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TROPICAL VERTEBRATES IN A CHANGING WORLD

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RANGE CHANGE AMONG NEW WORLD TROPICAL AND SUBTROPICAL BIRDS

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This paper is dedicated to the memory of our dear friends and colleagues, Gary Waggerman, 1942-2009, and James Cox, 1952-2008

ABSTRACT

Range change is occurring at a rapid rate for tropical, subtropical, and warm desert birds in Texas. Comparisons between former (1974) and current avian distributions for the region show significant breeding range extension of 40-220 km to the N, NE, or E for at least 68 species, many of which cross major biogeographic boundaries. Fieldwork at the northern end of the subtropics along the coastal plain of the Gulf of Mexico has provided extensive documentation of breeding populations in new areas (e.g., nests, eggs, nestlings, fledglings, pairs, singing males on territory, and response to playback) for nine subtropical species (e.g., Green Jay *Cyanocorax yncas* and White-tipped Dove *Leptotila verreauxi*), as well as photographic evidence of seasonal persistence derived from use of a novel, web-based collaborative online robotic wildlife camera. Poor previous documentation, population change, habitat loss in the former range, and habitat change in the new range are considered as possible explanations. We conclude that change in key parameters of habitat, e.g. seasonal food availability, as affected by factors related to climatic change, e.g., mean annual precipitation, temporal distribution of precipitation (monthly means), or monthly means for nighttime-low temperatures during the breeding season, provide the most likely explanations for observed range extensions. At present, movement of a large segment of the subtropical avian community into temperate habitats has not been met with a corresponding shift of temperate species as had been predicted by a number of models; rather the communities now overlap, creating, in effect, novel communities. Results of this overlap are likely to produce profound changes that may first be evident in the genetics of subtropical/temperate species pairs, e.g., Black-crested Titmouse *Baeolophus atricapillus* and Tufted Titmouse *Baeolophus bicolor*.

Key words: Biogeography, biome, breeding ecology, climate change, novel communities, range shift, wildlife camera.

INTRODUCTION

Range shift in a number of organisms in apparent response to climate change has been treated in an increasing number of studies (e.g., Parmesan 2006) since a seminal paper in Nature provided prominent documentation for the phenomenon in English avian communities (Thomas & Lennon 1999). Based almost entirely upon anecdotal information derived from observations by amateur naturalists, avian data sets have served as the core for a number of modeling papers, several of which predict the shrinking and eventual disappearance of ecological communities at higher latitude or elevation (Jetz *et al.* 2007, Sekercioglu et al. 2008).

Texas has unique properties that make the study of the process and effects of range change especially informative, e.g., relatively abrupt boundaries between major biogeographic realms and historically well-documented avian species distributions (Cope 1880, Strecker 1912, Blair 1950, Oberholser 1974, Lockwood & Freeman 2004, Rappole *et al.* 2007). The purpose of this study is to use recently-published information along with fieldwork to test whether or not substantial changes in avian breeding ranges have

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occurred over the past four decades in Texas, and, if present, to consider what the long-term effects of such changes on existing communities might be.

METHODS

Oberholser's *The Bird Life of Texas* (1974), provided a thorough summary of the distribution of Texas birds as of 1973, including highly detailed maps of breeding distribution. The Texas Ornithological Society published updated maps for Texas breeding birds in 2004 (Lockwood & Freeman 2004). For each species in which range change was evident, we used the mapping program DeLorme (2007) to plot the northern, northeastern, or easternmost breeding record by county from Oberholser (1974) and the northern, northeastern, or easternmost extent of breeding range according to Lockwood & Freeman (2004). We then measured the distance between these points (to the nearest 10 km) and the approximate cardinal or intermediate direction from the Oberholser point to the Lockwood & Freeman point.

In addition to examining data in the literature, we conducted a three-year field study on ranch land of the Welder Wildlife Refuge along a 30-km stretch of the Aransas River (15 km on a straight west-to-east line) from the bridge across U.S. Highway 77 (28° 7' 37.69" N, 97° 25' 39.85" W) east to within 5 km (by air) from the river's mouth in Copano Bay (28° 6' 31.92" N, 97° 18' 57.24" W) in San Patricio and Refugio counties, at the northern end of the New World subtropics (Fig. 1).

The principal habitats surveyed included mesquite chaparral, oak chaparral, coastal prairie (maintained by fire and cell grazing by cattle), riparian forest, bridge abutments (for swallow nesting), vertical stream and river banks (for kingfisher nesting), and fresh and brackish water (tidal influence) marshes (Box & Chamrad 1966, Rappole & Blacklock 1985). Audiovisual surveys were conducted during 16 Apr - 14 May 2007, 3-10 Jun 2007, 4-30 Sep 2007, 13-19 Jan 2008, 28 Mar - 5 May 2008, and 18 Mar - 4 May 2009. Surveys were conducted at least once each year in April or May on all roads or trails on foot or on bicycle and on the Aransas River and Moody Creek by canoe. Sites where singing males or flocks of target species were found by surveys were visited repeated times each season to search for additional evidence of breeding (female, agitated pair, nests, fledged young, adults carrying food or nesting material, response to playback). The data gathered included GPS (Garmin 76) localities for displaying

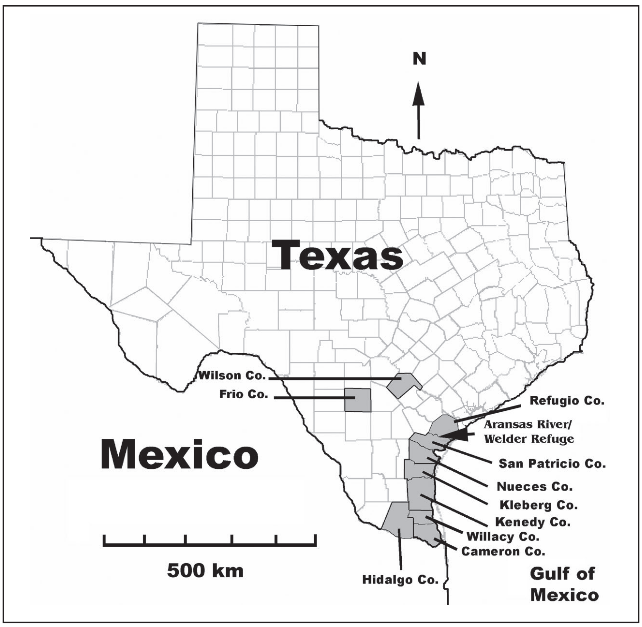

FIG. 1. US state of Texas, with the location of the Aransas River and Welder Wildlife Refuge (arrow) and the counties (shaded) mentioned in the text.

