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HISTORICAL ZOOGEOGRAPHY AND CURRENT STATUS OF TWO SPECIES OF HYBRIDIZING GROUND SQUIRRELS (*ICTIDOMYS PARVIDENS* AND *I. TRIDECIMLINEATUS*) ON THE SOUTHERN PLAINS OF TEXAS

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ABSTRACT

Zimmerman and Cothran (1976) and a series of their follow-up studies documented hybridization between the Rio Grande (*Ictidomys parvidens*) and thirteen-lined ground squirrels (*I. tridecemlineatus*). More than 20 years after their work, we applied a series of morphological characters obtained from captive-born F₁ animals and field-collected specimens from across north Texas. Hybridization remains a localized phenomenon, with hybrid individuals comprising the majority of resident animals in Baylor County, Texas. Ranges have changed little in the intervening decades, but our collecting efforts have generated marginal county records for *I. parvidens* from Jones, Shackelford, Stonewall, and Throckmorton counties. Extirpation of two populations of *I. tridecemlineatus* sampled by Cothran (1982, 1983) were documented in Wilbarger and Motley counties -- the latter site now occupied by the Rio Grande squirrel. Historical accounts suggest that hybridization between the two taxa likely was initiated in the mid-1900s by range expansion of *I. parvidens*, a mid-Holocene immigrant into Texas from Mexico.

Key words: ground squirrels, hybridization, *Ictidomys parvidens*, *Ictidomys tridecemlineatus*, Southern Plains, sibling species, zoogeography

INTRODUCTION

The recent revision of Holarctic ground squirrels by Helgen et al. (2009) recognizes eight genera, while restricting the use of *Spermophilus* to Old World taxa. As presently defined, *Ictidomys* is now restricted to three species: the thirteen-lined ground squirrel (*I. tridecemlineatus*), and each of the two previously recognized subspecies of Mexican ground squirrel (*I. mexicanus* [Mexican ground squirrel] of

central Mexico, and the newly elevated *I. parvidens* [Rio Grande ground squirrel] of Texas, New Mexico, and northeastern Mexico). Two of these species, *I. tridecemlineatus* and *I. parvidens*, maintain a nearly parapatric distribution in Texas, with the exception of an area of broad apparent sympatry from northcentral Texas into eastern New Mexico.

The point of departure for this zoogeographic discussion of *Ictidomys* from the Southern Plains is the late Pleistocene. Most regional fossil and subfossil faunas from the study area are from alluvial sediments of the Kansan Province in Texas and Oklahoma and the limestone cave silts of the Balconian and Chihuahuan provinces in Texas and New Mexico. Although ground squirrel dentition is usually distinctive at the generic level *sensu* Helgen et al. (2009; e.g., Bryant 1945; Goodwin 2009), identifiable ground squirrel material is often scarce, and such remains are commonly edentulous jaws or isolated teeth that may be sufficiently worn or weathered as to obliterate distinctive dental characters. Further, there is no single diagnostic character distinguishing *Ictidomys parvidens* from *I. tridecemlineatus*. Size alone is of limited utility (Cothran 1982, 1983), and the potential for temporal size variation has been demonstrated for sciurids and a variety of other taxa (Martin and Barnosky 1993, and citations therein). A final confounding factor is the purported regional Pleistocene presence of at least two other ground squirrels with dentition comparable in size to *I. parvidens* — Richardson's ground squirrel of the *Urocitellus richardsonii-elegans* complex, and the larger Franklin's ground squirrel with proportionally smaller teeth, *Poliocitellus franklinii*. These sciurids occur no closer today than the High Plains of Colorado and Kansas, respectively, but fossil material attributed to these sciurids are recorded from the mesic Pleistocene grasslands and savannas south into Oklahoma (Graham et al. 1987; Smith and Cifelli 2000), Texas (Graham et al. 1987; Dalquest and Schultz 1992) and New Mexico (Harris 1989).

