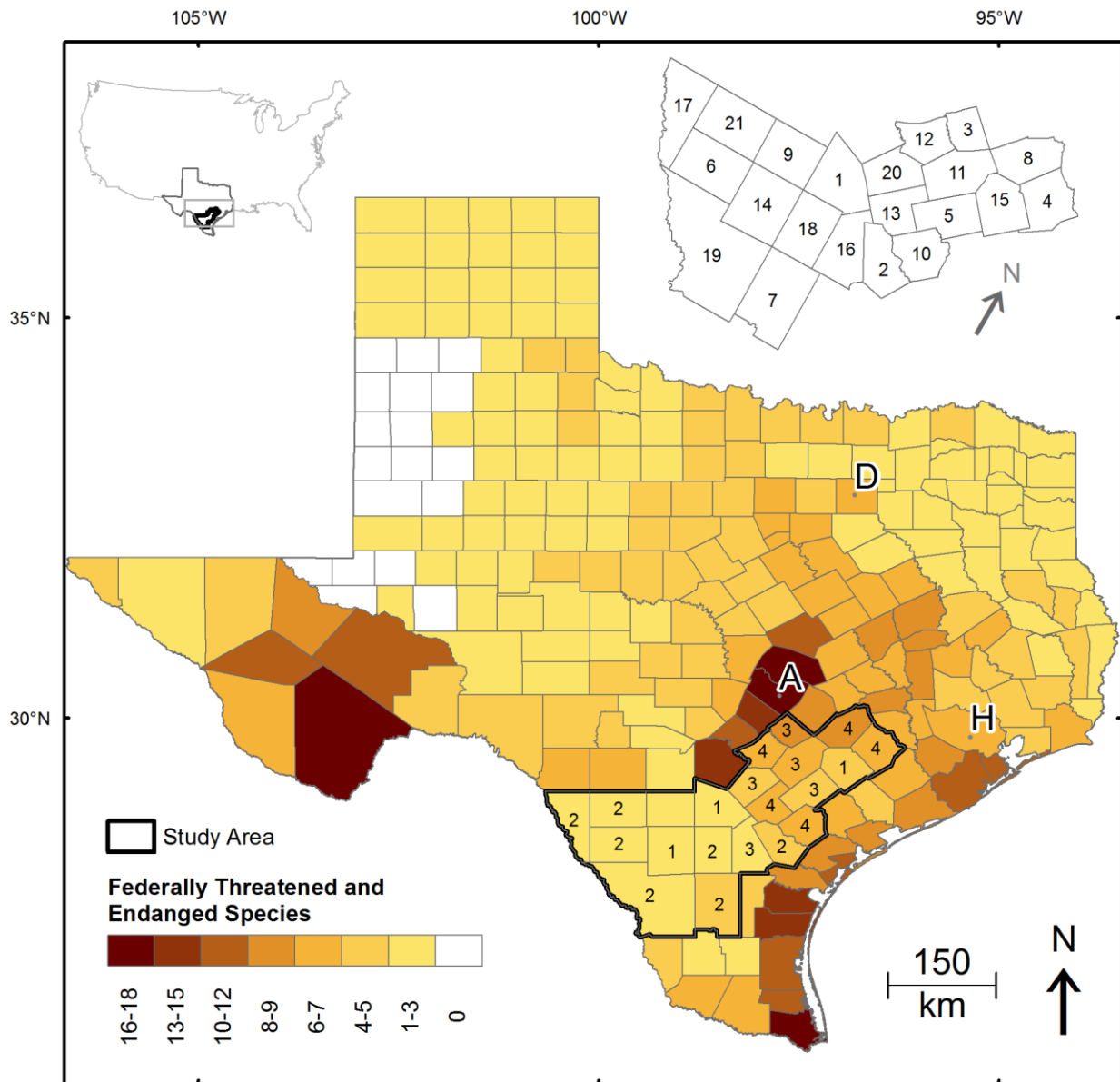
Figure 11.4. Species listed as federally threatened or endangered under the Endangered Species Act (Table 11.2)

A county is considered to potentially include a listed species where it contains an elemental occurrence for a species based on records from the Texas Natural Diversity Database (TNDD; TPWD 2018). The number of candidate species awaiting federal listing determination as threatened or endangered is labeled on counties within the study area (where present). As *Holbrookia lacerata subcaudalis* is not formerly included as a candidate species in TNDD, the historic range is from Axtell (1998). Note that TNDD may not include the results of all population surveys for all species of potential interest and that some federally listed or candidate species may currently be extirpated in some portions (or all) of their historic ranges. The names of counties in study area, which correspond to those in Table 2, are indicated as numbers on the inset map at the top left of this figure and are: 1. Atascosa, 2. Bee, 3. Caldwell, 4. Colorado, 5.

DeWitt, 6. Dimmit, 7. Duval, 8. Fayette, 9. Frio, 10. Goliad, 11. Gonzales, 12. Guadalupe, 13. Karnes, 14. La Salle, 15. Lavaca, 16. Live Oak, 17. Maverick, 18. McMullen, 19. Webb, 20. Wilson, 21. Zavala. A=Austin, D=Dallas, H=Houston.

Table 11.1. Estimated vegetation conversion
Shown as reduction of current hectares from well pad construction through 2045 by ecoregion. Price scenarios are low ($40/barrel), medium ($50/barrel), and high ($80/barrel)

Ecoregion	South Texas Plains				East Central Texas Plains				Texas Blackland Prairies			
	2006 Estimate	2045 Estimate (ha reduction)			2006 Estimate	2045 Estimate (ha reduction)			2006 Estimate	2045 Estimate (ha reduction)		
Vegetation type	(Ha)	Low	Med.	High	(Ha)	Low	Med.	High	(Ha)	Low	Med.	High
CD shrub	1,396,532	8,126	12,269	24,125	167,693	1,494	2,329	3,771	24,203	346	429	510
Grassland	473,479	3,587	5,572	10,536	483,737	4,245	6,256	11,116	198,107	2,642	3,472	4,557
CD forest	239,511	1,709	2,744	4,716	148,071	1,160	1,808	3,265	35,255	534	568	771
EG shrub	190,758	1,008	1,453	2,787	9,469	93	110	203	2,600	14	21	23
Row crops	59,031	369	574	1,318	21,796	211	314	475	3,894	73	90	110
BLEG forest	18,538	102	172	388	20,749	105	159	302	12,202	143	182	269
Urban low	17,849	90	123	217	10,696	61	85	125	3,291	12	21	31
Barren	9,724	75	108	214	4,723	25	71	102	121	0	0	1
Urban high	8,654	26	40	86	2,077	11	11	22	456	1	1	3
NLEG forest	3,493	22	34	63	495	3	4	9	1,185	10	16	18
Open water	12,776	16	24	56	1,014	8	13	19	61	1	0	1
CD mixed forest	2,908	14	16	24	13,567	68	118	232	6,773	61	84	104
Marsh	1,822	8	10	22	1,206	13	13	27	363	3	5	6
Total	2,435,077	15,152	23,139	44,551	885,291	7,496	11,291	19,669	288,511	3,837	4,889	6,402

Notes: BLEG = broadleaf evergreen, CD = cold-deciduous, EG = evergreen, NLEG = needle-leaf evergreen. Swamp and Grass Farm vegetation types had <50 ha for 2006 estimate and were omitted.

Table 11.2. Species of conservation interest within Eagle Ford footprint
Listed as federally threatened or endangered under the Endangered Species Act or candidates for federal listing.
T=Threatened, E=Endangered, C=Candidate for federal listing. Names of counties in study area correspond to those in Figure 4 inset map are: 1. Atascosa, 2. Bee, 3. Caldwell, 4. Colorado, 5. DeWitt, 6. Dimmit, 7. Duval, 8. Fayette, 9. Frio, 10. Goliad, 11. Gonzales, 12. Guadalupe, 13. Karnes, 14. La Salle, 15. Lavaca, 16. Live Oak, 17. Maverick, 18. McMullen, 19. Webb, 20. Wilson, 21. Zavala.

Federal Status	Taxon	Common Name	Scientific Name	Counties which may have species[†]
T	Amphibian	San Marcos Salamander	*Eurycea nana*	3
T	Bird	Piping Plover	*Charadrius melodus*	1, 2, 3, 4, 5, 7, 8, 10, 11, 12, 13, 15, 16, 18, 20
T	Bird	Red Knot	*Calidris canutus rufa*	2, 3, 4, 5, 8, 10, 11, 13, 15
T	Fish	Devils River minnow	*Dionda diaboli*	6, 17
E	Amphibian	Houston Toad	*Anaxyrus houstonensis*	3, 4, 8, 15
E	Amphibian	Texas Blind Salamander	*Eurycea rathbuni*	3, 12
E	Bird	Attwater's Greater Prairie-chicken	*Tympanuchus cupido attwateri*	4, 10
E	Bird	Golden-cheeked Warbler	*Setophaga chrysoparia*	8, 13
E	Bird	Northern Aplomado Falcon	*Falco femoralis septentrionalis*	7
E	Bird	Whooping Crane	*Grus americana*	1, 2, 3, 4, 5, 8, 10, 11, 12, 13, 15, 16, 20
E	Fish	Fountain darter	*Etheostoma fonticola*	3, 11, 12
E	Fish	Sharpnose Shiner	*Notropis oxyrhynchus*	3, 4, 5, 8, 10, 11, 12, 13, 15, 20
E	Fish	Smalleye Shiner	*Notropis buccula*	3, 4, 5, 8, 10, 11, 12, 13, 20
E	Mammal	Ocelot	*Leopardus pardalis*	1, 2, 6, 7, 9, 13, 14, 16, 17, 18, 19, 21
E	Plants	Ashy dogweed	*Thymophylla tephroleuca*	19
E	Plants	Black lace cactus	*Echinocereus reichenbachii var. albertii*	7
E	Plants	Navasota ladies'-tresses	*Spiranthes parksii*	8
E	Plants	Texas prairie dawn	*Hymenoxys texana*	14
E	Plants	Walker's manioc	*Manihot walkerae*	7

C	Bird	Black Rail	*Laterallus jamaicensis*	2, 3, 4, 5, 8, 10, 11, 12, 13, 15, 20
C	Mollusks	Golden Orb	*Quadrula aurea*	1, 3, 5, 10, 11, 12, 13, 16, 18, 20
C	Mollusks	Smooth Pimpleback	*Quadrula houstonensis*	4, 8
C	Mollusks	Texas Fawnsfoot	*Truncilla macrodon*	4, 8
C	Mollusks	Texas Hornshell	*Popenaias popeii*	17, 19
C	Mollusks	Texas Pimpleback	*Quadrula petrina*	3, 4, 5, 8, 10, 11, 12, 13, 20
C	Plants	Bracted twistflower	*Streptanthus bracteatus*	12
C[††]	Reptile	Spot-tailed Earless Lizard	*Holbrookia lacerata*	2, 6, 7, 10, 13, 14, 16, 17, 18, 19, 21