FIG. 2. Interface of the website (http://cone.berkeley.edu) for the collaborative telerobotic wildlife camera system, CONE Welder. The top panorama illustrates the camera field of view, which allows users to draw rectangles to control the camera. The camera window on the right side of the frame shows the live view. Each user can capture a picture by clicking on the camera button to the right of the live view. The image is then stored and displayed in the list at the left side of the live view, where users can enter their comments to annotate the image or comment on photos taken. Each user logs on to the system to draw rectangles on the panorama to indicate where they want the camera to observe. Details regarding camera operation can be found in Song (2009).

or singing males or birds responding to playback of recorded song, pairs, flocks, nests, eggs, fledglings or juveniles accompanied by adults. Exemplary nests, eggs and/or nestlings were collected and preserved as museum specimens (stored in the collection of the Welder Wildlife Foundation), and photos were taken of all nest sites discovered. *Ad hoc* mist-netting was done in attempts to capture specific individuals or species representatives. Mist nets were 12 m x 2.6 m of various mesh sizes (24 mm, 30 mm, 36 mm, 61 mm, or 121 mm) depending on the target species (AFO Mist Nets, Manomet, Massachusetts). Captives were banded with USFWS numbered bands and color-banded for individual recognition. Blood was drawn from the brachial vein using a small syringe to be used to determine whether birds captured earlier in the study were parents of birds captured in subsequent years. These data will be presented in a later paper. GPS localities were plotted and displayed on maps of Welder and vicinity using DeLorme Topo USA, version 6 (DeLorme 2006).

Seasonal persistence for several species was documented by means of a networked telerobotic camera set up at a lighted feeding and watering site established in mesquite chaparral about 100 m NW of the Welder Headquarters building. Online public access to the camera is controlled through a website titled “CONE-Welder” (CONE-Welder 2011) (Fig. 2). Building on the recent system and algorithmic development of collaborative observation (Song 2009), this novel web-based wildlife camera system was deployed on 12 May 2008, and has engaged citizen scientists to take photos of birds (and other animals) visiting the site 24 hours a day, seven days a week, except for brief downtimes for occasional maintenance and repair. Photos taken are logged automatically as to date, time, and photographer, and the users vote to classify each photo according to species (Faridani *et al.* 2009).

The conclusions in this paper are based on presence/absence data. Presence of breeding populations of target species is documented by the methods described above. It is not possible to document the historical absence of breeding populations with the same level of certainty. However, in addition to thorough documentation of the historical ranges of the species under consideration presented in the distributional literature (Strecker 1912, American Ornithologists' Union 1957, 1983, 1998; Packard 1951, Oberholser 1974, Rappole & Blacklock 1985, 1994; Vega & Rappole 1994), as well as in the appropriate species accounts from the *Birds of North America* (Poole 2011), there is extensive information on the historical bird community, and specifically for the area along the Aransas River, based on ornithological work done by several generations of researchers dating back over half a century (Roth 1971, Cottam & Blacklock 1972, Emlen 1972, Woodard 1975, Rappole 1978, Blacklock 1984, Blankenship & Glasscock 2007). Data in Oberholser (1974) are the principal source used for comparison of former nearest known breeding sites with current localities. These data are based on Oberholser's notes, published literature, major museum collections, personal fieldwork, observations by the senior editor of the volume (E.B. Kincaid, Jr.) and his associates, and thousands of records from Audubon Field Notes, Spoonbill (newsletter of the Houston Outdoor Club), *Bulletin of the Texas Ornithological Society*, and local and regional checklists and reports.

For bird taxonomy and species sequence we followed the *Check-List of North American Birds* (American Ornithologists' Union 2011).

RESULTS

For 68 species a considerable change in Texas range over a 35-year period is evident (Appendix 1). Recent documentation by photo of a Texas breeding record for the Mangrove Warbler (*Dendroica petechia erithachorides*), a tropical taxon (Lowther *et al.* 1999) is exemplary (Fig. 3).

National Breeding Bird Survey data trends for 1966-2007 (Sauer *et al.* 2008) show that populations of 20 species increased, eight of which increased significantly; 13 decreased, one significantly; three show no change; and there are no data for 32. The mean distance of range expansion was 205 km. The approximate direction of furthest expansion was N for 31, NE for 28, E for 7, and NW for 2 species.

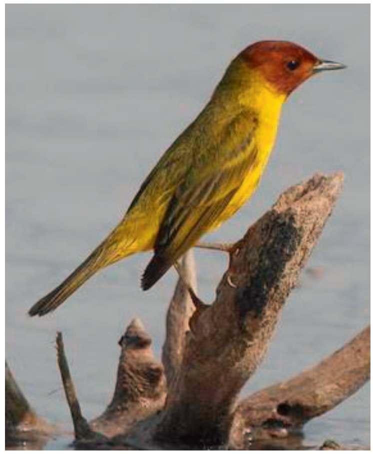

FIG. 3. Male member of a breeding pair (nest photographed) of Mangrove Warblers at the mouth of the Rio Grande River in South Texas. Photo by Scarlet Colley.

Data documenting presence of new breeding populations in San Patricio and Refugio counties and vicinity at the northern end of the subtropics are summarized below by species.

White-tipped Dove *Leptotila verreauxi* - Evidence of breeding for this species was observed at 21 new localities, 190 km N of the nearest known breeding area in the region (Cameron County) according to Oberholser (1974: 428) (Fig. 4). The majority of these were singing birds (> 500 m apart or birds heard simultaneously); however, at two sites (#7 and 5, Fig. 4) birds responded to playback (approach to < 10 m) and were captured and banded; one site (#13) was an observation of two adult birds with a juvenile; and one site (#9, Fig. 4) was a singing bird sitting on a nest. In addition, White-tipped Doves were photographed at the CONE feeding site in March of 2008 and May and June of 2009 (Table 1), although it is a woodland species that only rarely feeds at such open sites.

