

USING MUSEUM AND CITIZEN-SCIENCE DATA TO
EXAMINE THE RANGE CONTRACTION OF A
THREATENED LIZARD SPECIES

by

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DEDICATION

I dedicate this entire endeavor to my parents, Larry and Jami, for the unending support and love throughout my entire life. I would be nothing without them, both literally and figuratively. I also dedicate this to the long line of broad-shouldered Giants who have spread the fire; may it burn forever.

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	v
LIST OF TABLES	vii
LIST OF FIGURES	viii
ABSTRACT	ix
CHAPTER	
I. INTRODUCTION	1
II. METHODS.....	4
Study Species	4
Data Sources – VertNet and iNaturalist.....	5
Obtaining the Data from VertNet and iNaturalist.....	6
Measuring Range Characteristics	9
Statistical Analysis.....	11
III. RESULTS	13
Time Period Range Maps.....	13
Quantitative Assessment of MCP Range Characteristics	14
Quantitative Assessment of Contraction Directionality	15
IV. DISCUSSION.....	16
V. CONCLUSIONS.....	27
LITERATURE CITED	36

LIST OF TABLES

Table	Page
1. Characteristics of the Geographic Range of <i>Phrynosoma cornutum</i> for Each Time Period	28
2. Geographic Coordinates for the Centroid and Extreme Directional Points in Each Time Period's Minimum Convex Polygon	29
3. Values of the metrics assessing the geographical extent of each quadrant of the <i>Phrynosoma cornutum</i> range in each time period.	30

LIST OF FIGURES

Figure	Page
1. Time period range maps for <i>Phrynosoma cornutum</i> divided into directional quadrants originating from the historical center	31
2. Area (km ²) of Each Directional Quadrant for Each Time Period's Range Map for <i>Phrynosoma cornutum</i>	32
3. Change in the Geographic Range of <i>Phrynosoma cornutum</i> over time.	34

ABSTRACT

To assess the utility of museum and citizen-science databases in observing range dynamics of a species that is suspected to have experienced a significant contraction in recent decades, the Texas horned lizard (*Phrynosoma cornutum*). By integrating the spatial data from two sources, VertNet and iNaturalist, into a GIS computing environment and segregating observations by time periods, I calculated several metrics to characterize the size and location of the *P. cornutum* range over time. In particular I compared the location of the range edge for consecutive time periods so as to test whether the range has been contracting in each of the four cardinal directions. My study also illustrates a method that could be applied to other species that may be undergoing range contraction or expansion.

I. INTRODUCTION

Extinction of a species usually begins with the extirpation of vulnerable populations and continues until no populations remain. In theory, the geographical range of a species should center on one or more areas that contain the most ideal environmental conditions and necessary resources for survival and reproduction (Lawton, 1993; Brown, 1984). Because natural resources are spatially autocorrelated, regions further from this “abundant center” should be of poorer quality with regard to the species’ fundamental niche requirements. Because of this difference in habitat quality, populations located further from the center (and nearer the periphery) are expected to have lower population sizes and densities than more central populations (Hengeveld & Haeck, 1981; Brown, 1984), leaving them more susceptible than central populations to local extinction. Therefore, the contractions of species’ geographical ranges often precede the extinction of species (Lucas, Gonzales-Suarez, & Revila, 2016) during a process in which peripherally-located populations decline and go extinct thereby “setting” a new range boundary with a new set of peripheral populations vulnerable to extinction. The process is repetitive and leads to a shifting and inwardly contracting range boundary, particularly if peripheral populations are always at lower density and hence more prone to extinction than centrally-located populations. Therefore, it is essential that ecologists and biogeographers studying extinction understand the dynamics of range contraction. Such knowledge can be used to develop effective conservation strategies, plan successful reintroductions, suggest where to survey for persisting populations (Lomolino & Channell, 1995, 1998), predict future range changes (Lucas et al., 2016) and assess the

effects of new threats (Newbold, et al., 2014; Selwood, McGeoch, & Mac Nally, 2015; Thomas, Franco, & Hill, 2006; Thomas, et al., 2011).

Factors that influence the trajectory of a range contraction include the size and shape of the range, the distribution of the species within, geographic characteristics of the occupied or surrounding areas, and the relative location and intensity of the extinction driver. For example, a species with a relatively large geographic range, such as the eastern fox squirrel (*Sciurus carolinensis*) occurring throughout North America, should contain multiple regions of high-density populations (including some not at the geographic center), whereas an endemic species with a relatively small range, such as the Kaibab squirrel (*Sciurus aberti kaibabensis*) may have only one particular area of relatively high density that is perhaps at or near the center. With regard to species undergoing range contraction, if the historic geographic range was composed of one high-abundance center, then contraction may occur towards that area. However if the historic range contained multiple regions of high abundance then the species may contract to multiple areas, leading to fragmentation of the original range.

The task of accurately quantifying and comparing species geographic ranges over time has long-confronted ecologists and biogeographers (Brown, 1995; Gaston & Blackburn, 2003; Vandermeer & Goldberg, 2013). Understandably, it is difficult to obtain detailed data on spatial locations of individuals and populations over the entire range of the species. Moreover, to study range contraction, we need distributional data from different time periods.

Although we are unable to track all individuals through space and time, we now have computational tools and databases to more accurately monitor range characteristics.

Today there exist online databases that record, store, and freely provide substantial amounts of spatiotemporal observational data for thousands of species. These databases include eBird and iNaturalist, which provide a social network platform for users to upload their own observations, and also VertNet, which provides historic data on where and when museum specimens were collected, often spanning five decades or more. By integrating these data into another modern technology, a Geographic Information System (GIS), the capability of researchers to effectively reference, map, and analyze patterns of range dynamics as they change over time is greatly enhanced.

II. METHODS

Study Species

The Texas horned lizard (*Phrynosoma cornutum*) is the largest and most widespread of the fourteen species of horned lizards (Genus: *Phrynosoma*), all of which are endemic to western North America. It is the easternmost *Phrynosoma* species with a range that historically extended from extreme southeastern Arizona to eastern Texas and from Kansas to northeastern Mexico (Price, 1990; Sherbrooke, 2002). They are flat-bodied lizards characterized by the spikes that line their abdomen and the bony occipital horns atop their heads. *P. cornutum* can range in size from 60-120mm SVL and may vary in color between geographic location and substrate type, allowing them to cryptically camouflage themselves (Price, 1990). It is well documented that Texas horned lizards feed primarily on Red Harvester Ants (*Pogonomyrmex barbatus*), though they also feed opportunistically on other small insects (Pianka & Parker, 1975). Texas horned lizards have likely been extirpated from locations in east and central Texas where they were relatively common several decades ago (Price, 1990; Donaldson, Price, & Morse, 1994). Although biologists have been aware of this possible range contraction since at least the early 1990s, it has not been quantitatively analyzed and it is unknown if range contraction has occurred from the west, north, and south as well.