Notes: ([†]) The Texas Natural Diversity Database (TNDD; TPWD 2018) may not necessarily include the results of all population surveys for all species of potential interest and some federally listed or candidate species may currently be extirpated in some portions (or all) of their historic ranges; ([††]) As *Holbrookia lacerata* is not formerly included as a candidate species in TNDD, the historic range of this species is from Axtell (1998).
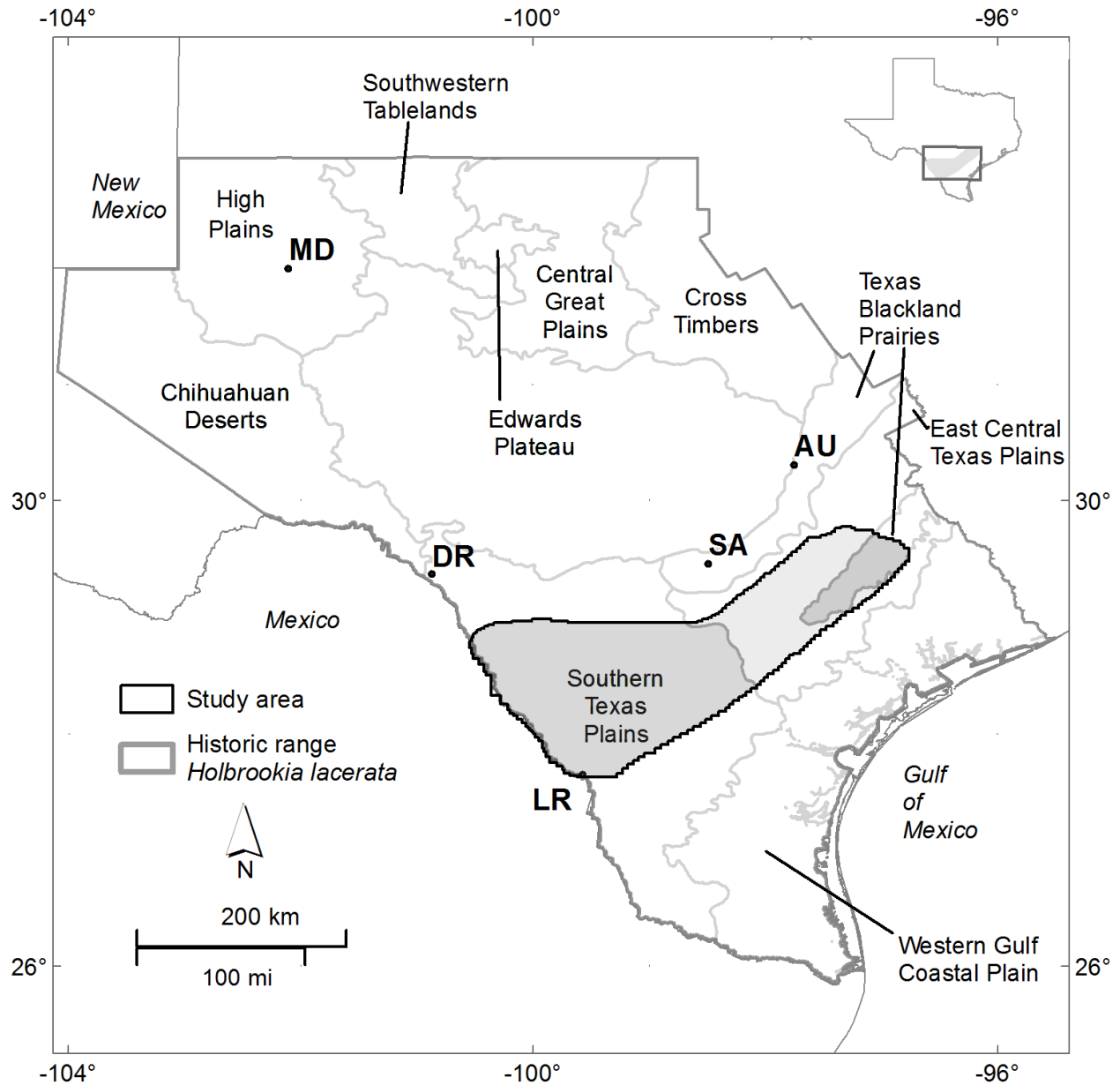
Figure 11.S1. Study area with ecoregions
AU=Austin, DR=Del Rio, LR=Laredo, MD=Midland, SA=San Antonio. Note, historic range of H. lacerata is after Axtell (1998). Counties included in study area: Atascosa, Bee, DeWitt, Dimmit, Frio, Gonzales, Guadalupe, Karnes, La Salle, Lavaca, Live Oak, Maverick, McMullen, Webb, Wilson, Zavala.

(a) Fluid region
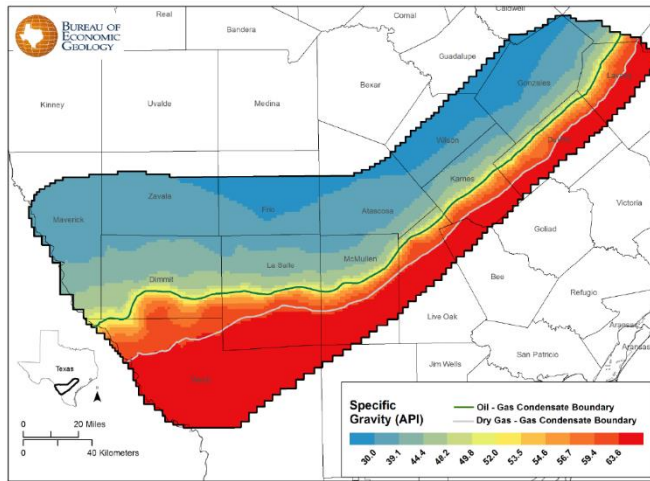
(b) Productivity tiers
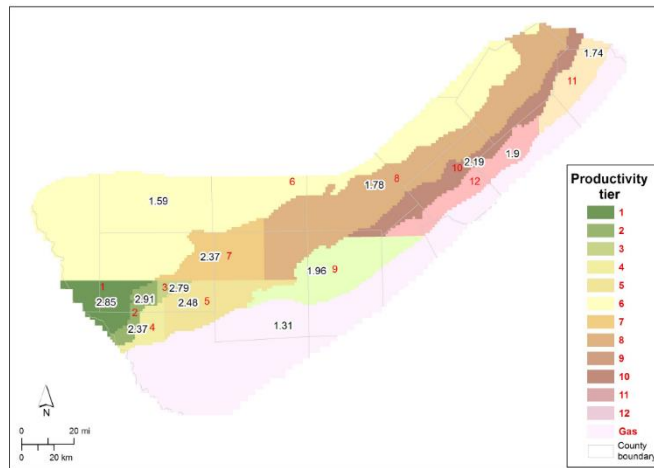
Figure 11.S2. Eagle Ford hydrocarbon quality fluid region
Indicated by American Petroleum Institute (API) specific gravity (a) and productivity tiers of similar fluid and well productivity characteristics (b). Mean number of wells per drilling pad for each tier as of 2014 are labeled and shown in Table 11.S1.
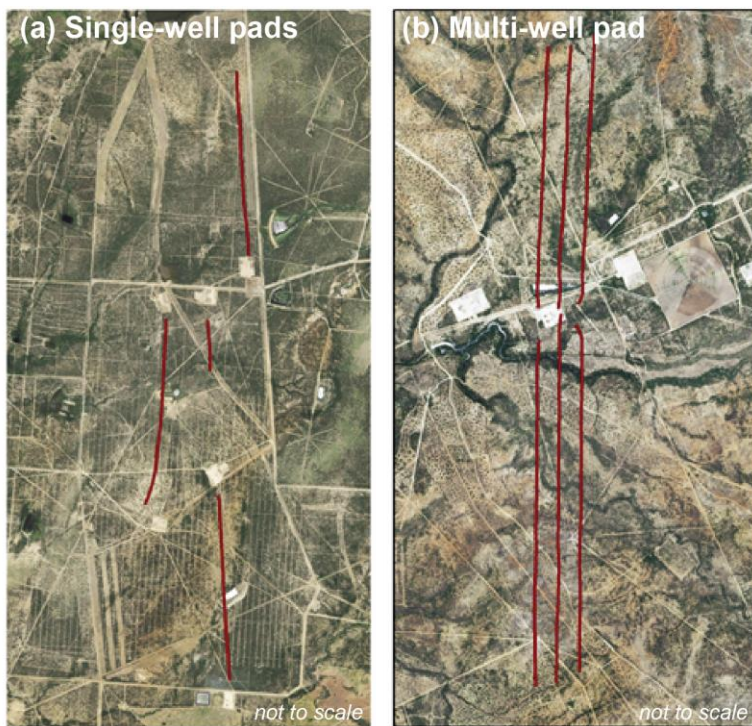
Figure 11.S3. Examples of single-well (a) and multi-well (b) pads
From a representative portion of the Eagle Ford in in La Salle County showing horizontal well laterals (red lines). Mitigation approaches may include using multi-well pads (b) for future drilling. Imagery: Landsat/Google Earth Pro.

Table 11.S1. Estimated wells to be drilled and well pads to be constructed
Well pads needed to accommodate wells to be drilled by 2045

Productivity Tier	2014 Estimate		2045 Estimate Wells to be Drilled			2045 Estimate Well Pads to be Constructed		
	Mean wells per pad	Mean pad size (Ha)	Low	Med.	High	Low	Med.	High
1	2.8	1.8	1,198	1,818	3,137	421	638	1,101
2	2.9	1.8	581	819	1,169	200	281	402
3	2.8	1.5	173	239	347	62	86	124
4	2.4	1.8	549	701	931	232	295	393
5	2.5	1.8	1,197	1,964	3,799	482	791	1,530
6	1.6	1.5	6,078	10,065	26,646	3,813	6,313	16,714
7	2.4	1.5	2,355	3,330	4,848	993	1,404	2,045
8	1.8	1.6	7,808	12,494	19,551	4,392	7,028	10,997
9	2.0	1.8	3,068	4,343	6,389	1,564	2,213	3,256
10	2.2	1.7	3,341	4,248	5,278	1,526	1,940	2,411
11	1.7	1.7	1,913	2,600	3,585	1,099	1,494	2,060
12	1.9	1.9	2,926	3,519	4,153	1,541	1,854	2,188
13	1.3	1.5	998	1,485	3,197	761	1,133	2,438
Total			**32,186**	**47,624**	**83,031**	**17,086**	**25,471**	**45,659**

Table 11.S2. Estimated vegetation conversion
Shown as percent reduction of current hectares for each vegetation type from well pad construction through 2045 by ecoregion.
Price scenarios are low ($40/barrel), medium ($50/barrel), and high ($80/barrel)

Ecoregion	South Texas Plains				East Central Texas Plains				Texas Blackland Prairies			
	2006 Estimate (Ha)	2045 Estimate (% reduction)			2006 Estimate (Ha)	2045 Estimate (% reduction)			2006 Estimate (Ha)	2045 Estimate (% reduction)		
Vegetation type		Low	Med.	High		Low	Med.	High		Low	Med.	High
CD shrub	1,396,532	0.58	0.88	1.73	167,693	0.89	1.39	2.25	24,203	1.43	1.77	2.11
Grassland	473,479	0.76	1.18	2.23	483,737	0.88	1.29	2.30	198,107	1.33	1.75	2.30
CD forest	239,511	0.71	1.15	1.97	148,071	0.78	1.22	2.21	35,255	1.51	1.61	2.19
EG shrub	190,758	0.53	0.76	1.46	9,469	0.99	1.17	2.14	2,600	0.52	0.81	0.90
Row crops	59,031	0.63	0.97	2.23	21,796	0.97	1.44	2.18	3,894	1.87	2.31	2.82
BLEG forest	18,538	0.55	0.93	2.09	20,749	0.51	0.77	1.45	12,202	1.17	1.49	2.21
Urban low	17,849	0.50	0.69	1.22	10,696	0.57	0.79	1.17	3,291	0.36	0.63	0.93
Barren	9,724	0.77	1.12	2.20	4,723	0.52	1.51	2.16	121	0.33	0.21	0.56
Urban high	8,654	0.30	0.46	0.99	2,077	0.53	0.51	1.05	456	0.12	0.13	0.60
NLEG forest	3,493	0.62	0.97	1.80	495	0.68	0.71	1.86	1,185	0.84	1.36	1.48
Open water	12,776	0.13	0.18	0.44	1,014	0.76	1.23	1.90	61	1.26	0.39	0.84
CD mixed forest	2,908	0.49	0.55	0.82	13,567	0.50	0.87	1.71	6,773	0.89	1.24	1.53
Marsh	1,822	0.46	0.54	1.22	1,206	1.05	1.10	2.27	363	0.72	1.48	1.55
Total*	2,435,077	0.62	0.95	1.83	885,291	0.85	1.28	2.22	288,511	1.33	1.69	2.22

Notes: BLEG = broadleaf evergreen, CD = cold-deciduous, EG = evergreen, NLEG = needle-leaf evergreen. Swamp and Grass Farm vegetation types had <50 ha for 2006 estimate and were omitted. *Total percent reduction of vegetation conversion is not a sum of the percent reduction of individual vegetation types.

CHAPTER 11.2. EFFECTS OF FUTURE PERMIAN BASIN DEVELOPMENT ON LANDSCAPE

The objective of this task was to forecast potential future drilling patterns in the Permian Basin. As with the parallel task for the Eagle Ford (Chapter 11.1; Wolaver et al., 2018), the results of this task could be used to understand future vegetation conversion from well pad construction within the historic range *Holbrookia lacerata* to inform development of a Species Status Assessment. We initially investigated the potential of using a similar energy production outlook model to map future drilling patterns and evaluate the spatial distribution of vegetation conversion and habitat impacts. However, well productivity expectations and geologic and petrophysical analyses from existing wells—in addition to economic assumptions, which would include oil and natural gas prices and cost projections—were not available to us. In fact, a large-scale reservoir characterization study needed to apply the same approach used for the Eagle Ford is currently underway by the Bureau of Economic Geology at The University of Texas at Austin, but results will not be available for several years.

Instead of generating forecasts of potential future drilling patterns using an economic model, our literature review of best practices for forecasting future drilling patters revealed that a Maxent model using geologic layers as inputs may be an appropriate approach. This approach associates the location of recently drilled wells (i.e., 2008–2016; IHS, 2016) with a suite of regional geologic and physiogeographic parameters to estimate where future wells are likely to be drilled (following the general approaches of Brand et al. 2014; Copeland et al. 2009; Evans and Kiesecker 2014; Johnson et al. 2010). We would then assess low, medium, high drilling scenarios, informed by the current range of well densities in the Permian Basin.