Buff-bellied Hummingbird *Amazilia yucatanensis* - Males were observed calling and displaying at four localities (Fig. 5), three of which were in the vicinity of feeders. Extensive photo evidence documents presence of this species at the CONE site during Apr-Oct 2008 and Apr-Oct 2009 (Table 1). The absence of records from Nov 2008 - Mar 2009 and 1-30 Nov 2009 (up to date of manuscript submission) likely

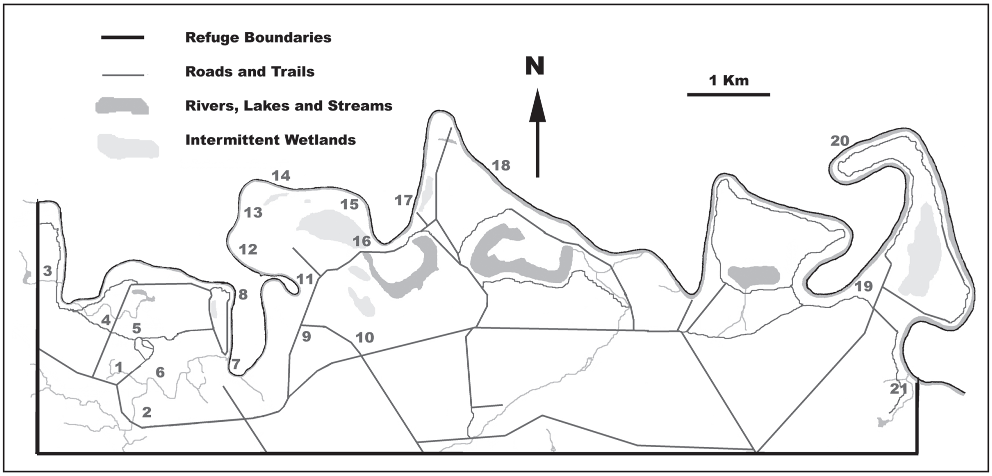

FIG. 4. White-tipped Dove *Leptotila verreauxi* localities in the main study area in the vicinity of the Aransas River and Welder Wildlife Refuge in San Patricio and Refugio counties, showing rivers, streams, roads, and trails where surveys were conducted, 2007-2009.

indicates migration for the majority of the population of this species.

Green Kingfisher *Chloroceryle americana* - Pairs of this species were observed at five localities on the Aransas River and two on Moody Creek (a tributary of the Aransas) (Fig. 5). In addition, a pair was seen on a creek in Sinton (#6, Fig. 5) and at Paradise Pond (#7, Fig. 5) in Port Aransas. Both members of one of the pairs on Moody Creek (#2, Fig. 5) were captured and banded; the female was captured and banded on 22 Apr 2007 and recaptured on 10 Apr 2009 at the same locality. Active nest holes (adults entering carrying food) were located at #1 and #4 (Fig. 5).

Great Kiskadee *Pitangus sulphuratus* - Pairs were observed at 22 separate localities in 2007-2009, 21 of which were along the Aransas River or nearby wetlands, and one in Sinton, 7 km S of the Aransas; active nests (adults constructing or visiting) were found at 12 sites (Fig. 6) most of which were over or near open water. Eggs were collected from site #2 (Fig. 6). Birds responded to playback (calling, approach) at two sites (#13 and 17, Fig. 6). Photos were recorded at the CONE site during several months in 2008 and 2009 (Table 1), although the only attractions at the site were bathing areas and foraging perches.

TABLE 1. Number of days by month on which photos were recorded by CONE website visitors for species new to the Welder avifauna. during 20 April 2008 – 30 November 2009. Photos can be viewed at http://cone.berkeley.edu.

	Month																			
	2008									2009										
Species	A	M	J	J	A	S	O	N	D[1]	J[1]	F	M[2]	A[2]	M	J	J	A	S	O	N
White-tipped Dove	0	3	0	0	0	0	0	0	0	0	0	0	0	5	0	1	0	0	0	0
Buff-bellied Hummingbird	0	26	21	21	28	26	13	0	0	0	0	0	19	31	30	31	27	29	13	0
Great Kiskadee	0	0	5	5	2	0	9	6	2	2	13	1	0	0	15	11	6	2	0	0
Couch's Kingbird	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0
Green Jay	4	29	18	27	31	29	31	30	16	11	26	2	18	22	10	9	18	30	13	12
Audubon's Oriole	0	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0

[1] Camera was not functioning during 17 Dec 2008 - 14 Jan 2009.
[2] Camera was not functioning during 4 Mar - 3 Apr 2009.

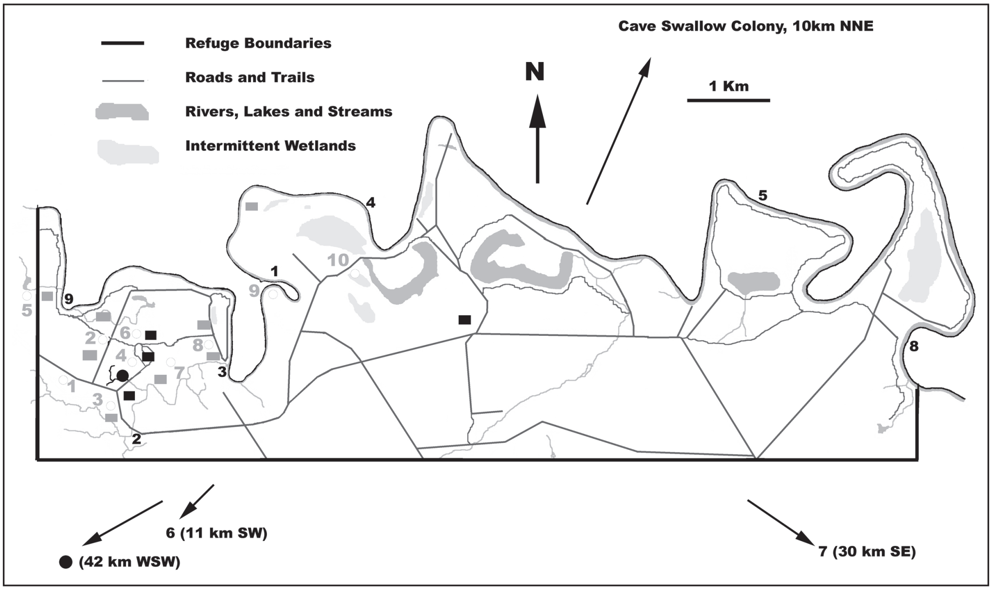

FIG. 5. Buff-bellied Hummingbird *Amazilia yucatanensis* (black rectangles), Green Kingfisher *Chloroceryle americana* (black numbers), Couch's Kingbird *Tyrannus couchii* (gray numbers), Tropical Parula *Parula pitiayumi* (black circle and arrow), Audubon's Oriole *Icterus graduacauda* (gray rectangles), and Cave Swallow *Petrochelidon fulva* (arrow) localities in the main study area (see Fig. 4 for details).