Although there has not been a thorough analysis of the range contraction biologists have nonetheless speculated as to its causes. To the extent that it exists, it may be attributed to a combination of factors. According to various authors these factors include: habitat alteration (Donaldson et al., 1994; Johnson-Linam, 2008), invasion and range expansion by the red imported fire ant (*Solenopsis invictus*) (Allen, Epperson, &

Garmestani, 2004; Johnson-Linam, 2008; Webb & Henke, 2008), widespread pesticide application used in agriculture or in controlling fire ants (Donaldson et al., 1994) and over collection for the pet trade (Manaster, 2002). Due to concerns for its long-term conservation, *P. cornutum* is listed as a threatened species by the state of Texas (Texas Parks and Wildlife Department 2012).

Data Sources – VertNet and iNaturalist

All of the data used in my study were downloaded from two repositories of crowd-sourced, spatiotemporal biodiversity data, VertNet and iNaturalist. VertNet is a conglomerate of four global networks of vertebrate distribution (Mammal Network Information, Ornithological Information System, HerpNET, and FishNet 2) that, collectively, contain more than 20 million records from 372 collections worldwide. VertNet is funded by the USA National Science Foundation (NSF), Global Biodiversity Information Facility (GBIF), and organized by a committee of researchers from the Universities of California, Colorado, Kansas and Tulane University. VertNet provides archived data primarily obtained from museum specimens. Hence, the VertNet database contains observations from as far back as the mid-19th century all the way to present day. These observations can, in some cases, be used to provide a historical view of the geographic distribution of a species.

iNaturalist is an online social network began in 2008 with the goal of recording and sharing observations of biodiversity around the world. iNaturalist allows people to record their own observations, get assistance with identifications, and access observational data collected by other users. Users submit observations with supposed

species identification, date, GPS location, a brief description and preferably photographic evidence. Once submitted, the online community can peer review submissions, offer ID suggestions, and comment to ask questions about the observation. Each observation is classified based on an assessment of data quality. All submitted observations are classified as “Casual Grade” by default. However, an observation can improve to “Needs Identification” if the user provides a date, GPS coordinates, and photos or sounds. An observation then becomes “Research Grade” when two out of the first three comments (ie. the user community) confirms the species identification based on the provided information. Once “Research Grade” is attained, the observation is recommended for use in research and can be featured on other biodiversity data websites. Due to the method of data acquisition, iNaturalist has an immense number of records with a relatively rapid rate of increase in new records overall. However it does not have the temporal depth that VertNet has.

Obtaining the data from VertNet and iNaturalist

I downloaded data for *P. cornutum* from VertNet in October 2017 following the procedure on the data request portal (www.vertnet.org). VertNet returned 3,589 specimen records for *P. cornutum* spanning the years 1859–2014. Each observation record had 51 fields of associated data but for subsequent data filtering I retained only “ObjectID”, “Year”, “Latitude”, “Longitude”, “EventDate”, “State”, “County”, “Specific_Location”, and “Geodeticdatum”. Next, I removed all observation records that did not have at least one field containing spatial information pertaining to geographic coordinates, city, or county. If an observation contained a city or county name, but no geographic coordinates,

then I used the geographic coordinates of the city or county center. Any observation that lacked information on the year or decade of collection was discarded. Finally, I removed all completely duplicated observations. A complete duplicate was considered to be any two or more observations that contained identical values for all fields, or observations containing identical fields for “EventDate”, “Latitude” and “Longitude”. Duplicates were discarded because the range metrics that I calculated required only a single observation of the species at a given location in a given year. Observations from the same location (but not with the same date) were not considered duplicates and were retained.

For most species, VertNet data tends to be most plentiful for the time span from about 1950–2000 whereas iNaturalist data are nearly non-existent for this time period. iNaturalist observations do not become very abundant until around 2010, after which they become much more numerous on a per year basis than any VertNet year. Therefore, I only used VertNet data up to 2009, a total of 1,631 observations.

Data for *P. cornutum* from iNaturalist were also obtained in October 2017, downloaded from www.inaturalist.org. iNaturalist returned 1,523 observations of *P. cornutum*. Because I had requested only “Research-Grade” observations, I did little amending of the iNaturalist data. The only data filtering involved removing observations preceding 2010. This amending left 1,207 observations for analysis.

Finally, for both datasets, I removed outlier observations. Outliers were determined by using the “Near” tool in ArcMap (ArcGIS 10.6) to determine the closest distance of one observation to its nearest neighbor. The 5% of observations with the largest values for nearest-neighbor distance were characterized as outliers and removed. This procedure mostly filtered out old VertNet observations that likely represented

mislabeling on a museum specimen tag as the specimen was said to be collected in regions far from the range of the species (eg. in northwestern Colorado, Indiana, Washington, D.C., and Alberta, Canada). Also worth noting, iNaturalist returned observations from a small, introduced population on the east coast of the USA (Georgia and South Carolina). These observations were also removed.

Once all of the observations were projected into ArcMap, the next step was to create separate layers containing observations for consecutive time periods. My initial intention was to divide observations up into consecutive decade-long time periods beginning with the 1960s, so that I would have seven time periods and a pre-1960s time period representing the historic range. However the number of observations per decade varied considerably. For instance, in the 1960s there were 388 observations from VertNet whereas in the 1990s and 2000s there were only 79 observations per time period. In order to adjust for these low sample sizes, I divided observations in a way to provide me with sample sizes of at least 200 observations in each time period. The best way to achieve this was by using five time periods, four of which came from VertNet and one from iNaturalist. The latter represents the current range. The time periods and sample sizes were as follows: VertNet observations preceding 1960 ($n=605$), 1960 – 1969 ($n = 383$), 1970 – 1979 ($n = 251$), 1980 – 2009 ($n = 392$), and iNaturalist observations 2010 – October 2017 ($n = 1,207$).

Measuring Range Characteristics

For each of the time periods I used several different metrics to measure characteristics of the geographic range. These characteristics were size and location of the range, and directionality of the contraction. Size was estimated as the MCP (Minimum Convex Polygon), which is the convex hull that bounds all spatial observations of the species. Given that the MCP is based on spatially-explicit locations, it also indicates geographic location of the range. The directionality metrics were based on linear distances between the historic center of the range and either the recorded observations or the MCP edge. These metrics were used to determine if there was a directionality component to the contraction.