The post-Pleistocene shift towards a warmer and more arid environment was a complex, gradual, and regionally variable phenomenon for the Southern Plains states of Texas, Oklahoma, and New Mexico (e.g., Semken 1983; Wright 1983; Davis 1987; Graham et al. 1987; Harris 1990; Gehlbach 1991). The mid-Holocene shift (3-8,000 YBP) seems especially critical to the regional displacement of resident flora and fauna by incursions of both xeric-adapted western species and subtropical species from the south that continue to this day. A series of woodrat midden studies (e.g., Van Devender et al. 1987a, b; Elias and Van Devender 1990) have chronicled the Trans-Pecos Texas transition of the prevailing early Holocene pinyon-oak-juniper wood-

lands and savanna to mid-Holocene desert grasslands, and the nearly complete emplacement by about 4,000 YBP of the modern desert flora and fauna.

Our knowledge of the earlier historical distributions of the two *Ictidomys* is limited, but given a predilection for the altered habitats around early settlements, military installations, and individual homesteads, *I. parvidens* and *I. tridecemlineatus* were conspicuous residents to early European immigrants. The fanciful vernacular terms applied by early settlers to *I. tridecemlineatus* are evidence for their degree of familiarity with the distinctive pattern (e.g., "leopard spermophile" of Goodrich and Winchell 1894; "federation squirrel" of Baird 1857—the latter a reference to the alternating rows of spots and stripes resembling the American flag). Common names for *I. parvidens* usually referred to the presumed northern limits of the species' geographic distribution in Texas (e.g., Mexican ground squirrel of Baird 1857; Rio Grande squirrel of Bailey 1905).

Congruence of molecular (Herron et al. 2004) and dental (Goodwin 2009) studies suggest that *I. parvidens* (Rio Grande ground squirrel, *sensu* Helgen et al. 2009) is related more closely to *I. tridecemlineatus* than to the previously conspecific *I. mexicanus*. The largely exclusive ranges of *I. parvidens* and *I. tridecemlineatus* encompass much of the Great Plains and converge in the Southern Plains of north Texas and eastern New Mexico (Hall 1981; Schmidly 2004). The thirteen-lined ground squirrel is largely a prairie animal, ranging from Texas to southern provinces of Canada, although along the western margins of its range, isolated populations occupy high montane parklands. The Rio Grande ground squirrel occurs from the semiarid scrub and desert grasslands of northeastern Mexico to the mesquite savannas of northern Texas.

The two taxa have accumulated little differentiation since their late Pleistocene divergence at the morphological (Bryant 1945; Black 1972; Cothran 1983; Goodwin 2009), chromosomal (Nadler and Hughes 1966; Zimmerman and Cothran 1976; Cothran and Honeycutt 1984), allozymic (Cothran et al. 1977; Cothran 1983) or molecular (Harrison et al. 2003; Herron et al. 2004) levels. Nevertheless, the two are superficially distinctive. The thirteen-lined ground squirrel is the smaller sciurid, seldom weighing in excess of 150

g. The dark dorsal pelage is marked by rows of white spots against a dark dorsum, with the spots of alternate rows confluent to form solid stripes. The Rio Grande ground squirrel is a larger and rangier animal that can exceed 300 g, and sports both a proportionally longer tail and series of distinct spots arranged in rows against a comparatively pale tan-to-gray dorsum.

Typical of ground squirrels, the two taxa are often conspicuous residents near human habitations, with their diurnal habits, preference for open terrain, and their characteristic alarm trills. While each species exhibits rather broad ecological tolerances, both prefer sparsely vegetated or short-grass settings. Densest populations today usually occur in artificially enhanced and manicured habitats (e.g., golf courses, parks, school campuses). Especially favored are cemeteries, which are often established at the edges of communities and smaller towns, experience light and sporadic human traffic, and provide favorable burrowing conditions related to the loosened and friable fill of grave sites—a feature especially useful in areas of compact or rocky soils. Animals living under more natural conditions (e.g., rangelands and pastures) tend to be sparsely distributed and more secretive, although local exceptions sometimes occur where moderate to heavy grazing regimes are practiced. Roadways and railroad rights-of-way provide seemingly logical dispersal routes across and through otherwise unsuitable terrain (e.g., dense brush, areas of monoculture), at least where vegetation is sparse or mowed regularly.