A great deal of time was invested parameterizing a Maxent model and doing initial runs. However, our modeling attempt using Maxent was not successful. When the Maxent model was run with a suite of input layer informed from previous studies (Table 11.2.1) the model failed to generate reasonable results (i.e., modeled forecasted drilling was random). We suspect that the geologic complexity of the Permian Basin, with over 20 major geologic formations producing hydrocarbons, caused the Maxent approach to fail. In contrast, the Eagle Ford and Marcellus Shale have only one primary producing horizon, which may simplify the geology sufficiently for a Maxent modeling approach to work. Thus, in the Permian Basin, we suspect that because there are so many targets and so many wells, the result of the modeling was not able to identify one or more predictors (i.e., depth to Wolfcamp, thickness of Wolfcamp, etc.) that could be used to forecast future well locations. Therefore, modeling likely future drilling locations in the Permian Basin may require the results of a rigorous large-scale geologic-economic analysis, which will not be available for several years, and using the approach of Wolaver et al. (2018)

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Table 11.2.1. Input Datasets for Maxent Model of Future Permian Basin Development

Datasets	References				Permian Basin Future Study
	1	2	3	4	
Depth of formation (structural contour map)	X	X	X		Top Ellenberger Group (Ordovician) and Top Precambrian (UT BEG datasets).
Thickness of formation (isopach map)	X	X	X		Wolfcamp (Permian). Simpson Group (UT BEG datasets).
Barrels of Oil Equivalent/km^2					Calculated from IHS (2016)
Gravity: Bouguer anomaly		X		X	USGS conterminous gravity anomaly map: https://mrdata.usgs.gov/geophysics/gravity.html
Gravity: With isostatic correction		X		X	USGS conterminous gravity anomaly map: https://mrdata.usgs.gov/geophysics/gravity.html
Magnetic anomaly		X		X	Magnetic Anomaly Map of North America https://crustal.usgs.gov/projects/namad/
Topography (30-m DEM)				X	USGS National Elevation Dataset (NED)
Percent slope (30-m DEM)	X				USGS National Elevation Dataset (NED)
Surface Geology				X	Mineral Resources On-Line Spatial Data, Geology by State: https://mrdata.usgs.gov/geology/state/map.html
Possible # target formations (plays)					Dutton et al. (2005)
Distance to Existing Wells			X		Calculated from IHS (2016)
Distance to pipelines	X				Pipelines digitized from screen captures of U.S. Energy Mapping System: https://www.eia.gov/state/maps.php
Well monitoring data		X			Not available
Thermal maturity (vitrinite reflectance values)	X	X	X		Not available

Notes:

1. Johnson (2010)

2. Evans and Kiesecker (2014)

3. Brand et al. (2014)

4. Copeland et al. (2009)

CHAPTER 11.3. EFFECTS OF ADDITIONAL CURRENT AND FUTURE ANTHROPOGENIC ACTIVITIES ON LANDSCAPE

Effects of other anthropogenic activities on landscape

The purpose of this task is to assess the spatial extent of additional current and future landscape-scale processes that may affect the target species, which are not specifically included in the prior tasks. We evaluated current and future invasive species and fire management as well as future agricultural activity, pesticide use, urbanization, road construction, and wind generation.

Current and Future Red Imported Fire Ants (RIFA)

Research indicates that Red Imported Fire Ants (RIFA) can alter the behavior of lizards and in some case cause lizard mortality (Langkilde, 2009). In Texas, current quarantines exist for RIFA in 188 counties and the City of Lubbock in Texas (USDA, 2016). Within our study area —the home range of *Holbrookia lacerata* buffered by ~one county—quarantines exist in 98 out of 111 counties. We followed the approach of Korzukhin (2001) to project where RIFA may spread within the 111-county study area. Because the study area is south of the high plains and has a warm enough mean annual temperature we did not need to incorporate temperatures into projections (Korzukhin et al., 2001; and personal communication with Sanford Porter co-author). We used the 30-year normal PRISM Climate Group data (PRISM, 2016) and limited projected spreading of RIFA to areas with at least 510 mm of rainfall. Results suggest that within the study area RIFA expansion is likely in Borden, Sterling, Menard, Sutton, Jim Hogg, and Zapata counties (Figure 11.3.1).

Current and future invasive grasses

We investigated the possibility of mapping current and future invasive vegetation, but these databases do not currently exist (Elliott et al., 2014; supporting document provided by Amie Treur-Kuehn via email).

Current and future fire management

We investigated current and future fire management practices in the study area; however, a unified approach for managing fire does not exist across the study area. The Texas A&M Forest Service (2018) notes that 80% of wildfires are responded to by rural fire departments.

Future agriculture

We considered forecasting future agricultural expansion; however, our discussions with Gene Richardson of the Texas Farm Bureau and others (e.g., TAMU land use studies [Anderson et al., 2014]) indicate that the footprint of agriculture is expected to shrink in the coming decades because of expected urbanization. Thus, our discussions suggest that agriculture will have a smaller footprint rather than expand in the future as Texas continues to urbanize.

Future pesticides

Similarly, to agriculture, we do not expect the spatial distribution of pesticide application to increase in area in the future (see Future Agriculture).

Effects of future urbanization on landscape

Urbanization has been identified as a primary cause of extinction in terrestrial ecosystems (Forman et al., 2003; Juffe-Bignoli et al., 2014; Torres et al., 2016). As part of our assessment of landscape alteration as of 2014 within the historic range of *H. lacerata*, we found ~7,800 km^2 of the landscape was converted to urban areas (Pierre et al., 2018). To assess possible future urbanization, we used the Theobald (Theobald, 2005) dataset of forecasted future changes in housing density. To provide low, medium, and high urbanization scenarios, we selected three classes of housing density (Table 11.3.1). Our medium future urbanization scenario most closely

reflects the urban classes used in the 2011 National Landcover Dataset (Jin et al., 2013) and visual inspection of aerial imagery. Results indicate that the southwest unit will continue to experience urban expansion (Figure 11.3.2). Under the low urbanization scenario, the northern study unit may experience very little change from current conditions. However, under the medium and high scenarios the landscape in the northern study area may experience some urbanization around San Angelo. We anticipate the southwest study unit will experience the least amount of landscape conversion due to future urbanization. With the low scenario, the southwestern study unit may not have much urbanization.

Future roads

We contacted TxDOT, but mapping of future roads is not publicly available. A PDF document of planned projects as of August 2015 for FY 2016 was provided to us; however, the individual mapping of each project is reported by district and the effort to contact each of the 25 districts to obtain and then georeference these maps is beyond the scope of this project.

Future wind generation

Wind energy development has been shown to fragment habitat and alter behavior patterns of wildlife (Diffendorfer and Compton, 2014; Kuvlesky et al., 2007). We mapped the 2014 footprint of wind development within the historic range of *H. lacerata* by interpreting aerial photography (Pierre et al., 2018). We used a Federal Aviation Administration (FAA) dataset (FAA, 2016) to map turbines built after 2014 and permitted but not yet built wind turbines. Results indicate that the northern *Holbrookia lacerata* unit will experience the greatest land change if these turbines are built (Figure 11.3.3). The southwest *Holbrookia lacerata* unit will also experience land change. The southwest unit will not be affected by construction of future turbines.

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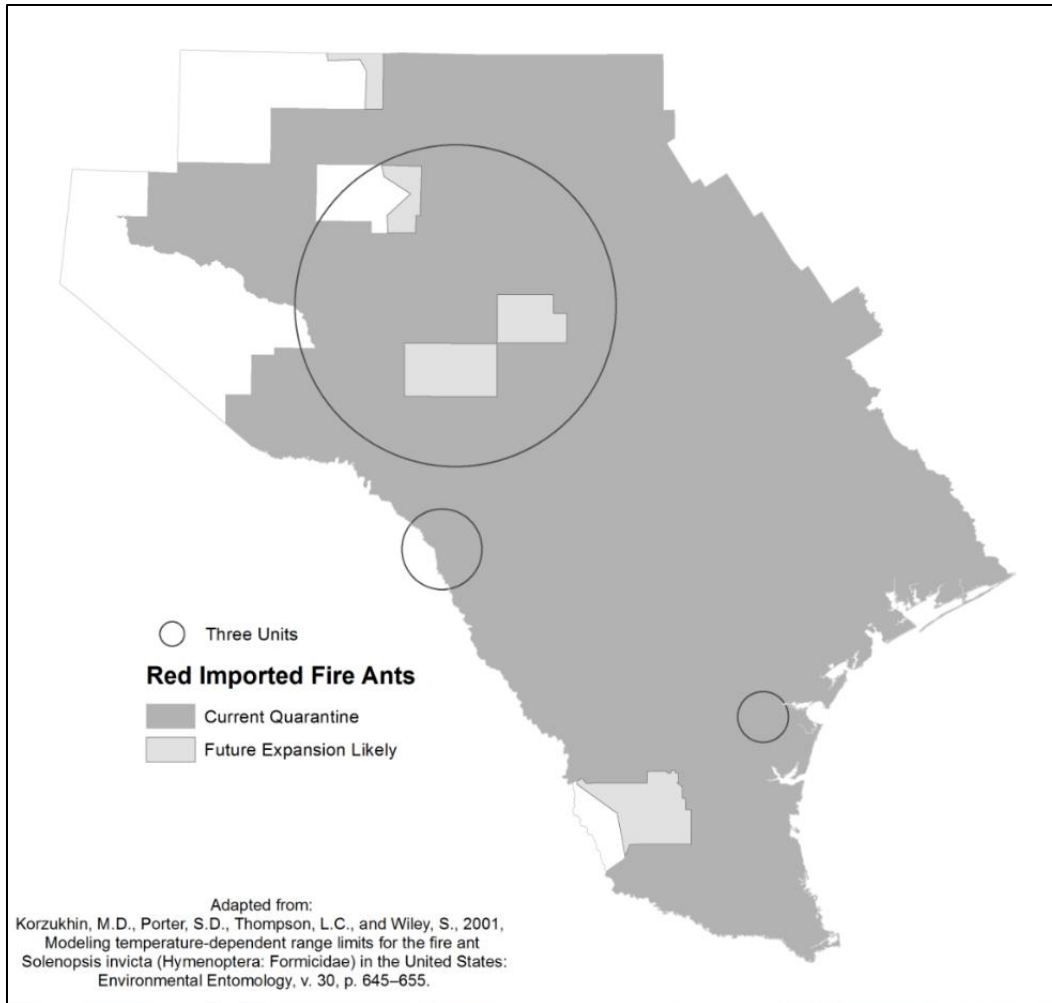
Figure 11.3.1. Forecasted future Red Imported Fire Ant (RIFA) locations

We forecast future red invasive fire ant locations using range limits from surveys and temperature-dependent habitat modeling (Korzukhin et al., 2001). Southeast, Southwest, and North study units indicated by circles.

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Figure 11.3.2. Forecasted future urbanization
We forecast future urbanization using housing density forecasts of Theobald (2005). Southeast, Southwest, and North study units indicated by circles.
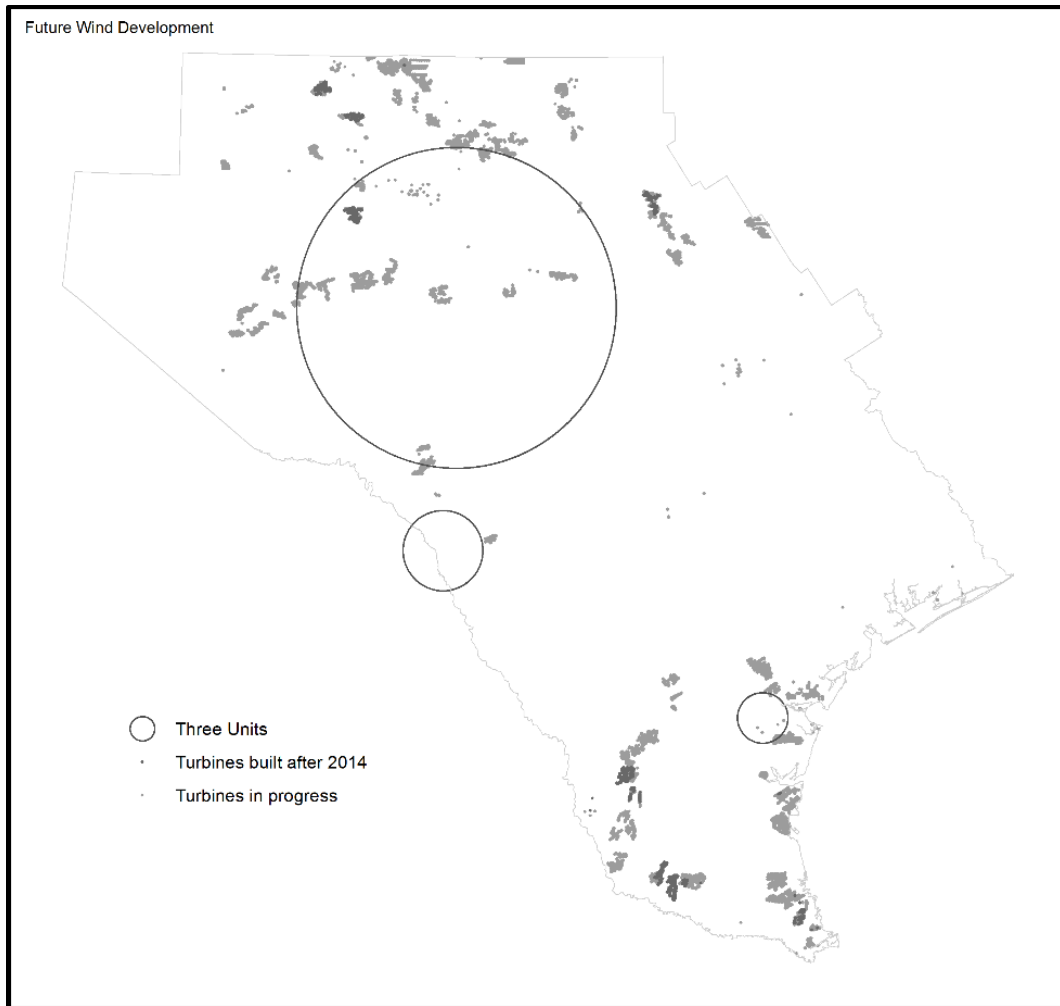
Figure 11.3.3. Forecasted future wind development
We forecast future wind power locations using wind turbines built after 2014 (which were not included in our 2014 landscape alteration study) and also FAA-permitted but unbuilt turbines (FAA, 2016). Southeast, Southwest, and North study units indicated by circles.