As my goal was to measure range change over time, I generated an MCP for all observations within a time period (Figure 1). This MCP acted as a proxy for the geographic range in each time period, so any change in the size of the MCP between time periods was taken as a change in size of the geographic range. To do this I used the “Minimum Bounding Geometry” tool in ArcMap, which creates a minimum convex polygon enclosing all observations by connecting the outermost observations to form a perimeter such that there are no internal angles $> 180^\circ$. Because of the geography of the greater region, the MCPs initially included portions that fell in the Gulf of Mexico due to observations in east Texas connecting to observations in southern Mexico. To remove these portions I used the intersect tool so to include only the MCP portions overlapping with mainland North America. These intersected MCPs were then regarded as the range of *P. cornutum* during each time period. Each map is divided into the directional

quadrants and contains the observations used to generate each MCP along with the points that were used to measure the distance to the edge from the historic center (Figure 1).

To generate the geometric center of each MCP, I used the “Feature to Point” tool. This tool generates the central point by determining the location within the polygon that is most equidistant from all vertices. Once the MCP was generated and the center was determined for each time period, I was able to measure and then compare the range characteristics as they changed over time. The metrics that were calculated are listed below: area of MCP (km^2), latitudinal and longitudinal extents of MCP (km), latitude and longitude of MCP center (decimal degrees), and latitudes and longitudes of northernmost, easternmost, southernmost and westernmost observations (decimal degrees).

To assess the directionality of any possible contraction, it was necessary to create a layer that would divide the MCPs from each time period into four portions, each corresponding to one of the cardinal directions. This required a central reference point to serve as the origin of the divider. Since my goal was to assess the contraction as it has happened since the 1960s, I used the centroid of the historic MCP (based on the pre-1960 observations) as the origin for the divider.

I then used the draw tool in ArcMap to create a “directional divider” that was simply a large “X” with its four arms extending towards the inter-cardinal directions (NE, SE, NW and SW). I used the “Feature to Polygon” tool to divide each MCP of each time period into northern, eastern, southern, and western quadrants (Figure 1). I then created a layer for each quadrant in each time period’s MCP that was then used to test for directionality of the range contraction. To do this I developed two directionality metrics, one that would measure the movement of the range (MCP) edge over time and one that

would measure the distance of all observations from the historic center in each quadrant in each time period. This latter metric assessed the extent that observations (i.e., sightings) of *P. cornutum* contracted toward the historic center over time.

For the directionality metric based on movement of the range edge, I calculated the distances from the historic center to multiple points along the MCP edge in each quadrant. To do this, I used the “Generate Points Along Line” tool to create points that traced the MCP boundary at 1% intervals of the perimeter. I then used the “Near” tool to measure the distance of each edge point to the historical center. Then by selecting the section of the boundary that intersected with each quadrant layer, I separated the edge points that corresponded to the eastern, southern, western and northern quadrants of the MCP for each time period. These data for edge distances were statistically analyzed with ANOVA to separately test for and compare edge contraction in each quadrant or direction (see next section). In order to test for and assess contraction as based on the observations, I again used the “Near” tool to measure the distance of each observation to the historic center. These distance data were then analyzed with ANOVA.

Statistical Analysis

For each quadrant, I used ANOVAs to determine if significant differences existed among time periods in either directionality metric (ie. For all quadrants, mean distance of the edge to the historic center and mean observation distance to the historic center). For either metric, if a quadrant produced significant p-values for the ANOVA, then Tukey’s post-hoc test was conducted on that dataset to determine which time periods within the quadrant were significantly different from one another. Both statistical tests were

conducted in R 3.4.1. Sample sizes for the ANOVAs were generally between 30 and 150 observations per quadrant per time period except that the western, northern, and southern quadrants each had >300 observations for the current time period (iNaturalist data). Sample sizes for the edge distances were more uniform, typically 20-40 per quadrant per time period (Table 3).

III. RESULTS

Time Period Range Maps

The portions of the geographic range within the western and northern quadrants are relatively stable in shape and area over time, whereas portions in the southern quadrant fluctuate more substantially from one time period to the next (Figures 1 and 2). In particular, the range edge in the southern quadrant contracts and expands repeatedly between the historic and 1980-2009 time periods, before extending back to nearly the historic extent in the current time period. As a result, the area of the historic southern portion is only 8% larger than the area of the southern portion in current time period (Figure 2). The southern quadrant contains the fewest number of observations in all time periods relative to the other quadrants, excluding the current time period, which accounts for >70% of all of the southern observations (Table 3).

Of the four quadrants, the portion of the geographic range in the eastern quadrant exhibited the most consistent change over time, primarily a decrease in area as the edge of the eastern quadrant contracted towards the historic center (Figures 1 and 2). Between the historic and current time period, the area of the eastern portion contracts about 35% (Figure 2). Additionally, in the historic and 1960-1969 periods, the observations are distributed throughout most of the eastern quadrant's area, whereas in the 1980-2009 and current time periods, the majority of the eastern observations are concentrated near the historic center and/or the border with the northern quadrant, leaving much of the eastern quadrant void of observations (Figure 1). The area of the range portions in the northern and western quadrants declined from historic to current, but by less than 6% (Figure 2).

Quantitative Assessment of MCP Range Characteristics

The MCP representing the entire current range is 10.1% smaller in area than the MCP representing the historic range (Table 1), although the MCPs representing the intervening time periods do contain area values that are slightly smaller than that of the current. The latitudinal extent for the current MCP is 16.2% smaller than the historic and two of the three intermediate time period's MCPs are smaller than the current. The longitudinal extent of the current MCP is 7.0% smaller than the historic, but two of the intervening time periods are 7.0% larger than the historic time period. It should also be noted that the current time period contains more than 40% of the total amount of observations.

The longitude of the MCP centroid trends west (becomes more negative) from the historic to 1980-2009 time period, though the current centroid's longitude is almost identical to the historic (Table 2). The latitude of the MCP centroid also fluctuates slightly over time but is very similar during the historic and current time periods. The longitude of the extreme observations in the east and west remain within one decimal degree over time and the same is true of the latitude of the northern extreme observations. However, the latitude of the extreme observations in the south varies between 21.20 and 26.03 through the five time periods and fluctuates at least one degree between each consecutive time period (Table 2).