Within the relatively broad band of mapped sympatry across southeastern New Mexico and north Texas (Figs. 1a, b), *I. tridecemlineatus* is the prevalent species across all but the southern periphery of the High Plains (Choate 1997), where *I. parvidens* is common. However, microallopatry seems a more accurate term here, for nowhere have the two taxa been taken simultaneously from the same locality. Contact has certainly occurred in places, for there are well documented instances of hybrid individuals—in each instance, coexisting with parental *I. parvidens*—within this area of apparent sympatry (Zimmerman and Cothran 1976; Cothran 1982, 1983; Cothran and Honeycutt 1984).

This study assesses the zoogeographic history and current status of *I. parvidens* and *I. tridecemlineatus* by comparing the results of an extensive systematic collecting effort with existing collection records and earlier literature. Documenting the current distributions of these species permits comparisons for the tracking of any future range shifts, as have been noted for other components of their respective faunas over the past several decades. During just the past century, mammals sharing subtropical affinities with *I. parvidens* (notably *Dasyopus novemcinctus*, Taulman and Robbins 1996; *Baiomys taylori*, Choate et al. 1990) have extended their ranges for hundreds of miles northward onto the Rolling Plains of Texas and beyond. *Ictidomys tridecemlineatus* is largely a species of more mesic prairie environs, and Frey (1992) provides examples of boreal species simultaneously extending their ranges southward into the Southern Plains (e.g., *Microtus pennsylvanicus*, *Zapus hudsonius*, *Mustela nivalis*). At least one Northern Plains mammal, *Microtus ochrogaster*, is actively reclaiming parts of its southern Pleistocene range in the Texas Panhandle (Choate and Killebrew 1991; Stangl et al. 2004; Poole and Matlack 2007).

A necessary corollary to documenting the present status of the two *Ictidomys* is the extent of detectable hybridization. While lacking fixed karyotypic or allozymic markers to distinguish the two species, Cothran (1982, 1983) was at least able to demonstrate the morphometrically intermediate distinctness of most of his “purported” hybrids. We provide a simple and reliable field method for distinguishing presumptive hybrid individuals from members of the parental species. While molecular analyses will provide a definitive determination of hybrid origin for any given specimen, identification of the distribution and numbers of purported hybrids by superficial or morphological means can certainly provide a coarse measure of the extent of hybridization and introgression between the two species (e.g., Homyack et al. 2008 for *Lynx rufus* x *L. canadensis*) and the geographic framework for the focus and design of subsequent genetic studies.