Table 11.3.1. Future urbanization scenarios

Future Urbanization Scenarios		
Low	**Medium**	**High**
Commercial and industrial institutions > 10 units per ac 5-9.9 units per ac	Commercial and industrial institutions > 10 units per ac 5-9.9 units per ac 2-4.9 units per ac 0.5-1.6 ac per unit 1.7-4.9 ac per unit	Commercial and industrial institutions > 10 units per ac 5-9.9 units per ac 2-4.9 units per ac 0.5-1.6 ac per unit 1.7-4.9 ac per unit 5-9.9 ac per unit 10-19.9 ac per unit 20-39.9 ac per unit

Note: We forecast urbanization using the classification of housing density of Theobald (2005). Our medium case best matches current urbanization from 2011 NLCD (Jin et al., 2013; MRLC, 2014) and air photo visual inspection.

CHAPTER 12. EFFECTS OF CLIMATE CHANGE AND FUTURE URBANIZATION ON THE SPOT-TAILED EARLESS LIZARD (*HOLBROOKIA LACERATA*)

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Introduction

Historically, *Holbrookia lacerata* occupied much of Central and South Texas (Fig. 1), in open native grasslands with gentle slopes and soils with low sand content (Axtell 1956; Duran et al. 2011). Anthropogenic activities in the lizard's historic range includes the Eagle Ford and the Permian Basin hydrocarbon provinces, in addition to areas that were converted to agriculture or experienced extensive urbanization. After 1970, however, populations of *Holbrookia lacerata* appear to have declined sharply (Axtell 1968; Axtell 1998; Duran and Axtell 2010; Duran et al. 2011). Hypotheses for this decline in *Holbrookia lacerata* reflect trends affecting reptiles globally (Gibbons et al. 2000), including: (1) agricultural practices and pesticide use (Axtell 1998; Chapin et al. 2000; Duran et al. 2011; Flanders et al. 2006; Fulbright et al. 2013; Sparling et al. 2010), (2) introduced invasive species (Duran and Axtell 2010), (3) road construction (direct vehicle contact and habitat fragmentations; Andrews et al. 2008), (4) urbanization (McKinney 2008; Wolf et al. 2013), and (5) energy development. The decline is not necessarily tied to energy expansion, but is potentially exacerbated by urbanization and invasive vegetation and fauna, which may follow land-use changes associated with energy development. Thus, in light of the species' historic decline in population, this species awaits a listing decision by U.S. Fish and Wildlife Service (USFWS) for possible protections under the Endangered Species Act (USFWS 2016).

Anthropogenic climate change is an immediate concern for global biodiversity conservation. It has been well established that changes in the variability and baseline values of climate parameters affect species' ranges; specifically, ranges may shift in space, and also change in size (Bellard et al. 2012; Parmesan 2006; Parmesan and Yohe 2003). These changes may be further affected by anthropogenic disturbances from multiple modalities (Ceballos et al. 2017; Dirzo et al. 2014).

Here we present an analysis of the potential effects of climate change and urbanization on the Spot-tailed Earless Lizard, *Holbrookia lacerata* (Cope 1880) in Texas, USA. The global range of *H. lacerata* is restricted to south and central Texas, as well as adjacent regions of northern Mexico; the majority of its range falls within Texas (Axtell 1968, 1998). *H. lacerata* is

considered to be Near Threatened by the IUCN, and is rare and sparsely distributed within its range. Previous work on the species has found their occurrence to be well predicted by factors related to urbanization, including soil type and vegetation; they are not found in built-up areas (LaDuc et al. 2018).

Methods

Surveys:

Data included in these analyses were collected from surveys conducted in 2010–2016. Surveys conducted in 2010–2014 were performed at sites near historical localities based on soils, slope, and land use (Duran and Axtell 2010). Surveys conducted in 2015–2016 were performed at sites selected through analyses of distribution models (created by The University of Texas on this project), aerial imagery, and historical localities (LaDuc et al. 2018). Surveys were a combination of driving and walking surveys and both types of surveys were conducted in each of the three survey units (e.g., North, Southwest, and Southeast).

Modeling:

We utilized a species distribution modeling framework to conduct this study. Species distribution models (SDMs) are a class of correlative models that predict the spatial patterns of a species' occurrence using a variety of biotic and abiotic factors (see Elith and Lethwick 2009; Guisan and Zimmerman 2000; Miller 2010). In order to understand the potential effects of climate change on the distribution of *H. lacerata*, we based our SDMs on the BIOCLIM variables, a set of climate parameters often used for this purpose (Gschwent et al. 2012; for a similar study using these variables see Langham et al. 2015). We averaged climate data from 2010–2016 from the PRISM climate group, and used this to derive the BIOCLIM variables for current conditions. For predicting future climate, we used a dataset that calculates yearly changes in the BIOCLIM variables under two different carbon emission scenarios, one assuming stabilization at an atmospheric concentration of 450 ppm and the other at 750 ppm (Pearson et al. 2014). These scenarios will be referred to as low emissions (LE) and high emissions (HE) in this manuscript. We chose the years 2050, 2075, and 2100 as our endpoints, in order to examine how the range of *H. lacerata* will shift over time.

Currently, the species exists as three disjunct populations, designated as North (N), Southeast (SE), and Southwest (SW). We analyzed the effects of climate change on the range of each population, as well as on the range of the species as a whole. For each population, we considered the potential range to be every county where *H. lacerata* was recorded during the surveys, plus a one-county buffer; we did the same for the entire range of the species. For the N population, the Pecos River and the Balcones escarpment were considered hard boundaries, and a one-county buffer was not considered.

In order to create maps for the present distribution of each population, we drew 1000 pseudo-absence points at random within the range of the population and extracted the BIOCLIM values at those locations (VanDerWal et al. 2009). These values were then used to create four different maps, using four separate modeling algorithms: support vector machines, random forest, boosted regression trees, and classification and regression trees. The maps were then averaged using the area under the receiver operating characteristic curve (AUC), a global accuracy metric, as a weight in order to obtain an ensemble prediction (Araújo and New 2007; Grenoillet et al. 2011); the AUC of this ensemble was calculated. This process was repeated for 250 distinct sets of

pseudoabsence points, resulting in 250 ensemble predictions, which were then averaged, weighted by their AUCs, to create a final prediction. The maps for future climate scenarios were created by projecting the results of the four modeling algorithms onto future climate maps for each set of pseudoabsences; averaging was then carried out as above, using the present climate AUCs as weights. These maps were also used to calculate the location of the centroid for each range by averaging the latitude and longitude for each raster cell, weighted by the model output (Langham et al. 2015).

In order to calculate the range size from each model, we discretized the output using a threshold, generating presence-absence maps. Threshold selection is a contentious issue in the literature (Liu et al. 2005). We used two different thresholds, corresponding to low-quality and high-quality habitat. In order to calculate these thresholds, we extracted the model output at each known present point; the lower threshold was set as the minimum of these values, and the higher threshold was set as the 10% quantile. This was done for both the present distribution and for future range projections; from this, we calculated the projected change in range size.

Urbanization:

Urbanization has been identified as a primary cause of extinction in terrestrial ecosystems (Foreman et al. 2003; Jueffe-Bignoli et al. 2014; Torres et al. 2016). As part of our assessment of landscape alteration as of 2014 within the historic range of *H. lacerata*, we found ~7,800 km^2 of the landscape was converted to urban areas (Pierre et al. 2018). To assess possible future urbanization, we used the Theobald (2005) dataset of forecasted future changes in housing density. To provide low, medium, and high urbanization scenarios, we selected three classes of housing density (for a complete description, see LaDuc et al. 2018). Our medium future urbanization scenario most closely reflects the urban classes used in the 2011 National Landcover Dataset (Jin et al. 2013) and visual inspection of aerial imagery.

In order to quantify the potential impacts of future urbanization on the range of *H. lacerata*, we overlaid the rasters onto the presence-absence maps described above. We considered areas of medium or high urbanization to be unsuitable for the species. We compared the range size for each population, as well as the entire species, before and after accounting for urban development; we also calculated the percentage of suitable habitat that would be lost to urbanization, both currently and under different climate scenarios.

Results

Figure 12.3 shows the predicted current distributions of *Holbrookia lacerata;* the maps for the current distribution are essentially composites of the maps for the separate populations, as would be expected. Projected distributions for *H. lacerata* are shown in Figure 4.

Our results show that populations of *H. lacerata* are expected to decline under most climate change scenarios (Fig. 12.4; Table 12.1). In particular, the SW population is predicted to lose all available habitat, both low and high quality, by 2050 under either emissions scenario (Fig. 12.4b; Table 12.1b). The North population is also predicted to lose all available high-quality habitat, although low-quality habitat will persist (Fig 12.4a; Table 12.1a). On the other hand, the SE population is predicted to undergo a range expansion (Fig. 12.4c); the bulk of this is expected to happen by the year 2050.

When considering the species as a whole, we expect to see an overall decline in the total available habitat for *H. lacerata* (Fig. 12.4d). The majority of the overall range contraction is

expected to occur before the year 2050 under either climate change scenario. The majority of suitable habitat is expected to coalesce into the SE part of the range; this is in accord with the results from the three populations when projected separately (Fig. 12.4a-c). The lack of concordance between the amount of high-quality habitat in the species-wide map and in the individual population maps is due to a difference in thresholding.

Table 12.2 shows the estimated shift in centroid for each population and for the species as a whole. The N population is expected to shift by over 21 kilometers by the year 2100, with similar shift for both the high and low emissions scenarios; the shift by the year 2050 is expected to be 19.9 kilometers (low emissions) or 14.6 kilometers (high emissions). For the SE population, the expected shift in range is over 9 kilometers by the year 2100 for both the high and low emissions scenarios; the shift by the year 2050 is expected to be 8.3 kilometers (low emissions) and 9.8 kilometers (high emissions). The large values for the SW population are likely a result of the projected extirpation of that population; the shifts for the entire species are a result of a change in the relative sizes of the three disjunct populations and cannot be interpreted directly.

The SE population is the most likely to expand. We therefore examined the projected effects upon this population. The proportion of climatically suitable habitat that overlaps with areas of projected urbanization is expected to increase relative to the present (Table 12.3; Fig. 12.5). Taking this into account, there is an increase expected in the overall habitat available for the SE population; however, almost a fifth of the climatically suitable habitat under certain climate change scenarios may not in fact be available for the species. Most of this urbanization centers around the town of Corpus Christi, which may represent a significant dispersal barrier for the species around the Nueces and Corpus Christi bays.

Our evaluation of urbanization found that recent urban expansion occurred primarily around major metropolitan areas and was focused along transportation corridors (Fig. 12.6a). However, the effects of urbanization on habitat varied spatially, as urbanization also occurred in widely distributed smaller towns across the study area. Results indicate that the southwest unit will continue to experience urban expansion. Under the low urbanization scenario, the northern study unit may experience very little change from current conditions. However, under the medium and high scenarios the landscape in the northern study area may experience some urbanization around San Angelo. We anticipate the southwest study unit will experience the least amount of landscape conversion due to future urbanization. With the low scenario, the southwestern study unit may not have much urbanization. We expect the trend of urbanization of metropolitan areas in Texas to continue in the future (Fig. 12.6c-d; Census 2016).