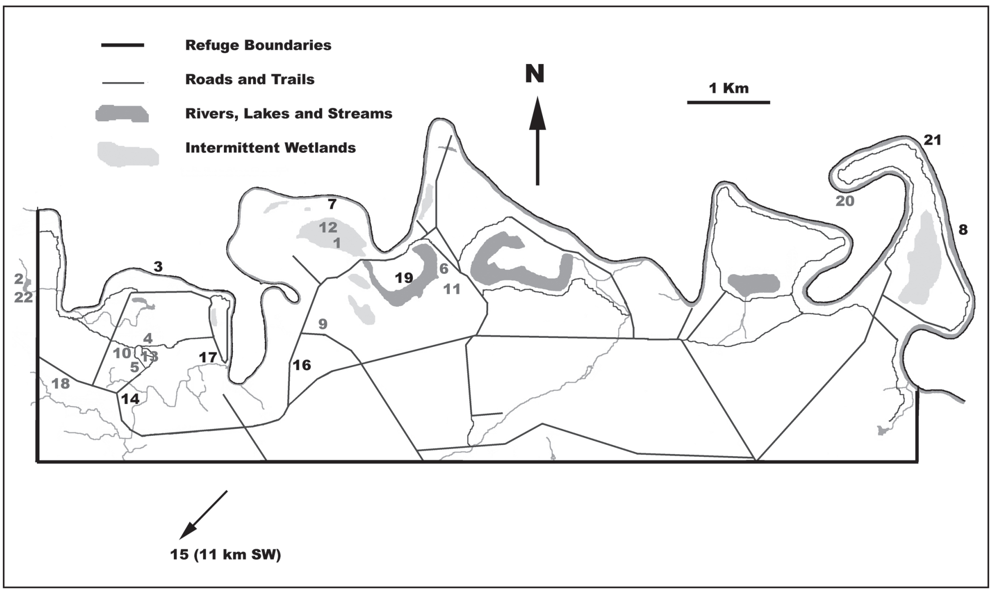

FIG. 6. Great Kiskadee *Pitangus sulphuratus* localities in main study area (see Fig. 4 for details). Black numbers are localities for calling birds; gray numbers are nest sites.

Couch's Kingbird *Tyrannus couchii* - Ten localities were found over the course of the study, five of which (#1,3,4,9,10, Fig. 5) were occupied by pairs in 2007, 2008, and 2009. Both members of one pair (#4, Fig. 5) were banded in 2008 and observed again in 2009. Individuals responded to playback (call, approach) at sites #3 and #4. Photos were taken at the CONE site in April 2008 and 2009 (Table 1).

Green Jay *Cyanocorax yncas* - Groups of this species were seen or heard at 25 separate localities in 2007-2009, 22 of which were in riparian forest, oak chaparral, or mesquite chaparral near the Aransas River (Fig. 7). In addition, groups were heard at Sous Creek (#23), Aransas National Wildlife Refuge (#24), and Paradise Pond at Port Aransas (#25). Most of the Aransas River area localities had Green Jay groups during all three field seasons. Green Jays were among the most common and regular visitors to the CONE feeding site, where they were photographed almost every day during every month of the year when the camera was operating (Table 1). A total of 17 jays was banded with both USFWS bands and color bands for individual recognition over the course of the study. Several of the color-banded birds were regular visitors to the CONE feeding site, where they were easily identified from photos. Both members of two pairs (from localities #4 and #5) were banded and color-marked. These birds were observed carrying food (cicadas mostly) in early May 2007, presumably to nestlings or recently-fledged young. The male from the pair captured and banded at locality #4 on 14 May 2007 was recaptured near that site 31 Mar 2009.

Cave Swallow *Petrochelidon fulva* - A nesting colony of this species was discovered under a bridge on Sous Creek in Refugio Co., 10 km NNE of Welder on 28 Apr 2007 (Fig. 5).

Tropical Parula *Parula pitiayumi* - Skoruppa & Blacklock (2007) reported pairs of both Tropical and Northern Parula warblers at Hibernia, San Patricio Co., 42 km SW of Welder. We found a pair of Tropical Parulas at Welder in May 2010 (Fig. 5), and also heard and saw a singing male of Northern Parula on several occasions during April and May 2010 in the vicinity of the Administration Building (28° 6' 48.86" N, 97° 25' 1.31" W) and at the south end of Hackberry Motte (28° 6' 42.54" N, 97° 24' 22.56" W).

Audubon's Oriole *Icterus graduacauda* - Eight localities for singing Audubon's Orioles were recorded during the course of the study, at least six of which were occupied during all three years (Fig. 5).

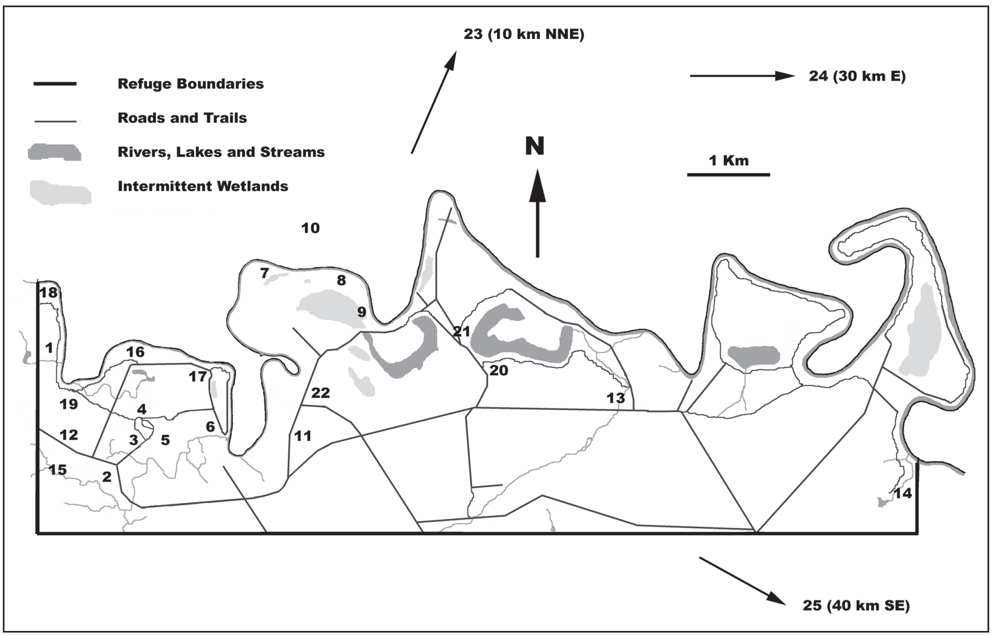

FIG. 7. Green Jay *Cyanocorax yncas* localities in the main study area (see Fig. 4 for details).