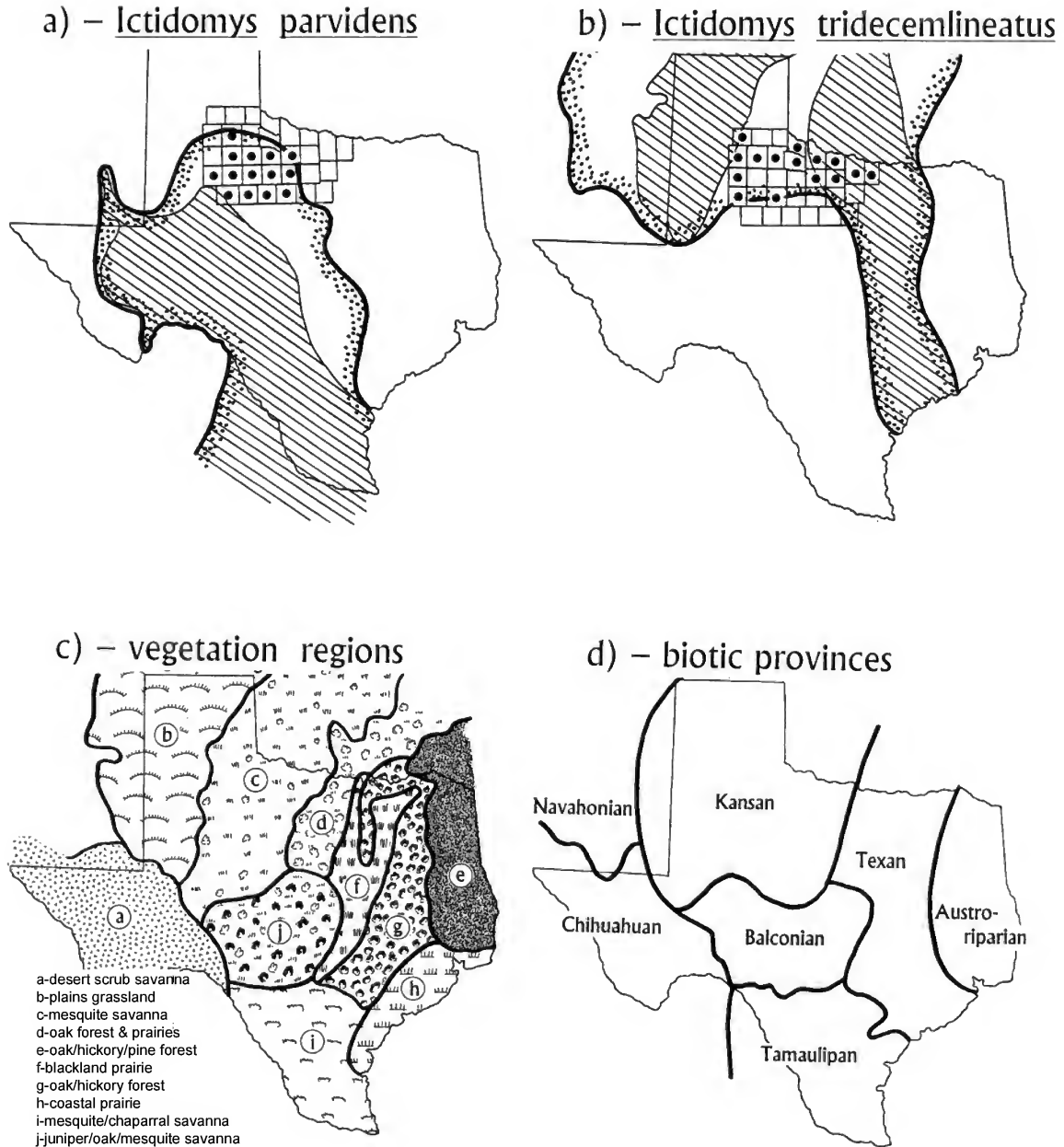


Figure 1. Current known distribution of *Ictidomys parvidens* (a) and *I. tridecemlineatus* (b) in Texas and proximal regions of adjoining states, superimposed over known range in early 1900s (hatched, from Bailey 1905); (c) regional vegetation map (modified from Kuchler 1964); and (d) biotic provinces (modified from Blair 1950). Closed circles from within the 31-county study area of north-central Texas represent counties where specimens are documented from literature records and from this study.

MATERIALS AND METHODS

The study area was designed to encompass the interface and overlap between northern populations of *Ictidomys parvidens* and the southern extent of the range of *I. tridecemlineatus* across the Southern Plains of north-central Texas. Cemeteries of mapped communities from 31 contiguous counties across the region were canvassed during the late spring to early fall months of 2004-2007 for ground squirrels.

Description of study area.—The terrain of the Southern Plains (Kansan and Balconian) and adjoining regions, combined with prevailing weather patterns, produce modern vegetation regions (Fig. 1c; from Kuchler 1964) coincidental with the distinct plant-animal associations recognized by Blair (1950) as biotic provinces (Fig. 1d). The effects of topography and edaphic considerations are also obvious: the Rocky Mountain flanks and foothills of the Navahonian that extend into the Chihuahuan; the Kansan, comprised of the semiarid and level High Plains (ca. 975+ m) of the west and the gently eroded Rolling Plains to the east of the Caprock Escarpment; the low and rugged terrain of the Edwards Plateau, comprising the Balconian; the desert mountain-and-basin system of the Chihuahuan; the subtropical Tamaulipan; and the Austroriparian woodlands that merge westward into the ecotonal Texan, with its alternating bands of prairies and forests.