Discussion

Our results suggest a decline in the range of *H. lacerata* during the remainder of the 21st century due to climate change. The reduction in the size of the species' range is predicted to be greatest for the Northern and Southwestern populations; the Southeastern population is predicted to experience a modest range expansion. In this context, we wish to highlight recent results examining the genetic divergence between the three populations, with the Northern population potentially representing a separate species. The decline in this population is therefore of particular concern.

Our maps of habitat suitability under current climate conditions are largely congruent between the three populations and the species as a whole (Fig. 3). However, the predictions under future conditions are less congruent, making it more difficult to draw conclusions (Fig. 4). This is a well-known issue when attempting to project habitat suitability onto future climate conditions in small geographic areas, since the variance in current climate parameters is small (Anderson 2013; Franklin et al. 2013). As a result, the future climate scenarios are novel from the perspective of the model, and therefore estimating habitat suitability becomes more difficult. As such, we believe that the results of the whole-range model are more indicative of future changes to *H. lacerata* habitat suitability; models based on larger geographical areas, when applied to subregions of that area, are more predictive than models based on smaller regions and extrapolated outwards (Vaughan and Ormerod 2003).

We urge caution in interpreting the results presented here. In particular, there may be factors that mitigate the effects of climate change on the species (Araújo and Peterson 2012). For example, *H. lacerata* may be able to adapt to novel climate conditions, either through evolutionary adaptation or else through trait plasticity (Pearson et al. 2014; Tingley et al. 2012). This may allow for the persistence of *H. lacerata* in areas that are predicted to be climatically unsuitable for the species in the future. On the other hand, it should also be noted that most biotic aspects of the ecological niche of *H. lacerata* have not been included in our models, due to the difficulty of projecting them into the future. For example, the climatic range of *H. lacerata* is expected to include the barrier islands just off the coast of Texas in the Gulf of Mexico, islands currently occupied by a closely related species, *Holbrookia propinqua*. However, *Holbrookia lacerata* has never been found on sandy soils; sandy soils are thought to be a major predictor in the distribution of *H. propinqua* (Axtell 1998). In addition, there is the question of whether *H. lacerata* will be able to disperse successfully to all areas that the model indicates will be climatically suitable (Anderson 2013; Schloss et al. 2012); including the previously highlighted part of the eastern Edwards Plateau where the species is currently absent. It is therefore plausible that our results concerning the N and SW populations are unduly pessimistic; it is however also plausible that our results concerning the SE population are unduly optimistic.

Field research using radio telemetry, initiated in 2017 and continuing through 2019, is focused on understanding habitat use and home range size in *Holbrookia lacerata* at different sites across the entire range of the lizard. Results from this work will better inform land managers as to the importance of abiotic and biotic factors unique to each population unit as well as those important factors that are shared by populations in all three units. Understanding habitat use at a fine scale in different habitats utilized by this species (e.g., disturbed grasslands, row crops) will allow future workers to more closely tailor evolving climate change emission scenarios to potential changes in specific habitat or microhabitat types. These refined predictions will in turn allow for more effective conservation efforts towards managing for quality habitat for *Holbrookia lacerata*.

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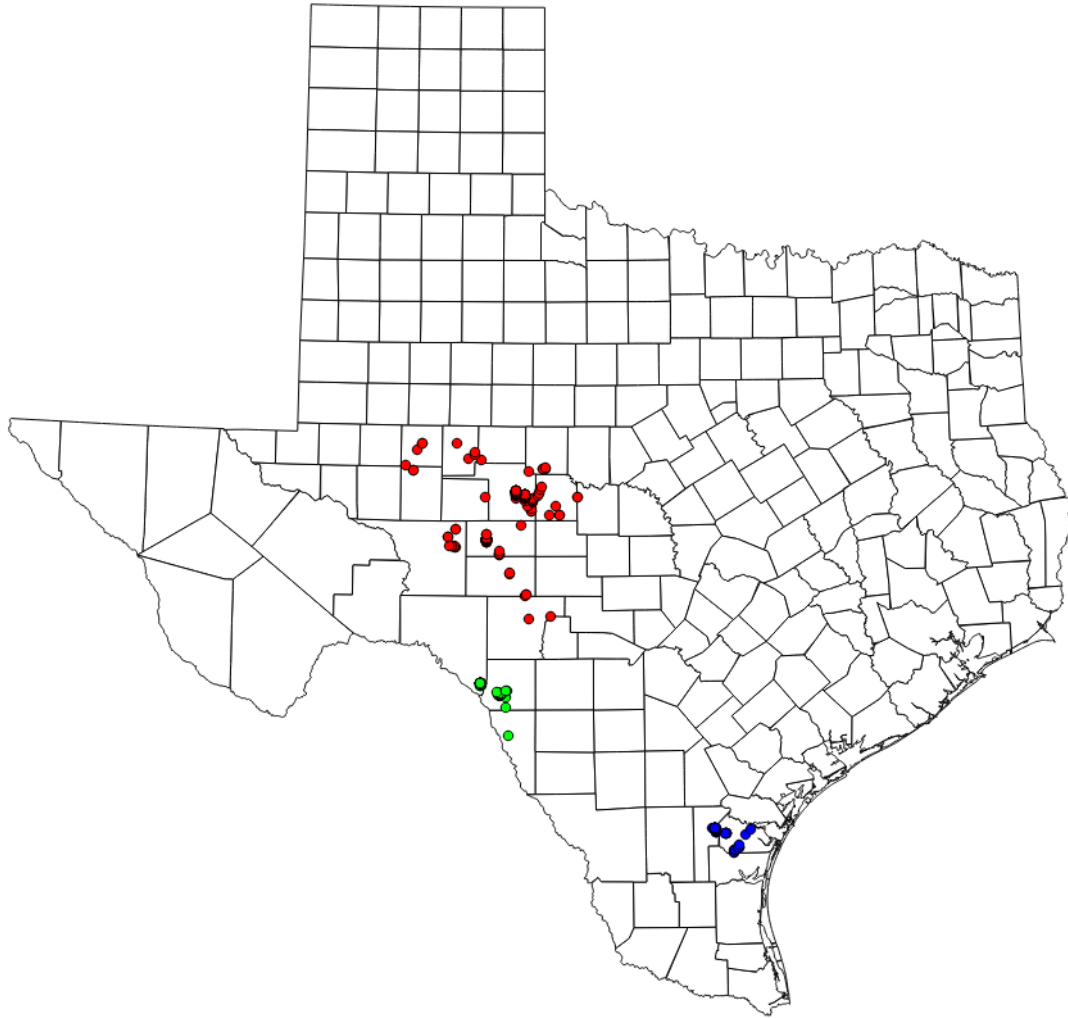
Figure. 12.1. County map of Texas showing survey points at which Holbrookia lacerata was found and localities used in this analysis
Colors correspond to the three separate populations: red = North, green = Southwest, blue = Southeast.

Figure 12.2. County maps showing the extent of the ranges considered for each population and for the species as a whole
 (a) The three subpopulations; the North population in red, Southwest in green and Southeast in blue. Points represent centroids of counties were the species was recorded on surveys. (b) The range for the entire species.
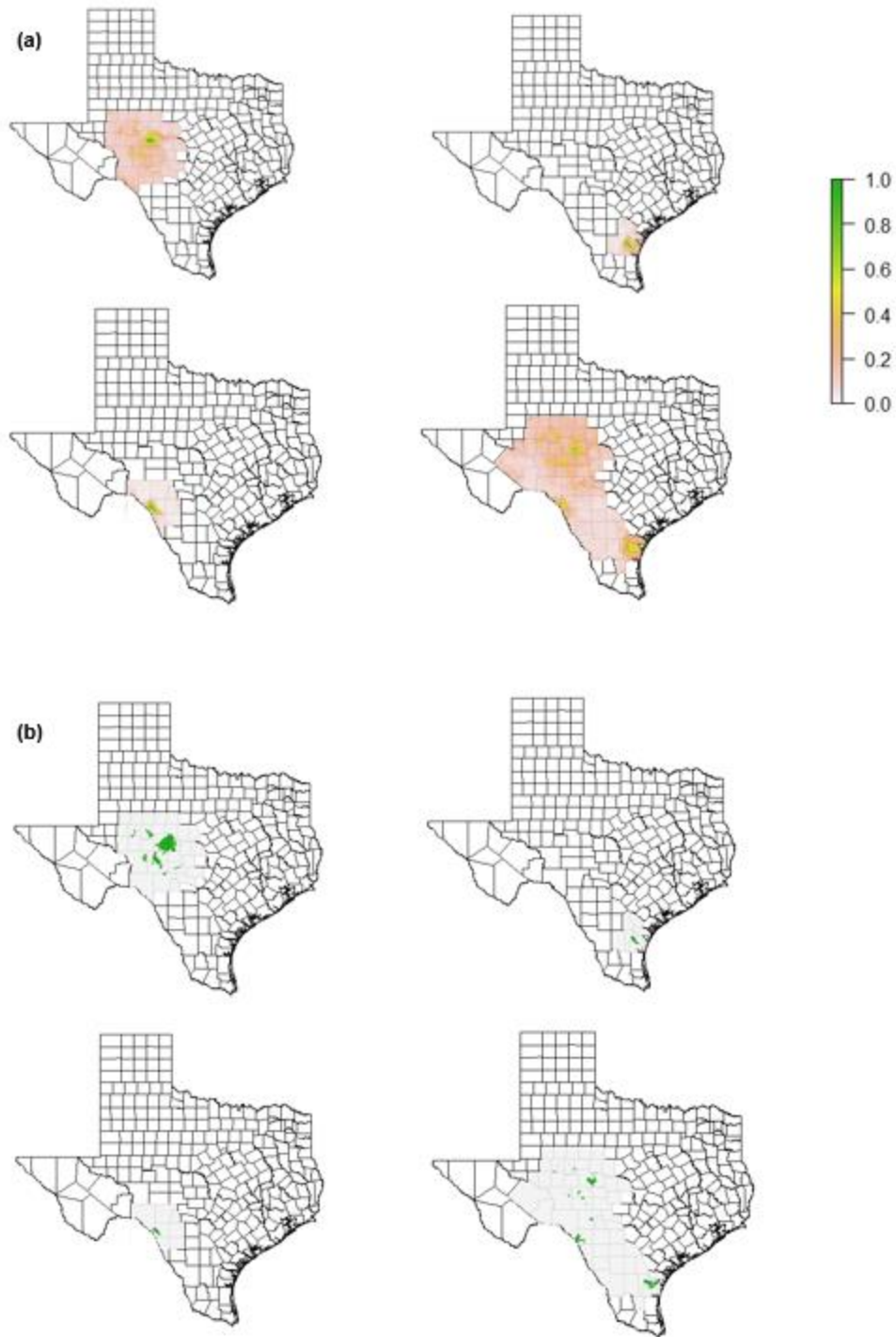
Figure 12.3. Predicted current distributions for each population of Holbrookia lacerata, as well as the species as a whole
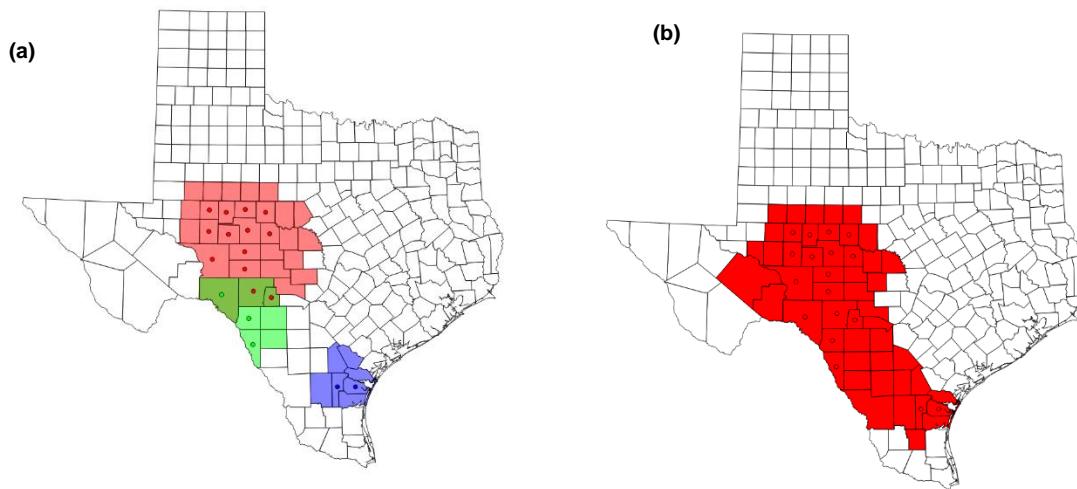
(a) Continuous ensemble output, which can be interpreted as habitat suitability, with high values indicating better habitat. (b) Thresholded presence-absence maps based on (a), with areas of predicted presence in green and areas of predicted absence in grey. Note the general congruence between the maps for the individual populations and the maps as a whole.

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Table 12.1. Change in range size of *Holbrookia lacerata* relative to the present, for each population and for the entire species
Values greater than 1 indicate a range contraction; values less than 1 indicate a range contraction; a value of 0 indicates no suitable climatic habitat.