Quantitative Assessment of Contraction Directionality

All four ANOVAs comparing mean distance of observations in the quadrants to the historic center among time periods were statistically significant (East, $F_{4,462} = 66.5$, $P < 0.00001$; West, $F_{4,835} = 20.8$, $P < 0.00001$; North, $F_{4,927} = 81.4$, $P < 0.00001$; South, $F_{4,594} = 4.7$, $P = 0.0009$). For mean distance to the edge, only two of the quadrants, the east ($F_{4,81} = 5.0$, $P = 0.001$) and south ($F_{4,194} = 23.5$, $P < 0.00001$) had significant differences among time periods (Figure 3). In the case of the observation metric, the east experienced the greatest reduction in value, declining nearly 60% from the historic to current time period. Additionally, the eastern historic time period was significantly larger than all later time periods. After the historic time period, the east's observation distances in all time periods were less than half the edge distance in the same time period. For the observation metric, the northern and western quadrants' current time periods contained significantly smaller values than all earlier time periods. Though the southern time period's current quadrant was significantly smaller than its historic and 1970s time period, it was not significantly different from either the 1960s nor 1980-2009 time periods.

In the east, mean edge distance for the current time period was 97.4 km less than the historic and 69.3 km less than the 1980-2009 time period (Figure 3). The southern quadrant showed significant decreases between the historic time period and all later time periods. Interestingly, the south contained the only significant increase in either of the directional metrics between consecutive time periods, as the edge distance increased more than 100km between the 1980-2009 and current time periods. The west and north contained no significant differences in mean edge distances between time periods.

IV. DISCUSSION

My study revealed some evidence of contraction in the geographic range of *P. cornutum* in all four directional quadrants, although this depended on which metric was used to measure contraction. Within each quadrant, the mean distance from the historic center to the lizard observations is significantly less during the current time period than in one or more preceding time periods, including the historic time period. However, the four quadrants did not exhibit the same level of temporal consistency in range contraction and for two quadrants (northern and western) the contraction was only evident from analysis of mean distance to the lizard observations, not mean distance to range edge or change in area of the range portion within the quadrant. Of the four cardinal directions, range contraction appears to be most evident in the east. The edge of the geographic range has been contracting westward (i.e., in the eastern quadrant) for at least six decades. Over this time, there has been a consistent decline in the mean distance from the historic center to the edge of the range. In addition, the mean distance from the historic center to recorded lizard (anywhere in the quadrant, not just the edge) has also declined.

This westward contraction of the eastern edge of the *P. cornutum* range has been strongly suspected by researchers since the 1990s (Price, 1990; Donaldson et al., 1994). The speculation was primarily based on anecdotal evidence from long-time residents that remarked about not having seen horned lizards in decades in areas where they previously occurred as well as the results of a citizen-science questionnaire survey (Donaldson et al., 1994). Field surveys have provided somewhat better empirical evidence of the species extirpation in east Texas (Donaldson et al., 1994; Henke, 2003). However, no previous

study has estimated range boundaries and tested for contraction in the range of *P. cornutum*.

As in the eastern quadrant, range contraction also may have occurred in the southern quadrant. Although the southern quadrant appears to have experienced a consistent contraction between the historic time period and the 1980-2009 time period (Figure 2), sample sizes for each time period (except the current) is < 70 observations (Table 3), and thus any corresponding metrics of range contraction may be somewhat imprecise. This clearly impacts the results obtained from the measurements of range size and location of the edge and may explain the irregular trends in the southern quadrant. For this reason, range contraction in the southern quadrant should be interpreted cautiously.

In the northern and western quadrants, the mean distance from the historic center to the observation declined between all time periods and the current. However, the mean distance to the edge did not vary among time periods. The portions of the geographic range in the northern and western quadrants currently have an area that is within 6% of their respective historic area (Figure 2), and the west and north both retain their general shape and extent between all time periods (Figure 1). This stability in area and edge distance for these quadrants indicates that the northern and western portions have not appreciably contracted over time. This could be due to the fact that the majority of both quadrants are in areas of relatively low human population density and perhaps greater availability of habitat, especially when compared with the eastern portion. The western portion extends through the Chihuahuan desert of New Mexico and northern Mexico, which has a relatively low human population density. The northern portion occupies the

southern reaches of the American Great Plains, which, though heavily altered over the last century for agricultural use, harbors some of the lowest human population densities in North America (Wilson, 2009).

There are a number of possible reasons why range contraction would be most severe in the eastern quadrant of the *P. cornutum* range. First, this region includes four of the most populous metropolitan areas in the United States -- Houston, Dallas-Fort Worth, San Antonio, and Austin that together contain more than 10 million people (US Census, 2010). There are also numerous other smaller cities and towns in this region such that the eastern quadrant has the greatest human population density. These urban areas are connected by transportation infrastructure (roads and highways) that likely further degrades *P. cornutum* habitat by way of fragmentation, automobile-related mortalities and increased predation (Barrow, Allen, & Rotenberry, 2006). In addition, range contraction in the eastern quadrant may stem from the invasion and range expansion of the red imported fire ant (*Solenopsis invicta*). These ants were accidentally introduced at Mobile, Alabama in the 1930s and have since spread to more than 125 million ha in the southern USA (Smith, Taylor, Whelan, Denight, & Stake, 2004) including the entire eastern quadrant. The most current version of the fire ant invasion map (USDA, 2017) indicates that fire ants also exist in the southern quadrant but less so in the western and northern quadrants where they are mostly absent. The westward contraction of *P. cornutum* in Texas (ongoing for several decades) may have been coincident with the westward spread of fire ants. Fire ants are notoriously aggressive and have been implicated in the decline of *P. cornutum* (Webb & Henke, 2008), as well as many other species of reptiles (Tuberville, Bodie, Jensen, Laclaire, & Whitfield, 2000; Wojcik, et al.,

2001), amphibians (Freed & Neitman, 1988), small mammals (Killion, Grant, & Vinson, 1995; Ferris, Killion, Ferris, Grant, & Vinson, 1998) and ground-nesting birds (Allen, Lutz, & Demarais, 1995; Kopachena, Buckley, & Potts, 2000). Aside from possible direct predation, fire ants may indirectly affect *P. cornutum* if they cause declines in the red harvester ant (*Pogonomyrmex barbatus*), a main prey source for horned lizards.