Males responded to playback (singing, approach) at two sites. Photos at the CONE site recorded presence of Audubon's Orioles during three months (Table 2), although no attraction other than water can be found at the site for this species.

Additional Species - Seven other subtropical, warm desert, or tropical birds were seen on or near the Welder Refuge within the past four years, but data are insufficient at present to document breeding: Groove-billed Ani *Crotophaga sulcirostris* - sightings at three localities in 2007 and 2008; Black-throated Sparrow *Amphispiza bilineata* - sighting in Apr 2009; Green-breasted Mango *Anthracothorax prevostii* - seen at SG's feeder each year from 2003-2008; Hooded Oriole *Icterus cucullatus* - male sighted on 18 Apr 2009; Gray Hawk *Buteo nitidus* - sightings at three localities by three different observers in 2007, 2008, and 2009; Lesser Nighthawk *Caprimulgus acutipennis* - seen and heard vocalizing on 17 Apr 2009, responded to playback (approach, call); Ringed Kingfisher *Megaceryle torquata* - seen on the Aransas River, E of Welder in 2006 by SG.

DISCUSSION

In this study, we document shift of breeding range for 68 species of birds, most of which fall into one of three major biogeographic categories in terms of their ecological communities: subtropical, tropical, and warm desert. The direction of range shift for nearly all of these species is into regions that historically were cooler and wetter than their original range (as of 1974) (Norwine & John 2007). Several reasons have been proposed for these or similar range changes that have occurred in other regions or taxa, which we discuss below:

1. Poor Historical Data - As Lockwood (2001: 108) has stated regarding the Gray Vireo, whether evidence of breeding populations from areas where they were not previously recorded "...is a result of an actual range expansion or if they were simply overlooked is open to speculation". Fall (1973) makes a case for "overlooked" for 10 subtropical species that he found on a huge private ranch (King Ranch) in Kenedy County, well north of their previously known ranges. Perhaps this explanation has some validity in situations where evidence of a range extension is based on observations of a few individuals at a few sites, but when the extension is documented for several individuals at several sites, the idea that a significant portion of the range was missed by earlier workers seems unlikely for one species let alone 68, at least in Texas where ornithological exploration has been conducted for well over a century (see review in Oberholser 1974). The ornithology of northeastern Mexico is less well-documented, making it difficult to assess the distances and rate of tropical species' range extensions. Nevertheless, the broad outlines of historical species distribution are well understood for the region (Friedman *et al.* 1950, 1957; Howell & Webb 1995), and certainly, the appearance of tropical bird species in Texas has been thoroughly recorded (Oberholser 1974, Lockwood & Freeman 2004).

2. Population Change - Populations of a species introduced to a new, suitable environment will expand to fill that environment, providing births exceed deaths. Rate of expansion will depend on factors affecting the relative rates of birth, e.g., food availability, and death, e.g., predators or disease (Wilson & Bossert 1971). For instance, since its introduction into the western hemisphere in 1851, the House Sparrow has expanded its range to include nearly all of North America south of the Arctic Circle, although in this case population increase and range expansion appear to have been a result of introduction into a suitable, vacant environment rather than a cause (Lowther & Cink 2006). Examples of species whose populations fill a new environment simply because of population pressure within their former environment are less obvious. Fretwell (1972) proposed that population density alone could affect habitat suitability. He argued that given two habitats, A and B, in which A has the higher quality for species X, the quality of habitat A can be reduced below that of habitat B simply by increasing the number of individuals occupying habitat A. Thus it is at least theoretically possible for population change within a species's existing range to force occupation of neighboring habitats formerly outside the range, providing these habitats are at least marginally suitable.

If avian range extension in Texas were a function of population change, a logical prediction would be that range would expand in some years for some species for those with increasing populations, contract in other years for those with decreasing populations, while showing no change for those with stable populations. However, this is not the pattern that has been recorded (Appendix 1). Rather, rapid range extension has occurred over a 30-year period for species in which some populations are decreasing, some are increasing, and others are showing no change. Therefore we conclude that population change does not provide an adequate explanation for the observed range expansions.

3. Habitat Destruction Within the Former Range - Replacement of large amounts of native habitat by agriculture is well documented for the northeastern Mexican state of Tamaulipas as well as for large parts of south Texas, particularly Hidalgo and Cameron counties of the Lower Rio Grande Valley (Dinnerstein *et al.* 1995: Map 6). This destruction has been suggested as a cause for the appearance of tropical species in Texas, e.g., Green Parakeet *Aratinga holochlora* and Red-crowned Parrot *Amazona viridigenalis* (Lockwood & Freeman 2004: 91), and might be considered as an explanation for range expansion in other species as well. However, most of this habitat destruction occurred more than 30 years ago (Purdy 1983), predating much of the observed range expansion.

Normal reproduction and dispersal provide sufficient impetus for occupation of nearby suitable habitat, at least in such well-adapted dispersers as birds (Fretwell 1972). In addition, there are many among the species in which range expansion has been observed, specifically those native to warm desert, for which no obvious change in habitat within the former breeding range has occurred. We conclude that habitat destruction in the former range does not provide a sound explanation for observed range expansion.