North

Climate scenario	Relative range size, low quality	Relative range size, high quality	Relative range size, combined
2050 Low	0.713	0.000	0.574
2050 High	0.662	0.000	0.533
2075 Low	0.762	0.000	0.613
2075 High	0.698	0.000	0.561
2100 Low	0.864	0.000	0.695
2100 High	0.942	0.000	0.758

Southeast

Climate scenario	Relative range size, low quality	Relative range size, high quality	Relative range size, combined
2050 Low	10.282	20.707	12.923
2050 High	11.408	18.289	13.151
2075 Low	11.246	18.514	13.087
2075 High	14.124	6.321	12.147
2100 Low	9.968	22.595	13.167
2100 High	11.943	13.745	12.400

Southwest

Climate scenario	Relative range size, low quality	Relative range size, high quality	Relative range size, combined
2050 Low	0.000	0.000	0.000
2050 High	0.000	0.000	0.000
2075 Low	0.000	0.000	0.000
2075 High	0.000	0.000	0.000
2100 Low	0.000	0.000	0.000
2100 High	0.000	0.000	0.000

Entire species

Climate scenario	Relative range size, low quality	Relative range size, high quality	Relative range size, combined
2050 Low	0.205	0.000	0.192
2050 High	0.205	0.000	0.192
2075 Low	0.205	0.000	0.192
2075 High	0.205	0.000	0.192
2100 Low	0.205	0.000	0.192
2100 High	0.205	0.000	0.192

Table 12.2. Shift in centroid of range of *Holbrookia lacerata* relative to the present, for each population and for the entire species

The high values for the SW population are likely due to the projected extirpation of that population; the large shift in the whole species by year 2050 is due to a shift in the relative range sizes of the three populations and cannot be directly interpreted.

North

Climate scenario	Centroid shift (km)
2050 Low	19.9
2050 High	14.6
2075 Low	20.6
2075 High	17.8
2100 Low	21.3
2100 High	22.0

Southeast

Climate scenario	Centroid shift (km)
2050 Low	8.3
2050 High	9.8
2075 Low	8.2
2075 High	8.5
2100 Low	9.3
2100 High	9.5

Southwest

Climate scenario	Centroid shift (km)
2050 Low	301.4
2050 High	293.5
2075 Low	301.2
2075 High	293.7
2100 Low	300.7
2100 High	302.3

Entire species

Climate scenario	Centroid shift (km)
2050 Low	106.6
2050 High	91.8
2075 Low	105.8
2075 High	93.7
2100 Low	105.2
2100 High	89.0

Table 12.3. Habitat in square kilometers of the SE population of *Holbrookia lacerata* predicted to be urbanized by the year 2075

At all time points and emissions scenarios, this amount increases relative to present, although this effect does not reverse the qualitative trend of range expansion for this population.

Climate scenario	Low-quality habitat urbanized	High-quality habitat urbanized
Present	200.6	63.6
2050 Low	1261.2	374.9
2050 High	1223.7	415.4
2075 Low	1337.4	301.7
2075 High	1421.7	210.6
2100 Low	1207.1	432.0
2100 High	1172.2	455.6

Figure 12.4a. Ensemble output for N population; the same color scale is used for all maps
Top image: present distribution. Left column – LE scenario, right column – HE scenario; top row
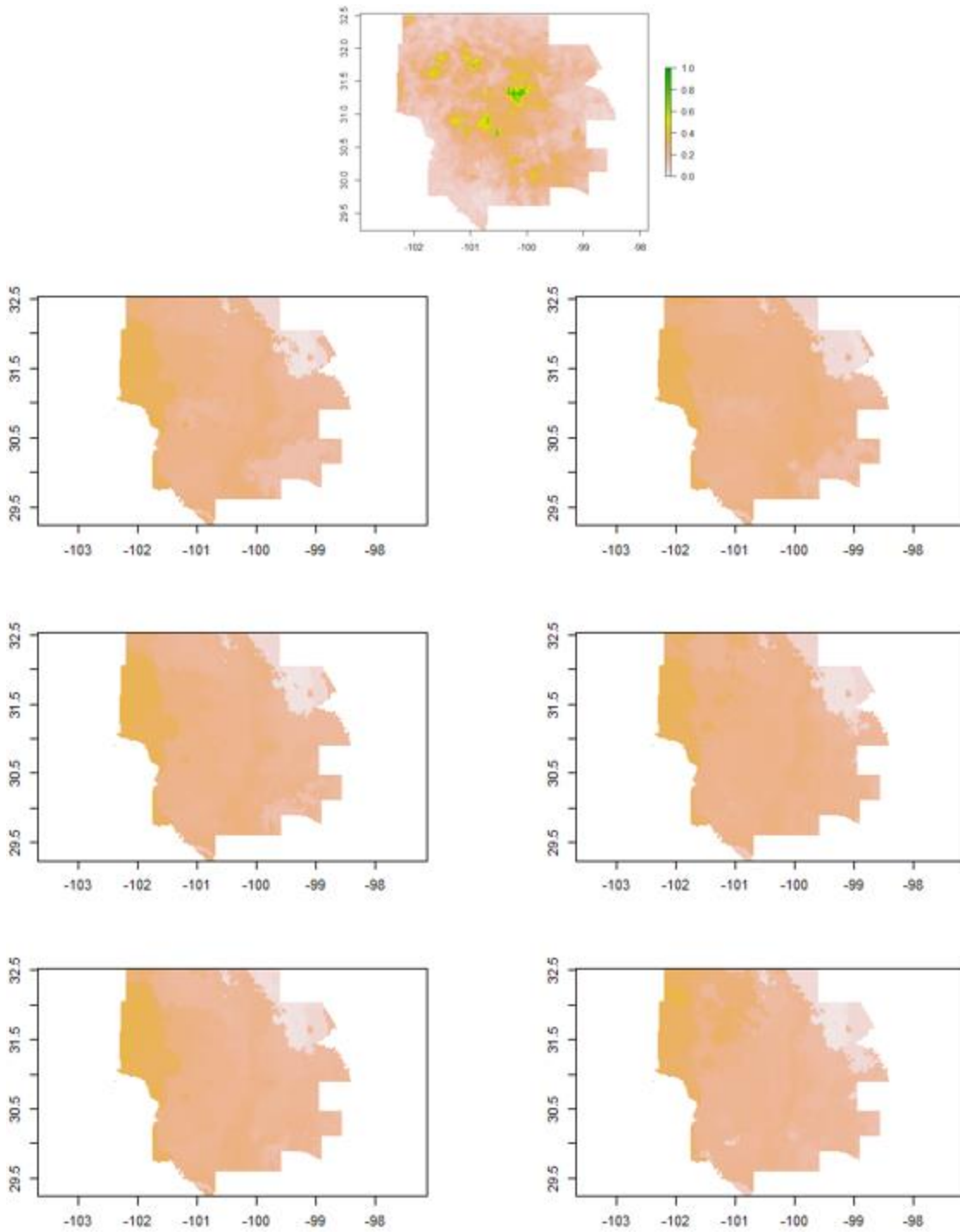year 2050, middle row year 2075, bottom row year 2100.
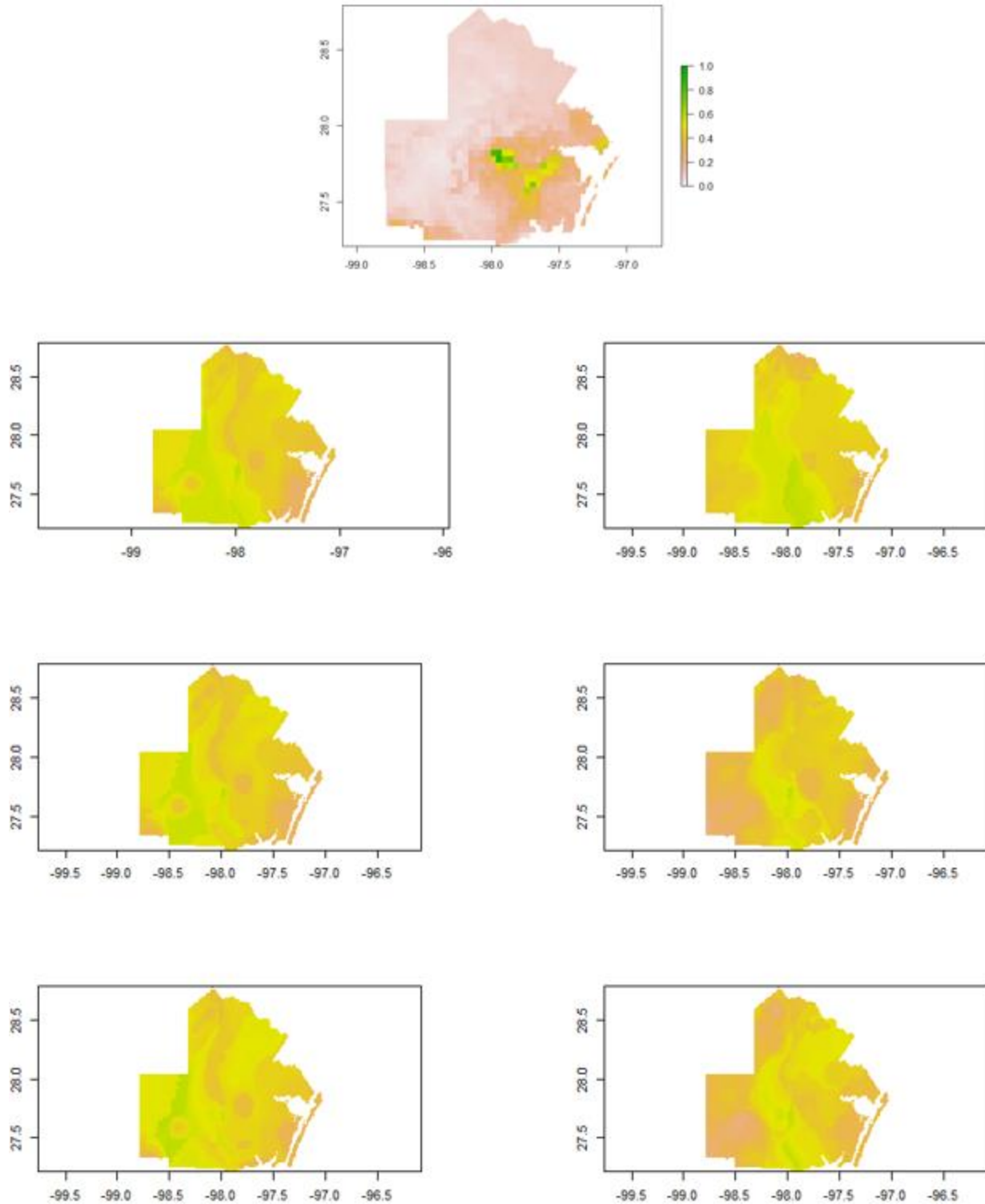
Figure 12.4b. Ensemble output for SE population; the same color scale is used for all maps
Top image: present distribution. Left column – LE scenario, right column – HE scenario; top row
year 2050, middle row year 2075, bottom row year 2100.