Range contraction in the eastern quadrant may also be explained by the relationship between the natural history of the *Phrynosoma* genus and climatic variability in the eastern portion of the *P. cornutum* range during the last century. Similar to all *Phrynosoma* species, *P. cornutum* is primarily a xeric-adapted lizard. The genus is native to arid and semi-arid regions of western North America and found within open habitats with minimal ground-level vegetation and scattered canopy cover. Of all the *Phrynosoma* species, *P. cornutum* ranges the farthest east and into areas that receive more precipitation annually and are more densely vegetated at ground level than would be typical for the ranges occupied by other members of the genus. It is therefore somewhat peculiar that *P. cornutum* was native to areas of eastern and central Texas. A possible explanation for this oddity is that *P. cornutum* might have expanded its range eastward during the 1920s – 1950s when Texas was experiencing a series of prolonged and intense droughts (Texas Water Resource Institute, 2011) that may have led to development of favorable habitat, permitting dispersal of *P. cornutum* into areas formerly uninhabitable. Therefore, prior to the droughts, *P. cornutum* may not have entirely inhabited what is considered to be the historic eastern portion, but instead expanded into eastern and central Texas during the droughts. If this is correct, then the observed range contraction in the eastern quadrant was preceded by a range expansion, and the species may simply be

retreating back toward the more western portions of its range, where the habitat is more suited to its long-term survival. This hypothesis, while intriguing, is difficult to test given that observational data prior to the 1950s is extremely limited. It does present the notion, however, that the assumptions of a range contraction in the eastern portion of the *P. cornutum* range may be limited in scope and that even studies looking at “long-term” trends may still be subject to misinterpretation due to a lack of prior data that may be impossible to overcome. Nonetheless, this climate/habitat-based explanation does introduce the idea that when the range of a species contracts, the contraction will proceed toward the center of the geographic distribution of the genus – an idea worth testing in future studies.

Even when extensive temporal and spatial data are available for analyzing range contraction, other issues of study design need to be considered. For example, the metrics used in this study might be susceptible to errors from small sample sizes and sampling bias in the spatial distribution of lizard observations. For instance, both directionality metrics might potentially misrepresent the “true” extent of the range portion in each of the quadrants. The edge metric is dictated by the bounding hull of the MCP that essentially traces the extreme outlying points (observations) in each time period to generate a perimeter that encloses all observations. A vagrant observation could skew the MCP edge, leaving large spaces in the quadrant void of observations, resulting in the mean distance to edge possibly being an inaccurate indicator of the actual extent of the range. The mean distance-to-observations metric could be overly influenced by clustered observations. For instance, if survey effort was concentrated near the edge in one time period and then near the historic center in later time periods, the mean distance to

observations might show a decline over time and mistakenly be regarded as indicating a range contraction even though the actual edge of the range may have remained unchanged. In reality, such a result would be a consequence of inconsistent or spatially-biased sampling coverage. Alternatively, a cluster of observations might represent an actual area of high density of the species such that the mean distance-to-observation metric is appropriately capturing the gradient in the species density over the extent of the range. With regard to my study, the two directionality metrics generally follow the same trend as they change among time periods (Figure 3), indicating a certain degree of precision, at least when used in tandem. Ideally, when examining changes in the range of a species, the MCP and distance metrics are based on as many points (locations of the species) as possible and points that reflect the species' actual spatial distribution rather than the distribution of survey effort.

Metrics based on one or a few points, such as the latitudinal and longitudinal extents or the geographic coordinates of the extreme directional points, are not very informative. These metrics simply assess the location and distance between extreme points and indicate nothing about the interior fill or shape of the range. Moreover, the latitudinal and longitudinal extents can be very misleading properties of the range in situations where they derive from vagrant locations of the species. As such they might be poor indicators of range contraction. In the present study, range contraction appeared to be most pronounced and consistent in the eastern quadrant, yet the longitude of the easternmost location of *P. cornutum* fluctuated among the time periods without a consistent trend moving west (Table 2).

Other limitations of my study include the use of inconsistent and sometimes low sample sizes to monitor the range over time. Ideally, all subsets being compared (ie. time period MCPs and quadrants) would be large and equivalent in size. Increasing sample size in subset populations supplies more information about the whole population and therefore reduces uncertainty in measurements, increasing the power to detect differences amongst subsets. However, if some subsets are much larger than others (i.e. unequal sample sizes), then the data may be heteroscedastic leading to larger error in and among measurements from different subsets. This error could be minimized by randomly resampling datasets based on a sampling threshold that is smaller than the smallest dataset being compared. For each resample, an MCP could be projected around the observations and each metric could be repeatedly measured, producing an increasingly precise probability distribution for each metric every time the datasets were resampled. This resampling would also allow a statistical comparison of all metrics, not just the two directionality metrics.

Further improvements on range estimation could be achieved by using a different bounding geometry to enclose the range, instead of the minimum convex polygon. The MCP is a continuous bounding configuration and does not allow for disjoint regions of occupancy, which might be necessary to represent the “true” range of many species, especially those with large ranges. The MCP also does not allow for any concave edges (i.e. curving inward); by definition of a convex polygon, all interior angles must be $\leq 180^\circ$. Both of these issues, depending on the shape of the distribution, cause the MCP to overestimate the range size and include large areas void of observations. In this study, four of the five time period MCPs extended into the Gulf of Mexico; these ocean portions

were objectively and easily removed using the intersect tool in ArcMap. However, the need for such removal and modification of the MCP is not always as apparent as in the case of the land-sea interface. Knowing which areas to include and exclude is usually more difficult to objectively determine. For example, each time period also included portions in alpine regions of northeastern New Mexico that contain no observations (Figure 1). These regions are lacking observations likely because the area lacks habitat and is climatically inhospitable to *P. cornutum*. However, the lack of observations could be due to inadequate sampling in this region. Field surveying to confidently conclude the species absence (a time-consuming and difficult task) or mapping of habitat would be required to validate the removal of that portion of the MCP.

Other bounding techniques that allow for the use of concave edges and discontinuity among regions of the range separated by uninhabited areas have been shown to reduce bias associated with convex hulls. These techniques include the alpha-hull (Burgman & Fox, 2003) and characteristic-hull (Downs & Horner, 2009); both use Delaunay triangulations to assemble the enclosing polygon(s). However, these methods are computationally complex and more difficult than my methods to perform in a standard GIS platform, as they require the use of coding techniques.