4. Habitat Creation Within the New Range - There are many examples of situations in which habitat change outside the former range of a species has resulted in expansion of the species into the newly-created habitat. Roberts (1936: 385), for instance, describes range change of the Greater Prairie Chicken *Tympanuchus cupido* in Minnesota as follows: "It entered the state from the east and south some time previous to the middle of the nineteenth century and spread rapidly west and north with the settlement of the country". What is noteworthy about most cases in which a species expands outward from former range into a neighboring new range is that obvious structural change in habitat in the newly colonized portion has taken place. This situation does not explain avian range expansion in Texas. Some small shifts (< 10%) in the relative amounts of native habitats have been documented in the region over the past decade (Wilkins *et al.* 2009), and shrub density has increased significantly in some South Texas prairie and savanna (Glasscock 2001), but for none of the 68 species documented as occupying new range in Texas has any obvious fundamental structural change in habitat within the new range occurred. Although the total amounts have increased for some habitats and decreased in others, all of the habitats into which these species moved were available before the range extensions occurred, even the specialized nesting habitats required by birds like the Cave Swallow (concrete bridge abutments), kingfishers (vertical banks of sandy loam soil), and Hooded Oriole (untrimmed palms with low-hanging fronds).

Despite the lack of obvious structural change in habitats within newly-occupied ranges, we suggest that habitat change remains the most probable explanation for the observed extensions in range for 68 Texas birds. Fretwell (1972: 80) defines "habitat" for a species as, "...any portion of the surface of the earth where the species is able to colonize and live (temporarily or permanently) at some density greater than zero". From an operational perspective, "habitat" for a given species is normally defined based on plant community (Odum 1971: 234), but clearly Fretwell's definition allows for multiple dimensions that relate to the species's niche. We suggest that some factor has influenced one or more critical habitat dimensions other than structure, causing a broad range of Texas habitats to become suitable that were previously unsuitable for a number of bird species.

The most obvious environmental factor associated with avian range shift in South Texas has been change in mean annual temperature (Fig. 8). Norwine & John (2007) provide extensive documentation of this fact, noting that the region is becoming warmer and dryer with a likelihood of longer droughts punctuated by more intense precipitation episodes. We hypothesize that climate change, exemplified by mean annual temperature changes, provides the ultimate cause for avian range change that we have documented in this paper. The proximate cause is unknown. However, we suggest that change in key parameters of habitat, e.g., seasonal food availability, as affected by factors related to climatic change, e.g., mean annual precipitation, temporal distribution of precipitation (monthly means), or monthly means for nighttime-low temperatures during the breeding season, provide the most likely explanations for observed range extensions.

Possible Effects of Range Extension on Avian Communities - In this paper we report on the immigration of 68 species of tropical, subtropical, and warm desert birds into avian communities of which they were not previously members, many of them in the

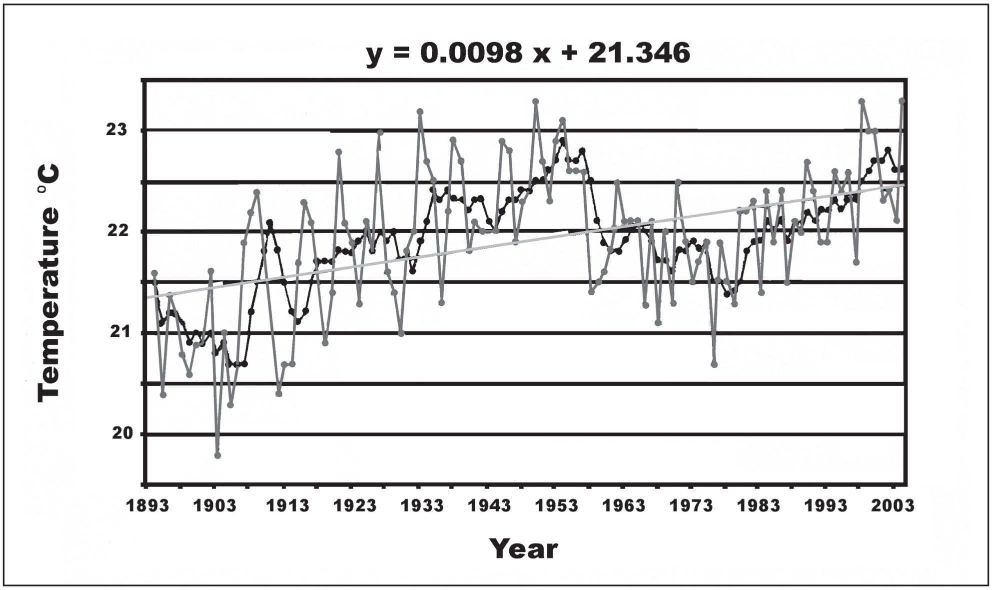

FIG. 8. Mean annual temperature for South Texas, 1893-2003. Dark gray dots = yearly average; black dots = 5-year running average; light gray line = trend line.

temperate biome. Expansion of the ranges of bird species of more "southern" or lower elevation communities into areas occupied by more "northern" or higher elevation communities is happening in many regions, although perhaps not so dramatically as in Texas. For instance, in New York State, publication of two breeding bird atlases at a 20-year interval (Andrle & Carroll 1988, McGowan & Corwin 2008) documents the movement of breeding populations of several species (e.g., Carolina Wren *Thryothorus ludovicianus*, Red-bellied Woodpecker *Melanerpes carolinus*, Tufted Titmouse *Baeolophus bicolor*) native to the Carolinean Zone (elevations < 300 m in southern New York) into breeding bird communities of the Transitional (300-600 m) and even the Canadian Zone (> 600 m) with no obvious change in the distribution or population size for members of the higher elevation communities (McGowan & Corwin 2008). Such range extensions would seem to have obvious implications for existing members of the invaded communities. Several models derived from avian range-shift data predict the disappearance of communities at higher elevation or latitude. For instance, Jetz *et al.* (2007: 1) state, "Even under environmentally benign scenarios, at least 400 [bird] species are projected to suffer > 50% range reductions by the year 2050 (over 900 by the year 2100)". Perhaps such changes will occur over the long term. At present, however, there is no evidence of such effects where subtropical species have invaded temperate bird communities in Texas. The same bird species that were present before the newcomers arrived are still present (Lockwood & Freeman 2004). It could be argued that since the avian range shifts have been so rapid and recent, and have not been accompanied by obvious changes in vegetation distribution, the predicted shift in habitat distribution will, in fact, occur over the years, decades, or centuries to come. However this argument simply begs the questions of how and why these range changes have occurred in the absence of structural change in existing habitat.