Some physical boundaries are more sharply demarcated than others (e.g., escarpments defining both the Edwards Plateau and the High Plains of the western Kansan Province). As the post-Pleistocene composition of floral and faunal associations changed in response to climatic shifts, the relatively static nature of such physical features as topography and soils appear to have continued to define the margins of what are essentially *in situ* evolving communities, even as their compositions changed. As such, we find it useful to retain the application of these biotic provinces dating back to the latest Pleistocene.

Two important compendia (Graham et al. 1987; Wright 1983) and a series of other studies (e.g., Hibbard and Taylor 1960; Van Devender et al. 1987 a, b; Elias and Van Devender 1990; Harris 1987, 1990; Gehlbach 1991; Dalquest and Schultz, 1992; Hafner 1993; Stangl et al. 1994; Smith and Cifelli 2000) have permitted our

following overview of the regional paleoecology and *Ictidomys* biogeography since our point of departure—the latest Pleistocene, when deciduous woodlands occupied the Texan and Austroriparian provinces. Mixed to tall-grass prairies dominated the High Plains of the Kansan, and along the northwestern margins of the Texan. Steppe conditions prevailed across lower elevations to the south and west, with sage dominating much of the Chihuahuan and Navahonian provinces, and chaparral throughout the Tamaulipan. Savannas of oak, juniper, and pinyon pine cloaked the Edwards Plateau and extended into more rugged parts of the southern Rolling Plains.

Sampling methods.—Our past field experiences have demonstrated that cemeteries would be ideal collecting localities for ground squirrels. We visited such sites for most mapped communities on a 2000 Texas roadmap. Cemeteries lacking evidence of ground squirrels and judged unsuitable for a variety of reasons (e.g., too small, overgrown with vegetation, surrounded by extensive areas of unsuitable habitat) were not revisited. Other cemeteries deemed suitable habitat were visited at least three times, and searched on foot for sign of squirrel activity, before concluding that no ground squirrels resided locally. Such instances occasioned the need to search for specimens at nearby fair grounds, school campuses, or golf courses. Three cemeteries with excessively sandy soils (Estelline of Hall County, Knox City of Knox County, and Roaring Springs of Motley County) supported only small populations of the spotted squirrel, *Xerospermophilus pilosoma*.

Animals were captured by hand after flooding of burrows and transported to the laboratory for processing. Sample sizes were determined by a subjective assessment of resident population size, with a minimum of two individuals whenever possible. Geographic samples of ≥ 6 represented sites collected over a period of two or more years. Each specimen was measured by the senior author and prepared as a study skin with skeleton for deposit in the Collection of Recent Mammals of Midwestern State University (MWSU). Tissues (liver, heart, kidney, muscle) were retained for deposit in the Genetic Resources Collection at the Museum of Texas Tech University.

Roadsides were visually surveyed during our travels over the entire three-year collecting effort and during the course of unrelated field studies. Particular vigilance was maintained in areas separating known populations of both species.

Determination of hybrid individuals.—A reference litter of three F_1 hybrid animals (MWSU 22564-22566) was obtained from the laboratory cross of a female *I. parvidens* with a male *I. tridecemlineatus*. Each possessed the paternal spot-and-stripe pattern against a background color only slightly darker than the maternal condition. Compared with reference series of comparable-aged (75 days-of-age) specimens of *I. parvidens* and *I. tridecemlineatus* in the MWSU collection, hybrids were intermediate in size for external body dimensions (Fig. 2). Attempts to produce offspring via reciprocal crosses failed.

Combined with geographic locality, pelage features, size, and ambulatory gait, we deemed it possible to identify many hybrids in the field. All field-caught specimens of suspected hybrid origin (e.g., backcrosses,

F_1 s, F_2 s) retained the alternating spot-and-stripe pattern, although background color intensity sometimes approached that of *I. tridecemlineatus*, and body dimensions sometimes approached the lower limits of *I. parvidens*. Most of these purported hybrids can be recognized in the field prior to capture and handling—providing the general impression of a large, rangy *I. tridecemlineatus* with the distinctive tail-held-high gallop of a Rio Grande ground squirrel. Examination of study skins from Cothran's Baylor County hybrid sample agree in appearance and dimensions with purported hybrids reported from our investigation.