The fact that the range of *P. cornutum* appears to be contracting in the eastern quadrant and possibly in the southern quadrant lends credibility to the notion that peripheral populations are more subject than central populations to undergo extirpation. However, as previously stated, the eastern portion also includes a number of factors that may have caused local extinctions, which peripheral populations in the other quadrants do not experience. It is therefore difficult to distinguish whether the range is contracting

because the peripheral populations are more sensitive to disturbances or because the anthropogenic factors in the eastern portion are so intense. Lucas et al. (2016) compared the range contraction patterns of 386 vertebrate species around the globe in the context of three models -- the demographic, contagion and refuge models. The models differ in assumptions concerning species' geographic range fill and extinction threats, as well as the predictions drawn from them. The demographic model assumes an abundant center and an extinction threat that is ubiquitous in extent and uniform in intensity throughout the range. Therefore in the demographic model, the contraction progresses towards the center from all directions, as peripheral populations progressively decline. The contagion model assumes that the extinction driver has a directionality component, but makes no assumption about abundance (distribution of populations) within the range. Under this model, the contraction begins within the regions nearest the extinction driver and gradually advances from one side of the range to the other and thus the contraction is directional. Finally, the refuge model assumes that extinction probability increases in areas used by humans, and so a species undergoing range contraction will persist longest in portions of its range that are least used by people. In the refuge model, range contraction does not necessarily have any directionality unless human density and land use is distributed along a gradient within the geographic range. Range contraction of *P. cornutum* is probably best explained by the contagion or refuge model given that both predict contraction in a given direction and such directionality was revealed for *P. cornutum*.

For the species analyzed in their study, Lucas et al. (2016) concluded that although extinction is more likely in human-impacted areas (in accordance with the

refuge model), some species persist in and perhaps benefit from such areas. They also found that the relative spatial location of a population within the range (i.e., nearer the periphery or center) also influenced extinction probability, independent of human land use. These findings indicate that human land use does not necessarily predict extinction of species in an area and that characteristics of the species and the relative locations of populations within the range are also important factors. Further, even when extinction is correlated with human land use, the land use itself may not be the direct cause of extinctions. Climate change, invasive species, or other factors correlated with human land use could lead to similar patterns of contraction, and therefore must be considered when developing strategies to manage declining species or mitigate threats.

Large-scale monitoring of species and habitat is necessary for the sake of conservation. In order to achieve logical and impactful conservation goals, researchers and conservationists need to determine the current status of species' range characteristics (eg. size, habitat structure, occupancy) and then compare these with past and predicted future states. This demands large amounts of observational data that could not be gathered using traditional methods of field surveying, but instead requires the crowd-sourced database approach, like that supplied by iNaturalist and VertNet. Museum collections have previously been used to show that the land conversion of prairies near Chicago preceded the declines of small mammals requiring prairie habitat (Pergams & Nyberg, 2001), to estimate diversity patterns (Grytnes & Romdal, 2008), and to reveal that genetic diversity has declined in Yellowstone Grizzly Bears (Miller & Waits, 2003). Citizen-science monitoring programs have proven useful in studying spread dynamics of invasive species (Mannino & Balistreri, 2018; Milko, 2012; Delaney, Sperling, Adams, &

Leung, 2006), detecting range shifts due to climate change (Lemoine, Schaefer, & Bohning-Gaese, 2007; Zuckerberg, Woods, & Porter, 2009) and observing phenological and elevational shifts in flowering times of plants (Miller-Rushing & Primack 2008, Crimmins, Kim, & Vasunilashorn, 2009). Therefore persistent use of these data sources and increasingly efficient data collection over time and space can only improve our ability to monitor range dynamics of species in the future.

V. CONCLUSIONS

My analysis shows that, between 1960 and 2017, the eastern portion of the *P. cornutum* range has contracted away from its historic edge. The range edge and observation density fluctuated in all the quadrants but a consistent range contraction was only apparent in the east. This westward range contraction may be due to any of various factors directly affecting *P. cornutum*, its habitat, and its prey base. Experimental evidence is needed to confirm the mechanisms causing the contraction. Range monitoring may be useful in developing effective conservation strategies. The use of MCPs and metrics assessing range extent and contraction directionality provide a relatively simple method to monitor changes in the geographic ranges of species. However, this approach necessarily generalizes complex spatial distributions and may not be useful in the case of species with irregularly shaped or disjoint distributions, or for species that may be too rare to generate sufficient observational data (museum records or citizen-science databases). Nonetheless, the future promise of this approach depends on the promotion and continued use of data from citizen-science networks worldwide.

Table 1. Characteristics of the geographic range of *Phrynosoma cornutum* for Each Time Period. Ranges were depicted as minimum convex polygons bounding the locations of the observations (n) from VertNet and iNaturalist.

Time Period	n	Area (km ²)	Latitudinal Extent (km)	Longitudinal Extent (km)
Historic	605	1,534,174	1,964	1,413
1960s	383	1,375,513	1,543	1,312
1970s	251	1,353,444	1,670	1,521
1980-2009	392	1,253,274	1,445	1,525
Current	1,207	1,379,877	1,645	1,314

Table 2. Geographic Coordinates for the Centroid and Extreme Directional Points in Each Time Period's Minimum Convex Polygon.

Time Period	Centroid		East	West	North	South
	Lat.	Long.	Long.	Long.	Lat.	Lat.
Historic	31.57	-101.28	-95.17	-110.45	39.62	21.20
1960s	31.76	-101.92	-95.64	-110.18	39.42	24.85
1970s	32.04	-101.99	-95.01	-110.42	39.14	23.70
1980-2009	32.97	-101.38	-95.12	-110.43	39.67	26.03
Current	31.65	-101.95	-95.97	-110.01	39.11	23.73

Table 3. Values of the metrics assessing the geographical extent of each quadrant of the *Phrynosoma cornutum* range in each time period.

North		Edge-to-Center Metric			Observation-to-Center Metric		
Time Period	Area (km ²)	n	Mean Dist. (km)	SD	n	Mean Dist. (km)	SD
Historic	518,506	13	774.9	105.5	258	549.3	169.8
1960s	462,148	22	725.3	82.2	105	562.3	227.2
1970s	497,192	29	756.5	103.0	37	584.9	213.7
1980-2009	527,439	25	784.9	117.1	175	591.0	205.5
Current	488,422	22	744.3	64.0	357	322.2	212.4

East		Edge-to-Center Metric			Observation-to-Center Metric		
Time Period	Area (km ²)	n	Mean Dist. (km)	SD	n	Mean Dist. (km)	SD
Historic	296,762	13	584.9	59.8	155	400.3	142.3
1960s	237,686	18	530.7	32.5	128	248.2	140.0
1970s	218,930	18	525.4	86.8	61	143.9	126.7
1980-2009	274,380	21	556.8	56.2	28	211.7	138.9
Current	193,939	16	487.5	65.6	93	160.3	117.3