The fact that in Texas a major portion of the subtropical avian community now breeds in temperate communities alongside temperate species may indicate that the result of range shift caused by climate change will not be simple replacement of a more "northern" natural community by a more "southern" one. Rather, this mixing of communities could lead to the evolution of entirely new sets of communities (Parmesan 2006). Of course it will likely take decades if not centuries for the community mixing process to evolve, but it may not take long before evidence of profound change can be detected. We propose that initial evidence of how communities will change will come from newly-overlapping pairs of closely-related, and formerly largely allopatric, congeners. For instance, the original northeastern range boundary for the subtropical Black-crested Titmouse *Baeolophus atricristatus* and Golden-fronted Woodpecker *Melanerpes aurifrons,* was the San Antonio River along the northern border of Refugio County (Fig. 1) (Oberholser 1974, Grubb & Pravasudov 1994, Husack & Maxwell 1998, Shackelford *et al.* 2000, Patten & Smith-Patten 2008). There is no evidence that this boundary has expanded northeastward for these species as yet, but some effect on populations or gene pools of their respective temperate congeners, the Tufted Titmouse *B. bicolor* and Red-bellied Woodpecker *M. carolinus* can certainly be expected: (1) one member of the species pair will push the other out of the new community, (2) both will occupy the new community, or (3) genetic mixing will occur. We believe that #3 is the most likely scenario, and we predict that genetic studies comparing DNA of historic specimens from border regions with those from the new region of overlap will show that the process is already well underway for superspecies pairs like the titmice and woodpeckers mentioned above. The Blue-winged Warbler *Vermivora cyanoptera*/Golden-winged Warbler *V. chrysoptera* situation, with *cyanoptera* DNA swamping *chrysoptera* populations (Gill 1997), may be a prototype for what we can expect in the future as more and more southern or low elevation congeners move into the ranges of their northern or higher-elevation counterparts.

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APPENDIX 1. Distance and cardinal or intermediate direction of range expansion[1], preferred habitat in biological region of origin, and evidence of recent population change based on National Breeding Bird Survey (BBS) data for avian species undergoing range expansion in Texas within the past 35 years (1974 - 2009). Species for which there is evidence of breeding within the new range as reported in this paper or the literature are shown in bold.

English name	Scientific name	Principal distance and direction of expansion	Preferred habitat in former range	BBS population trend
Black-bellied Whistling-Duck	*Dendrocygna autumnalis*	300 km N	Tropical and subtropical freshwater wetlands	Increase
Muscovy Duck	*Cairina moschata*	280 km N[2]	Tropical freshwater wetland	No data
Mottled Duck	*Anas fulvigula*	220 km NE	Subtropical freshwater wetland	Decrease
Plain Chachalaca	*Ortalis vetula*	180 km N	Tropical and subtropical woodlands, usually near water	No data
Neotropic Cormorant	*Phalacrocorax brasilianus*	220 km NE	Tropical and subtropical wetlands	No data
White-tailed Kite	*Elanus leucurus*	290 km N	Tropical, subtropical, and temperate savanna, thorn forest, and grassland	No change
Common Black-Hawk	*Buteogallus anthracinus*	410 km NE	Tropical and subtropical lowland woodland	No data
Short-tailed Hawk	*Buteo brachyurus*	370 km N[3]	Tropical savanna	No data
Crested Caracara	*Caracara cheriway*	220 km NE	Tropical and subtropical savanna, thorn forest and scrub	Increase[4]
White-winged Dove	*Zenaida asiatica*	480 km N	Tropical and subtropical thorn forest	Increase[4]
Inca Dove	*Columbina inca*	360 km N	Tropical and subtropical savanna and thorn forest	Increase[4]
White-tipped Dove	*Leptotila verreauxi*	190 km N	Tropical and subtropical woodland	No data
Green Parakeet	*Aratinga holochlora*	280 km N[5]	Tropical lowland woodland	No data
Red-crowned Parrot	*Amazona viridigenalis*	280 km N[5]	Tropical lowland woodland	No data
Greater Roadrunner	*Geococcyx californianus*	340 km NE[6]	Tropical, subtropical, and temperate semi-arid and arid scrub	Increase
Western Screech-Owl	*Megascops kennicottii*	330 km E	riparian woodland in temperate and subtropical semi-arid and arid lands	Decrease
Ferruginous Pygmy-Owl	*Glaucidium brasilianum*	70 km N	Tropical and subtropical riparian woodland	No data
Elf Owl	*Micrathene whitneyi*	300 km NE	Tropical and subtropical desert	No data
Common Pauraque	*Nyctidromus albicollis*	80 km N	Tropical and subtropical thorn forest and riparian woodland	No data
Common Poorwill	*Phalaenoptilus nuttallii*	80 km NE	Temperate and subtropical desert and thorn forest	Increase
White-throated Swift	*Aeronautes saxatalis*	140 km E	Temperate, subtropical, and tropical; aerial over montane and arid lands	Decrease
Buff-bellied Hummingbird	*Amazilia yucatanensis*	190 km N	Tropical and subtropical thorn forest and riparian woodland	No data

APPENDIX 1. Continued.