Confirmation of each presumed hybrid determination was obtained by greatest length of the hind foot, the most highly repeatable of the four standard external measurements, and the one which can even be obtained reliably from a live specimen in hand. The hind foot length achieves adult dimensions by 75-days-of-age (Stangl et al. 1995), permitting application of this method on all but the younger juveniles (*I. tridecemlineatus* < 90 g, *I. parvidens* < 130 g, purported hybrids < 100 g) taken in this study. A measure of the

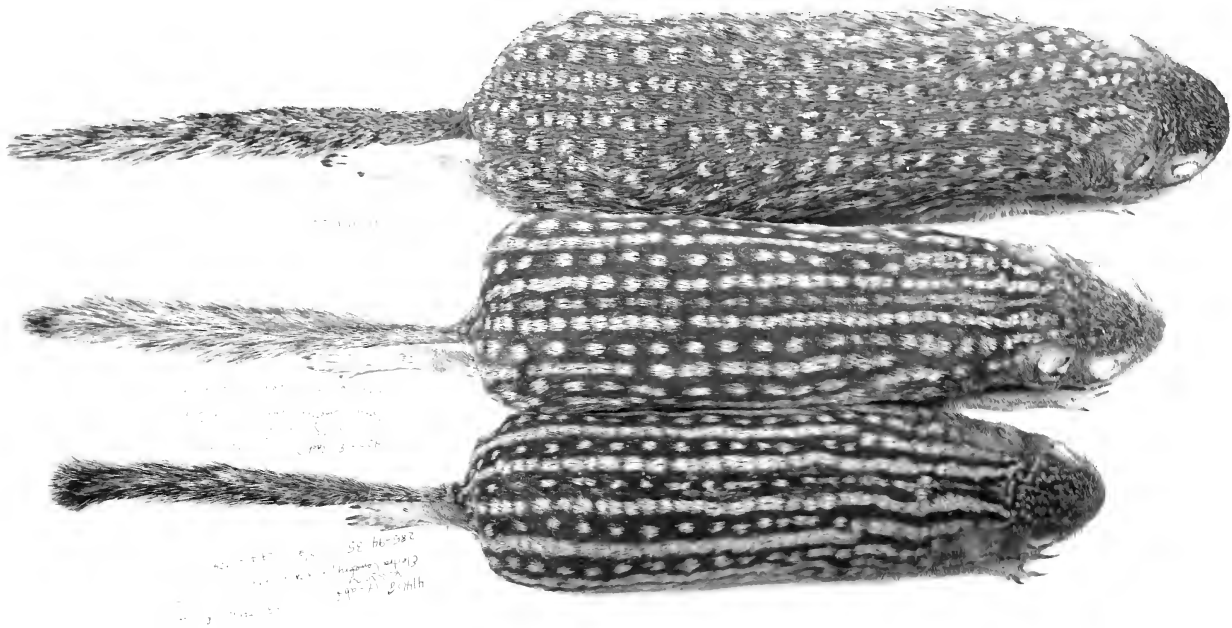


Figure 2. Study skins of *Ictidomys parvidens* from Stonewall County, Texas (top; MWSU 22373) and *I. tridecemlineatus* from Wichita County, Texas (bottom; MWSU 22303), bracketing field-taken hybrid ground squirrel from Baylor County, Texas (center; MWSU 22440). Hybrid animal closely resembles captive-born F_1 s in size, pelage features, and body dimensions.

repeatability of this character is the close agreement of our hind foot measurements (Table 1) with those for adults of the two species reported by Cothran (1983: mean of 34.3 ± 1.7 SD for *I. tridecemlineatus*; mean of 40.6 ± 2.6 SD for *I. parvidens*). Reliability of hind foot

measurements to distinguish parentals from individuals of hybrid origin among field-caught specimens was tested with a one-way analysis of variance and Duncan's multiple means tests, using the NCSS statistical package (Hintze 1990).