Figure 12.4c. Ensemble output for SW population; the same color scale is used for all maps
Top image: present distribution. Left column – LE scenario, right column – HE scenario; top row
year 2050, middle row year 2075, bottom row year 2100
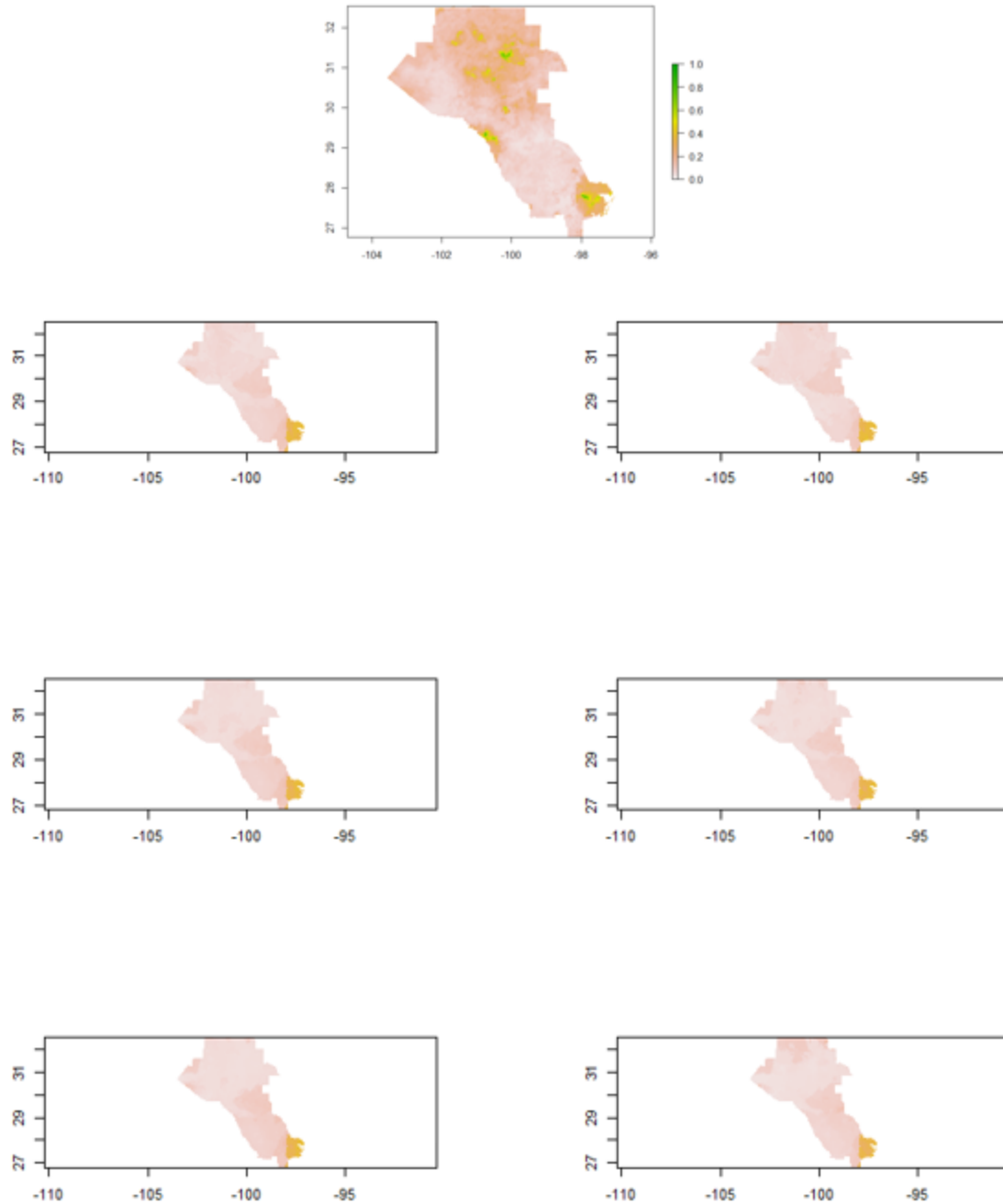
Figure 12.4d. Ensemble output for entire species; the same color scale is used for all maps
Top image: present distribution. Left column – LE scenario, right column – HE scenario; top row year 2050, middle row year 2075, bottom row year 2100.
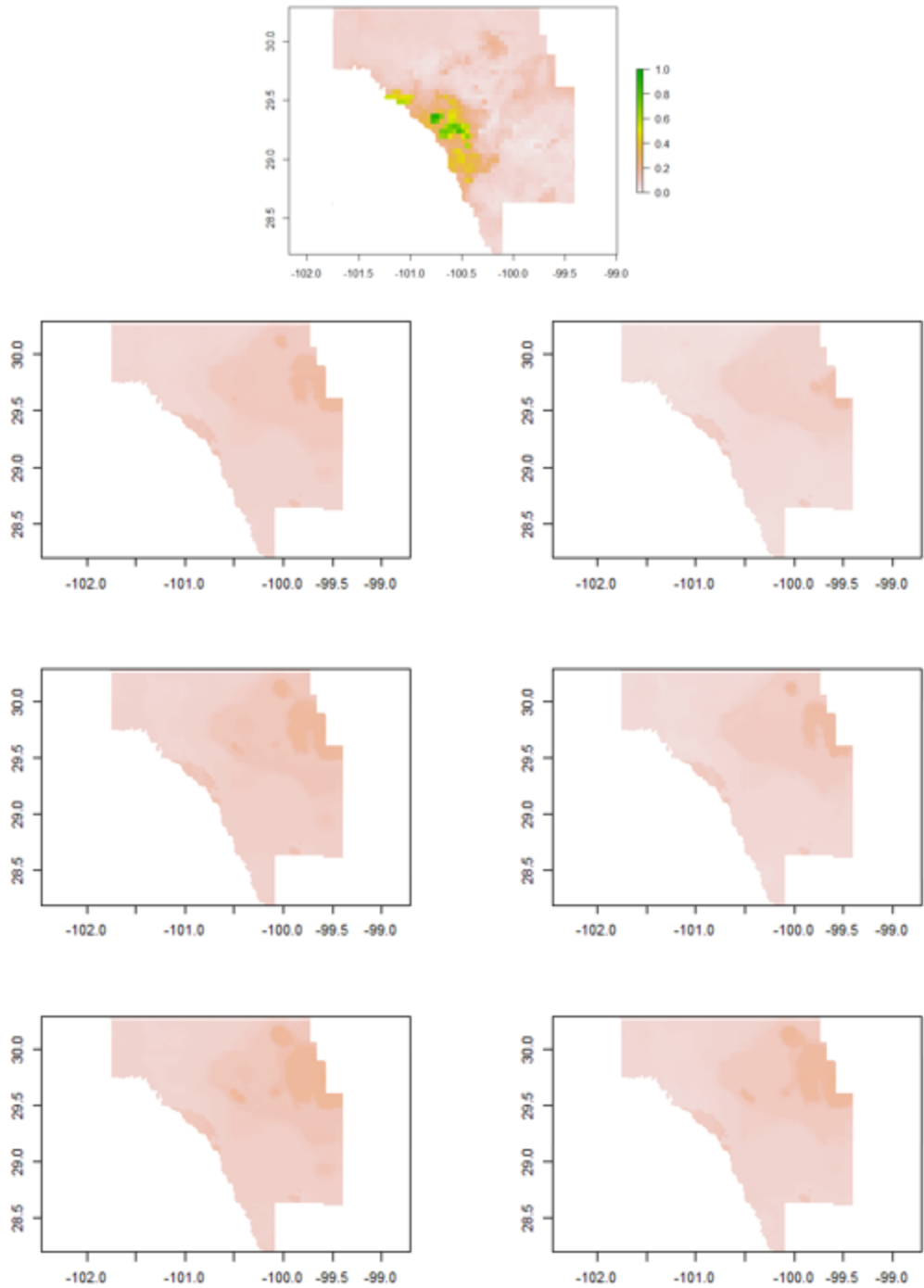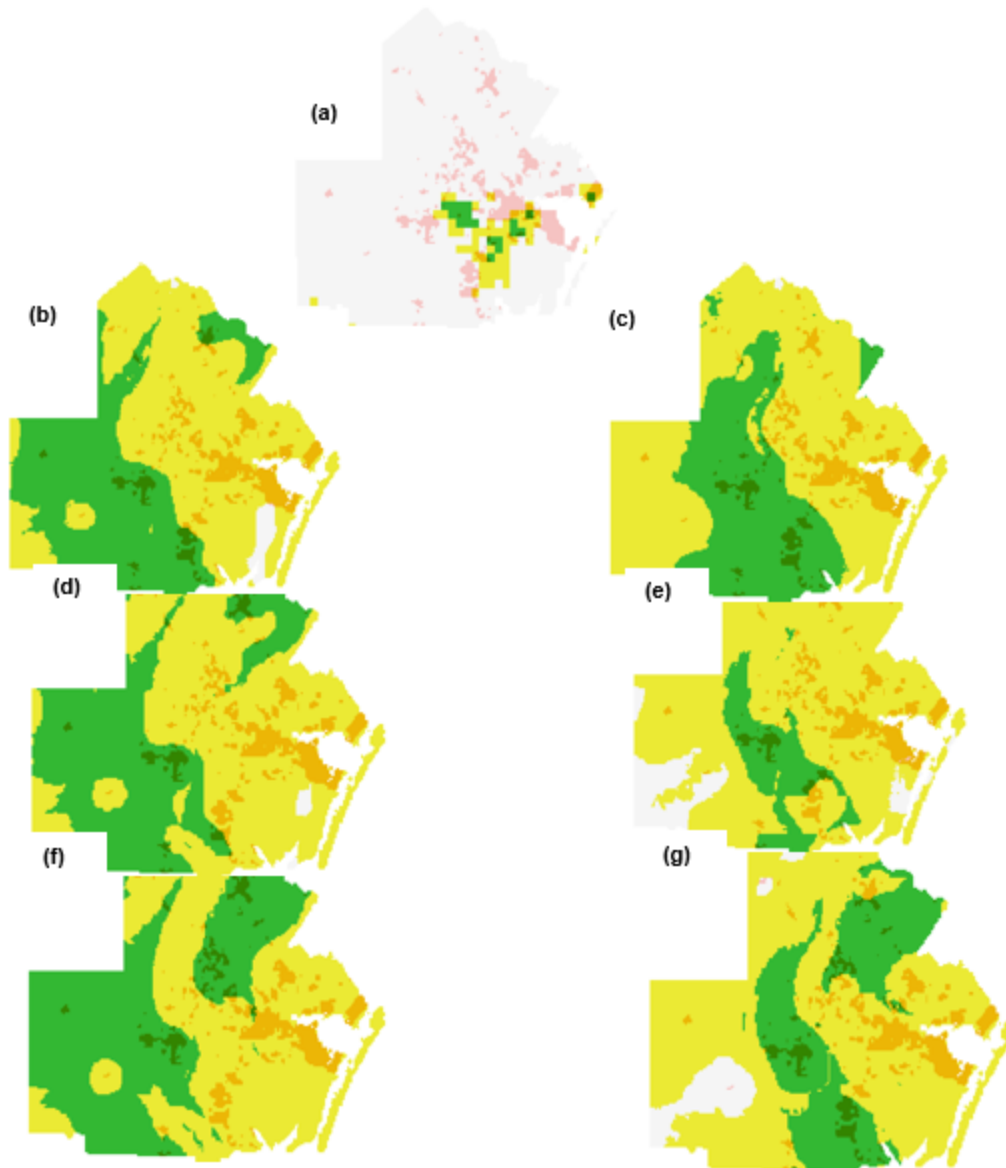
Figure 12.5. Overlap of range of SE population of Holbrookia lacerata and projected areas of urbanization

Yellow and green represent areas of low and high quality habitat respectively for H. lacerata; red represents urbanization. (a) Present, (b) 2050, low emissions, (c) 2050, high emissions, (d) 2075, low emissions, (e) 2075, high emissions, (f) 2100, low emissions, (g) 2100, high emissions. The urbanization on the east side of these maps represents Corpus Christi.

Figure 12.6. Future urbanization forecasted using Theobald future housing density projections Study units indicated by circles. A. Current urbanization (circa 2014). B. Low urbanization scenario (circa 2050). C. Medium urbanization scenario (circa 2050). D. High urbanization scenario (circa 2050).

CHAPTER 13. POPULATION VIABILITY ANALYSIS

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Fragmentation analyses, threat assessments, and scenario building

This task was designed to produce data and layers for their integration into a population viability analysis (PVA), now cancelled. Most layers identifying habitats that have been fragmented by current and future landscape threats have been prepared as part of previous tasks. The integration of these layers with the habitat model has been put on hold, due to the multiple comments and suggestions regarding the habitat model following its presentation in January 2017.

Population viability analysis

After further discussions between our group and Robert Gulley of the Texas Comptroller of Public Accounts, the decision was made not to pursue a formal PVA because of the significant uncertainty and data gaps that remain in our knowledge of the natural history and genetics of the lizard. In consultation with Robert Gulley, it was ultimately decided that a PVA based on best professional judgment would be drafted by a group of herpetologists. Under a new contract, we have asked a team of herpetologists from across the state with experience in studying Spot-tailed Earless Lizards or a related species to evaluate the telemetry results as well as the results all other existing, relevant scientific data. This group initially met on 20 October 2017 and will meet again in 2018 to discuss the status and results of ongoing field work, with two meetings scheduled for 2019. A final best professional judgment PVA report will be delivered to the TCPA by 31 October 2019.

CHAPTER 14. CONCLUSIONS

The goal of this multi-year research program was to develop science to inform the U.S. Fish and Wildlife Service's (USFWS) listing determination for *Holbrookia lacerata*. Thus, the objective of the studies presented in this document is to improve our understanding of (1) biology of the species, (2) current condition, and (3) future condition. The results of these studies are organized in a manner so that they may be incorporated into a Species Status Assessment (SSA) for *Holbrookia lacerata*. As these data were developed as part of an open, transparent process involving stakeholders, this final report details the results of the varied research program studies that were proposed over the course of the initial RFP and two iterative contract amendments.