English name	Scientific name	Principal distance and direction of expansion	Preferred habitat in former range	BBS population trend
Blue-throated Hummingbird	*Lampornis clemenciae*	290 km NW	Tropical and subtropical montane semi-arid and arid lands	No data
Magnificent Hummingbird	*Eugenes fulgens*	290 km NW	Tropical and subtropical montane and arid woodland	No data
Black-chinned Hummingbird	*Archilochus alexandri*	70 km NE	Temperate and subtropical semi-arid and arid woodland and thorn forest	Increase
Ringed Kingfisher	*Megaceryle torquata*	210 km N	Tropical and subtropical riparian	No data
Green Kingfisher	*Chloroceryle americana*	70 km NE	Tropical and subtropical riparian	No data
Northern Beardless-Tyrannulet	*Camptostoma imberbe*	180 km N	Tropical and subtropical riparian woodlands and thorn forest	No data
Buff-breasted Flycatcher	*Empidonax fulvifrons*	400 km E[7]	Tropical and subtropical pine and pine-oakwoodlands	No data
Vermilion Flycatcher	*Pyrocephalus rubinus*	110 km NE	Temperate, subtropical, and tropical semi-arid and arid lands	Decrease
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	370 km NE[8]	Tropical and subtropical lowland woodlands	No data
Ash-throated Flycatcher	*Myiarchus cinerascens*	90 km E	Temperate, subtropical, and tropical semi-arid and arid lands	Increase
Brown-crested Flycatcher	*Myiarchus tyrannulus*	130 km N	Tropical and subtropical woodlands	Increase[4]
Great Kiskadee	*Pitangus sulphuratus*	80 km NE	Tropical and subtropical freshwater wetlands	No data
Tropical Kingbird	*Tyrannus melancholichus*	110 km NE[9]	Tropical and subtropical savanna	No data
Couch's Kingbird	*Tyrannus couchii*	200 km N	Tropical and subtropical thorn forest and savanna	Increase[4]
Gray Vireo	*Vireo vicinior*	250 km NE	Temperate, subtropical, and tropical semi-arid and arid woodlands and thorn forest	Increase
Hutton's Vireo	*Vireo huttoni*	300 km E	Temperate, subtropical, and tropical pine-oak and juniper woodlands	Increase
Yellow-green Vireo	*Vireo flavoviridis*	30 km NE	Tropical and subtropical lowland woodlands	No data
Green Jay	*Cyanocorax yncas*	80 km NE	Tropical and subtropical savanna and woodlands	Increase
Western Scrub-Jay	*Aphelocoma californica*	310 km N	Temperate, subtropical, and tropical oak woodlands	Increase
Cave Swallow	*Petrochelidon fulva*	510 km NE	Tropical and subtropical open areas and wetlands (with bridge abutments or caves for nesting)	Increase[4]
Black-crested Titmouse	*Baeolophus atricristatus*	110 km N	Temperate, subtropical, and tropical riparian and oak woodlands in semi-arid lands	No data

APPENDIX 1. Continued.

English name	Scientific name	Principal distance and direction of expansion	Preferred habitat in former range	BBS population trend
Verdin	*Auriparus flaviceps*	120 km NE	Temperate, subtropical, and tropical thorn forest and oak woodlands in arid and semi-arid areas	Decrease
Bushtit	*Psaltriparus minimus*	400 km N	Temperate, subtropical, and tropical thorn forest and oak woodlands in arid and semi-arid areas	Decrease
Cactus Wren	*Campylorhynchus brunneicapillus*	160 km NE	Temperate, subtropical, and tropical thorn forest and desert	Decrease
Black-tailed Gnatcatcher	*Polioptila melanura*	260 km E	Temperate, subtropical, and tropical thorn forest and desert	Decrease
Clay-colored Thrush	*Turdus grayi*	280 km N[5]	Tropical lowland woodland and riparian forest	No data
Long-billed Thrasher	*Toxostoma longirostre*	90 km NE	Tropical and subtropical semi-arid woodlands	Increase[4]
Curve-billed Thrasher	*Toxostoma curvirostre*	310 km N	Temperate, tropical, and subtropical semi-arid and arid thorn forest and woodlands	Decrease
Crissal Thrasher	*Toxostoma crissale*	270 km NE	Temperate, tropical, and subtropical semi-arid and arid thorn forest and woodlands	Increase
Tropical Parula	*Parula pitiayumi*	150 km N[10]	Tropical and subtropical lowland woodlands	No data
Yellow Warbler (Mangrove Warbler race)	*Dendroica petechia erithachorides*	340 km N[11]	Tropical mangroves	No data
Rufous-capped Warbler	*Basileuterus rufifrons*	360 km N[12]	Tropical and subtropical semi-arid and arid woodland and scrub	No data
Olive Sparrow	*Arremonops rufivirgatus*	50 km N	Tropical and subtropical thorn forest and lowland woodlands	No data
Canyon Towhee	*Melozone fusca*	190 km NE	Tropical, subtropical, and temperate arid scrub	Decrease
Botteri's Sparrow	*Peucaea botterii*	90 km N	Tropical and subtropical grasslands	No data
Rufous-crowned Sparrow	*Aimophila ruficeps*	140 km NE	Tropical, subtropical, and temperate arid scrub	Decrease
Black-throated Sparrow	*Amphispiza bilineata*	120 km NE	Tropical, subtropical, and temperate arid scrub	Decrease4
Pyrrhuloxia	*Cardinalis sinuatus*	80 km NE	Tropical, subtropical, and temperate semi-arid and arid scrub	Decrease
Varied Bunting	*Passerina versicolor*	170 km E	Tropical, subtropical, and temperate semi-arid and arid woodlands	No data
Bronzed Cowbird	*Molothrus aeneus*	180 km N	Tropical and subtropical savanna	No change

APPENDIX 1. Continued.

English name	Scientific name	Principal distance and direction of expansion	Preferred habitat in former range	BBS population trend
Hooded Oriole	*Icterus cucullatus*	100 km NE	Temperate, tropical, and subtropical lowlands (with palms for nesting)	Increase
Altamira Oriole	*Icterus gularis*	80 km N	Tropical and subtropical lowland woodlands	No data
Audubon's Oriole	*Icterus graduacauda*	90 km NE	Tropical and subtropical semi-arid woodlands	No data
Scott's Oriole	*Icterus parisorum*	200 km N	Tropical, subtropical, and temperate semi-arid and arid woodlands	Increase
Lesser Goldfinch	*Spinus psaltria*	90 km N	Tropical, subtropical, and temperate semi-arid and arid woodlands and scrub	No change

1 Northern or easternmost extent of former Texas range is based on Oberholser (1974) unless otherwise noted. Current northern or easternmost extent of Texas range is based on Lockwood & Freeman (2004) or data presented in this paper. Cardinal and intermediate compass points are used for approximate direction of extension. Distance of extension is given to the nearest 10 km.

2 Former northern extent of range is based on Friedman *et al.* (1950, 1957).

3 Former northern extent of range is based on Miller & Meyer (2002).

4 $P < .05$ based on National Breeding Bird Survey data, 1966-2007, in Sauer *et al.* (2008).

5 Former northern extent of range based on Gehlbach et al. (1976).

6 Current northeastern edge of the Greater Roadrunner's range likely is well northeast of the Texas border (Hughes 1996).

7 Former eastern extent of range based on Bowers & Dunning (1994).

8 Former northeastern extent of range based on Tweit & Tweit (2002).

9 Former northeastern extent of range based on Stouffer & Chesser (1998).

10 Current northern extent based on Skoruppa & Blacklock (2007).

11 Current northern extent based on Colley (2006); former northern extent based on Lowther *et al.* (1999).

12 Former northern extent of range based on based on Howell & Webb (1995). There are over 20 Texas records for this species, but no confirmation of breeding to date.