Table 1. Hind foot measurements of adult *Ictidomys parvidens* (weights ≥ 130 g), adult *I. tridecemlineatus* (weights ≥ 90 g), and purported hybrid individuals initially identified on the basis of morphological characters from 19 counties in north-central Texas. Descriptive statistics are: sample size (n), mean, standard deviation (SD), range (minimum-maximum), confidence intervals (C.I.), and coefficients of variation (CV). Analysis of variance: $P < 0.0001$; Duncan's Multiple Means Test: each of three subsets (parental species and hybrids) significantly different from one another at $P < 0.05$ level.

County (n)	Hind foot measurement (mm)			
	mean \pm SD	range	95% C.I.	CV
<i>Ictidomys parvidens</i>				
Baylor (1)	39.0	--		
Cottle (4)	40.8	40-41		
Dickens (6)	41.7	40-44		
Fisher (2)	40.0	39-41		
Garza (4)	41.0	40-42		
Haskell (2)	41.5	41-42		
Jones (13)	40.9	40-45		
Kent (2)	42.0	41-43		
Knox (7)	40.1	38-42		
Motley (4)	39.8	37-42		
Shackleford (5)	41.2	39-43		
Stonewall (6)	42.5	41-43		
Throckmorton (9)	40.4	39-44		
Total (65)	40.9 ± 1.5	37-45	40.5-41.2	3.6
<i>Ictidomys tridecemlineatus</i>				
Archer (2)	35.5	35-36		
Floyd (2)	34.5	34-35		
Hardeman (4)	34.3	33-35		
Wichita (19)	33.3	32-35		
Wilbarger (3)	34.6	34-36		
Total (30)	33.5 ± 1.2	32-36	33.0-33.9	3.7
<i>Ictidomys</i> hybrids				
Baylor (9)	38.0	36-40		
Haskell (1)	38.0	--	--	
Knox (1)	38.0	--	--	
Throckmorton (3)	37.6	36-40		
Laboratory F ₁ s (3)	35.3	35-36		
Total (17)	38.0 ± 1.9	35-40	37.0-39.0	4.9

RESULTS

Most of the westernmost counties of our study area are dominated by large ranches or extensive monoculture (usually cotton) and comparatively few communities, thereby providing fewer collecting opportunities (i.e., fewer cemeteries or golf courses). Ground squirrels were collected from 21 of the 31 Texas counties surveyed (Appendix). No single county during the time of our survey provided both *Ictidomys parvidens* and *I. tridecemlineatus* (Fig. 3). The Rio Grande ground squirrel was taken from 14 counties, and four of these (Jones, Shackelford, Stonewall, and Throckmorton) are new county records. The thirteen-lined ground squirrel was taken from six counties. Two regions appeared to be uninhabited by either species of

Ictidomys: the northwesternmost corner (Briscoe, Childress, Hall counties), where rugged terrain or extensive sandy soils are prevalent; and the easternmost region (Clay, Jack, Montague, Palo Pinto, Stephens, Young counties) of the Cross Timbers. Specimens of the Rio Grande ground squirrel were obtained incidental to unrelated field studies from King (MWSU 22571) and Knox (MWSU 22570) counties. Visual sightings from along roadways during our travels were rare: single presumed *I. parvidens* were observed, but not collected, from each of Dickens, King, and Knox counties.

General distributions of the two taxa have not changed dramatically since Cothran's (1983) study,