Our results have filled in many gaps in our knowledge of this species and this contract has been a tremendous success towards providing data to the USFWS in their compilation of an SSA. Road surveys across 57 counties within the historical range revealed populations of this species in 19 counties, including populations from both subspecies. Two population units are present in the south (SW & SE) and a single unit in the north (N). Walking surveys were successful, but with lower success rates than road/driving surveys. When found, this species is often in early successional, disturbed habitats. Diet analyses of museum specimens indicate this species is an opportunistic generalist, with grasshoppers comprising over 1/3 of their diet; subsequent insect surveys in currently occupied habitat of *Holbrookia lacerata* demonstrate insect abundances match lizard diets. Initial genetic work using two genes supported the recognition of two separate species, elevating the subspecies to the species level: *Holbrookia lacerata* (north; N unit) and *Holbrookia subcaudalis* (south; both SW and SE units). A subsequent larger and more comprehensive molecular analysis supported these findings; morphological analyses found the same pattern with a division between the two taxa. Climate change models indicate that all three units will encounter significant habitat loss under a variety of emission scenarios. Iterations of a habitat model have identified areas of high and low quality habitat that will provide land managers information useful towards conservation measures, particularly when used in conjunction with future forecast models for energy development.

With our knowledge of current day distributions elucidated by survey work, significant gaps remain in our understanding of habitat use, home range size, and behavior in these taxa. A second separate contract focused wholly on radio telemetry work was signed in 2017 to cover field work across 2017-2019, concluding prior to the current listing decision date. Radio telemetry work initiated in 2017 demonstrated the effectiveness of small (0.2 g) transmitters for this small lizard (<6.0 g). An additional telemetry technique (harmonic radar) has been added to the radio telemetry protocol and both are being used at multiple field sites within the range of both taxa during both the 2018 and 2019 field seasons. As land access is granted, we will continue surveys for *Holbrookia lacerata* across the historical distribution, with particular emphasis south of the Edwards Plateau.

Four manuscripts have been published in peer-reviewed journals:

Wolaver, B. D., J. P. Pierre, S. A. Ikonnikova, J. R. Andrews, G. McDaid, W. A. Ryberg, T. J. Hibbitts, C. M. Duran, B. J. Labay, and T. J. LaDuc. An improved approach for forecasting ecological impacts from future drilling in unconventional shale oil and gas plays. Environmental Management, (accepted), first on-line 13 April 2018. [11 pp.] https://doi.org/10.1007/s00267-018-1042-5.

Pierre, J. P., B. D. Wolaver, B. J. Labay, T. J. LaDuc, C. M. Duran, W. A. Ryberg, T. J. Hibbitts, and J. R. Andrews. 2018. Comparison of recent oil and gas, wind energy, and other anthropogenic landscape alteration factors in Texas through 2014. Environmental Management 61:805–818. https://doi.org/10.1007/s00267-018-1000-2.

Wolaver, B. D., J. P. Pierre, B. J. Labay, T. J. LaDuc, C. M. Duran, W. A. Ryberg, and T. J. Hibbitts. 2018. Assessing recent anthropogenic infrastructure development within the historic range of the Spot-tailed Earless Lizard (*Holbrookia lacerata*) in Texas. Environmental Earth Sciences 77:171 [14 pp.]. https://doi.org/10.1007/s12665-018-7323-8.

Roelke, C. E., J. A. Maldonado, B. W. Pope, T. J. Firneno Jr., T. J. LaDuc, T. J. Hibbitts, W. A. Ryberg, N. D. Rains, and M. K. Fujita. 2018. Mitochondrial genetic variation within and between *Holbrookia lacerata lacerata* and *Holbrookia lacerata subcaudalis*, the spot-tailed earless lizards of Texas. Journal of Natural History 2018 [11 pp.]. https://doi.org/10.1080/00222933.2018.1436726.

One manuscript is currently in revisions following submission in 2017.

Hibbitts, T. J., W. A. Ryberg, J. Harvey, G. Voelker, M. Lawing, C. S. Adams, D. B. Neuharth, D. E. Dittmer, C. M. Duran, B. D. Wolaver, J. P. Pierre, B. J. Labay, T. J. LaDuc. Phylogenetic relationships within *Holbrookia lacerata* (Cope 1880) (Squamata: Phrynosomatidae). Submitted to Zootaxa, reviewed and returned for revisions.

At least three additional manuscripts are being developed: climate change, diet of *Holbrookia lacerata*, insect survey data.

GIS data sets generated from analyses shown in Chapters 9, 10, and 11 (Wolaver et al., 2018a, Pierre et al., 2018, and Wolaver et al., 2018b listed above) are available online at Texas Data Repository at: https://dataverse.tdl.org/dataverse/stel. If you download and use these mapping products, please cite the corresponding publication.

Current and future work (not included under this contract)

Radio telemetry 2017: Background
Private land access was obtained in Kimble County for several adjacent properties, totaling approximately 5,574 acres. These properties provide access to habitats that differ in biotic (vegetation) and abiotic (slope, elevation, canyons, mesa uplands, alluvial bottomlands)

characteristics. The properties also have been subjected to differing historical management practices, including prescribed fire, grazing by different types of livestock, planted fields, as well as the absence of management. 2017 research began in mid-July, unfortunately missing spring and early summer activity periods but observing mid to late summer activity of the species. VHF radio transmitters were attached to adult Spot-tailed Earless Lizards to determine movement, habitat use and home range size for the species.

Radio telemetry: Results

A total of 41 individual STEL were captured, 31 juveniles and 5 of the adults (4 male 1 female) large enough to be tagged with VHF transmitters. Nine individuals were recaptured during the study period of July 4 – October 17, and interestingly 2 new individuals were captured in October during vegetation surveys. Radio tracking concluded in August, as activity appeared to wane (no new adult individuals were captured) and attached transmitters reached the end of their battery life (because of their small size [0.2 grams], transmitter life: ~18-21 days). The number of locations collected per individual ranged from 7 (transmitter attachment failed) to 51. Three home ranges were calculated using Minimum Convex Polygons, using 21, 44 and 51 locations each. The resulting home range estimates were 0.52 acres, 1.3 acres, and 0.45 acres respectively. The home range of the female was the smallest, possibly because she was clearly gravid at the time of transmitter attachment. These are the first home ranges calculated for this species through the use of radio-telemetry, however it should be noted that these results mark the success of our proof of concept for the telemetry project and that these calculated ranges represent only ~1 month in the life of these three individuals in this particular population of STEL. Moreover, these are data collected from a single month at the end of a 4-5 month-long field season. We look forward to carrying this protocol over to 2018-2019 and conducting research for a continuous field season.

Radio telemetry: Habitat use

To assess habitat use of tagged Spot-tailed Earless Lizards, ten 2m quadrats were randomly placed within each of the three home ranges, and 10 were randomly placed up to 100m from the margin of each home range. Within each quadrat, all vegetation was identified to species and counted. In addition, percent cover of different vegetation classes and open area was estimated, as was canopy cover if present. Slope was also recorded. While only preliminary analyses of these data have been conducted, these preliminary results are reported here. Principal Components Analysis (PCA) of percent cover, canopy, and slope data suggests that the home ranges of Spot-tailed Earless Lizards generally included bare ground, the presence of small forbs and grasses, and lacked canopy cover or trees. Using Analysis of Similarity (ANOSIM) and Non-Metric Multi-Dimensional Scaling (NMDS) to investigate vegetative community data, there were no apparent patterns of large scale differences in vegetative communities within the home ranges of Spot-tailed Earless Lizards relative to samples collected outside the home range margins. Ordination of the data with NMDS and ANOSIM both suggest that the community data captured more variation in the home ranges than outside of them, and this may be due to some uniqueness in the vegetation of the largest home range. Overall, this likely indicates that home range and habitat use is not limited by availability in these areas.

Radio telemetry: Meeting: UT-Austin/BIOWEST and Texas A&M

In mid-October, an informal meeting was held at Texas A&M University between both groups currently conducting STEL telemetry studies. Six people from UT-Austin/BIOWEST and five people from Texas A&M attended the meeting with attendees included field technicians as

well as PIs. The goal of the meeting was to share information learned during the first year of telemetry research and to discuss potential collaborative project goals moving forward.

– UT-Austin/BIOWEST introduced preliminary findings from their field site (above) and suggested that a next step might be to compare differences in home range size and density across the varied management regimes at the Kimble County property.

– Texas A&M discussed their two telemetry projects. The first site, "Barnhart", covers ~3000 acres in the North Unit. This northern site was studied between the first week of May and 10 July. Gentle slopes, vegetation ranging from open forbs/grass to mesquite thickets. Some oil and gas activity present with a large number of roads bisecting the site; moderate grazing practices present. Lizards were not dense at this site but were distributed primarily along two main roads (caliche). In total, 11 lizards (7 male, 4 female) were radio-tracked over the course of 10 weeks, relocated 2–3 times/day between 0900-1700 hrs. Visual fixes were obtained for each relocation and a 1-m quadrat surrounding the lizard was photographed for subsequent vegetation analysis. Home ranges and vegetation variables had not yet been calculated. The team had two years of funding for telemetry work at this site (through 2018).

– The second Texas A&M telemetry site was at Laughlin Air Force Base (LAFB) in the Southwest Unit. This site covers ~1000 acres of primarily managed (mowed) grassy fields divided by roads/runways. Twenty-one individuals (roughly even between sexes) were studied using the same relocation protocols as at the Barnhart site. Home ranges and vegetation variables had not yet been calculated. The team had only secured a single year of funding at this site at the time of our meeting, but they have subsequently received an additional year of funding from Texas Parks and Wildlife.

– The UT-Austin/BIOWEST group thanked the Texas A&M team for their suggestions back in July on transmitter attachment. Both teams experienced transmitter attachment problems, but Texas A&M was able to troubleshoot the issue months before the other team started their work.

– We were all heartened that our protocols were not markedly different, allowing for future comparisons between the three sites. These comparisons would not focus solely on differences in home range size and behavior, but also on the broader similarities in habitat characteristics across the three sites.

– Both teams agreed to continue to keep the lines of communication open and work towards a series of multiple papers that would compare and contrast the natural history of Spot-tailed Earless Lizards at these three remarkably different habitats. The addition of one or more field sites by the UT-Austin/BIOWEST team would provide a more holistic description of this species across its entire Texas distribution.

Radio telemetry: Plans for field seasons 2&3: 2018–2019

Expand Kimble County field site to include additional management practices

We plan on taking advantage of the varied management regimes at our initial field site. By radio-tracking animals found in the differently managed habitats, we may begin to tease apart differences in the home range size and use Spot-tailed Earless Lizards that can be attributed to the different land-use practices across the ~5550 acre site.

Additional field site in Southeast Unit

Between the three Texas A&M and UT-Austin field sites, three markedly different habitats are being studied, however these three sites only cover habitats in the Northern and Southwest units. Finding a field site for telemetry in the Southeastern Unit (among row crops?) is a priority for the next two field seasons. A "row crop" site in the San Angelo/Tom Green County area

would make an interesting comparison to the desired but as-of-yet hypothetical Southeast Unit site.

Continued research at all three sites

Adding an additional year of research to the data collected last year will be important to identify trends and patterns in home range sizes at each of the three sites.

Additional marking techniques

Only a small fraction of the total number of STEL encountered during our 2017 research were large enough to carry VHF transmitters. The majority of lizards found were juveniles, sub-adults or adults too small to carry VHF transmitters without affecting their movement and survival. Understanding the dispersal and habitat use of these individuals is a critical aspect of the species biology that has been difficult to achieve with the methods available. Recently, however, Harmonic Radar technology has been applied with success to track small reptiles, amphibians, and insects. This technology uses a passive reflector that does not require a battery, and thus alleviates limitations of traditional radio telemetry tracking tags including weight, short battery life, and high cost. This technology could be applied to studies on Spot-tailed Earless Lizards to vastly increase the quality and quantity of tracking data we are able to collect.

APPENDIX 1. GIS FILES FROM PUBLISHED MANUSCRIPTS AVAILABLE ON TEXAS DATA REPOSITORY

Geographic information systems (GIS) included in published manuscripts are available here: https://dataverse.tdl.org/dataverse/stel

If you download and use these mapping products, please be sure to cite the following publications:

Wolaver, B.D., Pierre, J.P., Labay, B.L., LaDuc, T.J., Duran, C.M., Ryberg, W.A., Hibbitts, T.J. (2018) An approach for evaluating changes in land-use from energy sprawl and other anthropogenic activities with implications for biotic resource management. Environmental Earth Sciences, https://doi.org/10.1007/s12665-018-7323-8.

Pierre, J.P., Wolaver, B. D., Labay, B. J., LaDuc, T. J., Duran, C. M., Ryberg, W. A., Hibbitts, T. J. and Andrews, J. R. (2018) Comparison of recent oil and gas, wind energy, and other anthropogenic landscape alteration factors in Texas through 2014. Environmental Management, https://doi.org/10.1007/s00267-018-1000-2. doi: 10.1007/s00267-018-1000-2.

Wolaver, B. D., J. P. Pierre, S. A. Ikonnikova, J. R. Andrews, G. McDaid, W. A. Ryberg, T. J. Hibbitts, C. M. Duran, B. J. Labay, and T. J. LaDuc, 2018, An improved approach for forecasting ecological impacts from future drilling in unconventional shale oil and gas plays: Environmental Management. http://dx.doi.org/10.1007/s00267-018-1042-5.