South		Edge-to-Center Metric			Observation-to-Center Metric		
Time Period	Area (km ²)	n	Mean Dist. (km)	SD	n	Mean Dist. (km)	SD
Historic	485,606	61	788.8	156.4	65	453.9	229.3
1960s	404,522	39	645.0	74.6	58	397.9	202.0
1970s	369,390	27	671.8	102.0	32	502.5	161.9
1980-2009	244,580	32	560.8	53.2	24	343.8	196.0
Current	447,500	40	675.1	104.6	420	377.6	202.0

West		Edge-to-Center Metric			Observation-to-Center Metric		
Time Period	Area (km ²)	n	Mean Dist. (km)	SD	n	Mean Dist. (km)	SD
Historic	399,631	12	686.8	76.0	126	478.4	178.2
1960s	421,557	20	698.3	55.0	91	487.2	181.5
1970s	418,937	25	698.8	61.7	121	502.9	161.2
1980-2009	362,290	21	656.0	99.7	165	419.9	190.2
Current	398,079	21	679.3	62.6	337	353.5	214.8

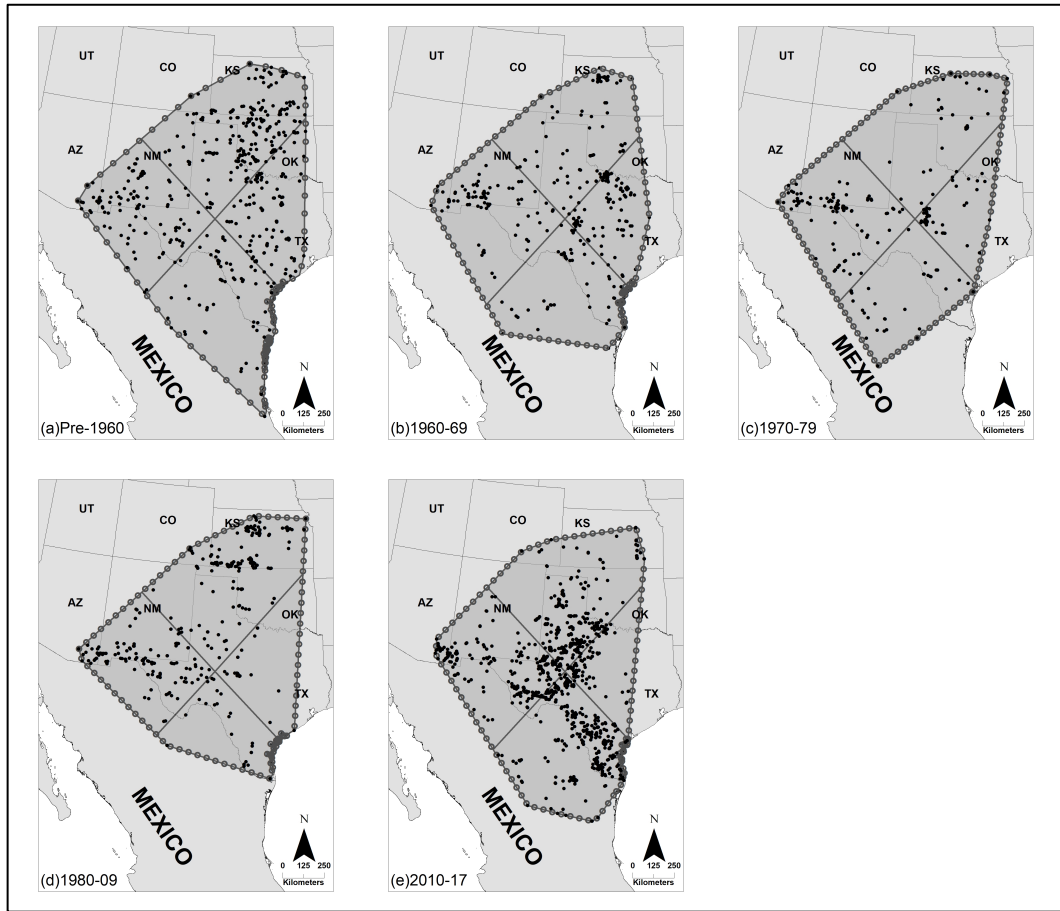


Figure 1. Time period range maps for *Phrynosoma cornutum* divided into directional quadrants originating from the historical center. Filled circles represent the location of each observation and hollow circles around the perimeter represent the points of measure for the metric assessing mean edge distance to the historic center.

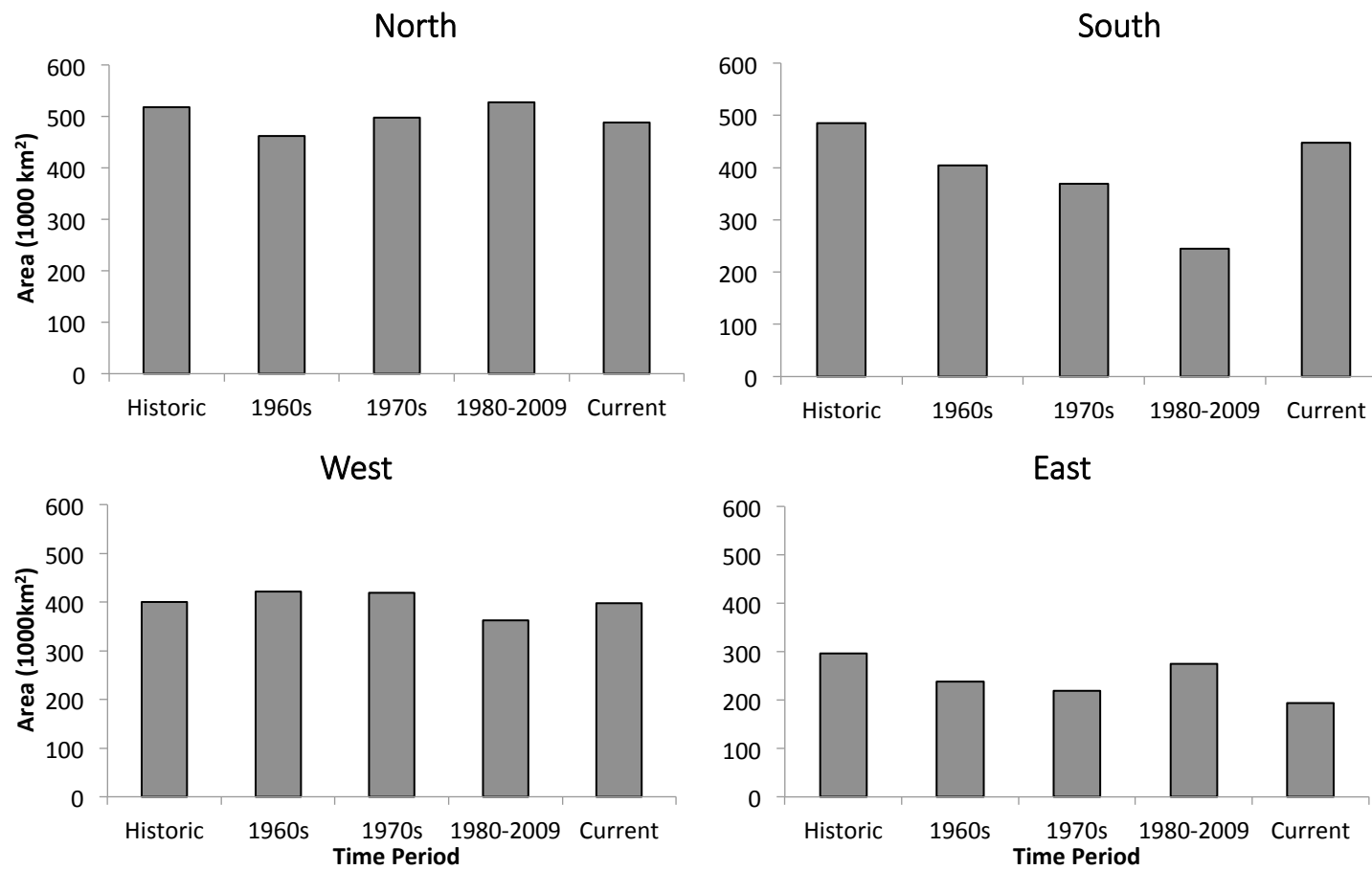


Figure 2. Area (km^2) of each directional quadrant for each time period's range map for *Phrynosoma cornutum*. The quadrants were created by dividing each time period's minimum convex polygon (MCP) into four portions by overlapping each MCP

Figure 2. Continued

historic (Pre-1960) time period's centroid was used as the origin of the 'X' as this was the starting reference point to which all later range maps were to be compared.

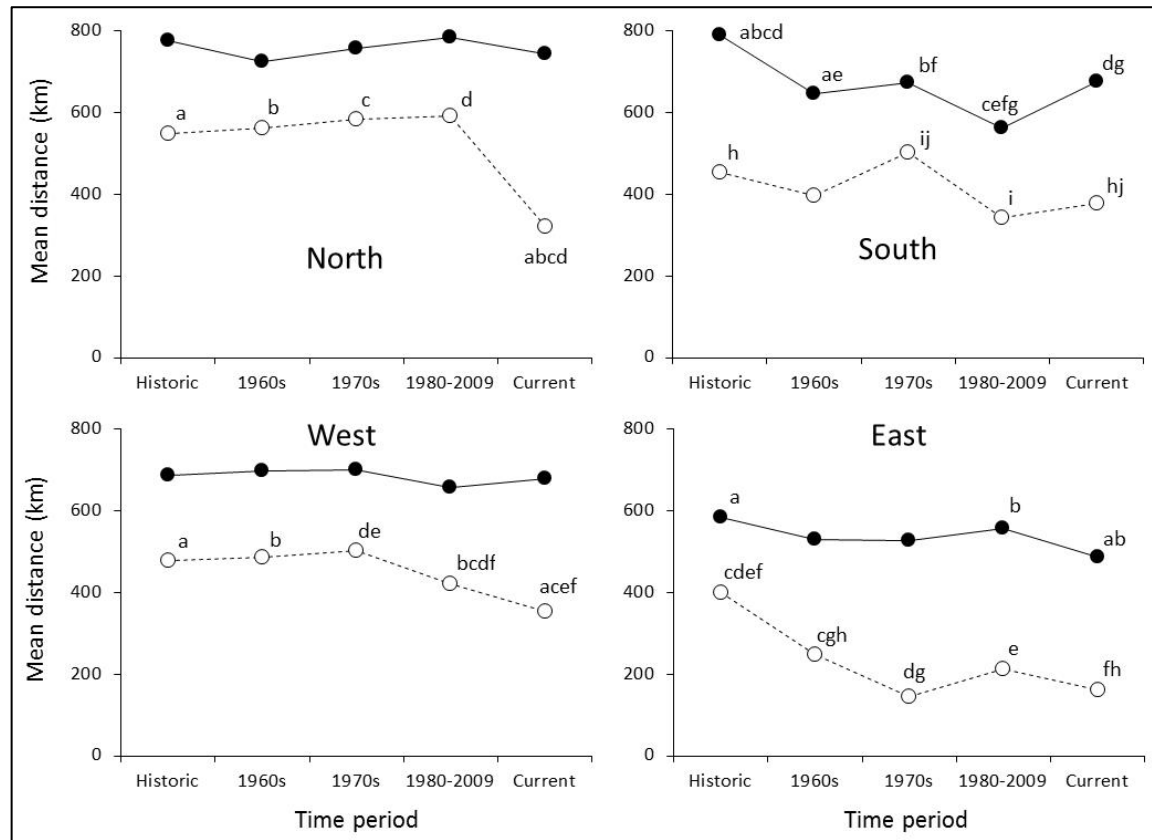


Figure 3. Change in the geographic range of *Phrynosoma cornutum* over time. Filled circles represent the mean distance between the center of the historic range and the edge of the range for each time period in each of the four directional quadrants. Open circles represent the mean distance between the center of the historic range and the observations within the given

Figure 3. Continued

quadrant. Shared letters indicate a statistically significant difference between two means as revealed by Tukey's post-hoc test; North, a-d: $P < 0.00001$; South, a: $P < 0.0001$, b: $P = 0.0001$, c: $P < 0.00001$, d: $P = 0.00002$, e: $P = 0.019$, f: $P = 0.002$, g: $P = 0.0004$, h: $P = 0.041$, i: $P = 0.033$, j: $P = 0.008$; West, a: $P < 0.00001$, b: $P = 0.063$, c: $P < 0.00001$, d: $P = 0.004$, e: $P < 0.00001$, f: $P = 0.003$; East, a: $P = 0.015$, b: $P = 0.0008$, c: $P < 0.00001$, d: $P = 0.074$, e-g: $P < 0.00001$, h: $P = 0.00002$. Note that Tukey's tests were not performed on the mean edge distances in the North and West quadrants as the ANOVAs were non-significant.

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