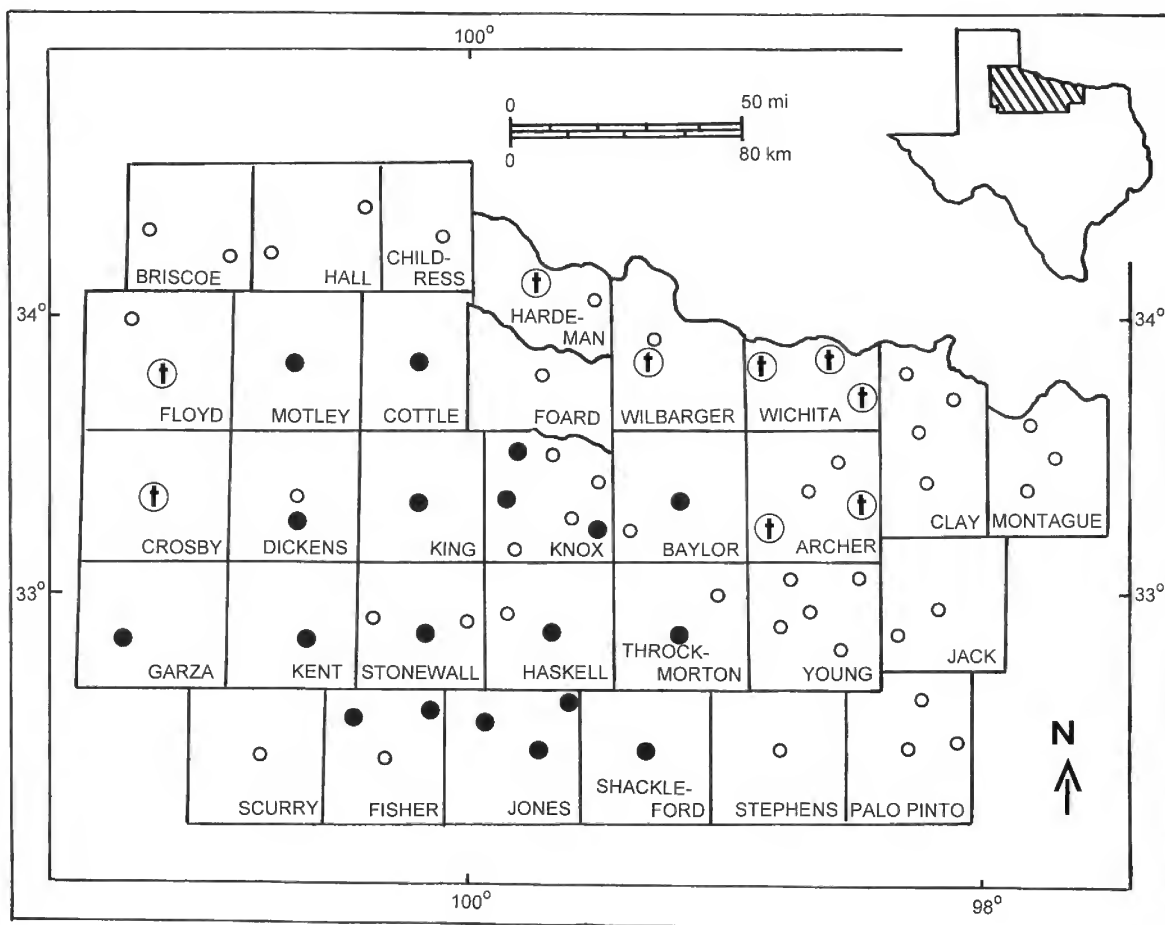


Figure 3. Map of 31-county study area and collecting localities in north-central Texas from 2004 to 2007. Results are: closed circles, *Ictidomys parvidens*; circles with enclosed "t", *I. tridecemlineatus*; open circles, absence of *Ictidomys*.

although specific findings worthy of note included: 1) extirpation of *I. tridecemlineatus* from Vernon in Wilbarger County since Cothran (1982); 2) extirpation of *I. tridecemlineatus* from Matador in Motley County since Cothran (1982), with subsequent replacement by *I. parvidens*; 3) occurrence of *I. tridecemlineatus* near Lockett of Wilbarger County, where Dalquest (1968) reported a specimen of *I. parvidens*; and 4) determined presence only of *I. parvidens* in Stonewall County, from where both species were taken earlier in close proximity (Ruhl and Stangl 1997).

Significant variation was observed for hind foot measurements (Table 1) of *I. parvidens*, *I. tridecemlineatus*, and individuals of hybrid origin (one-way ANOVA; $P < 0.0001$), with each of the three classes

varying significantly from one another (Duncan's multiple means test; $P < 0.05$). There was no overlap between the two parental species. Reflecting the array of recombinant possibilities, measurements from the hybrid sample demonstrated the greatest range of variation ($CV = 4.9$), were generally intermediate in size, and exhibited minimal overlap with the smaller *I. tridecemlineatus*.

Purported hybrids, as determined by our criteria, were taken from localities in four contiguous counties that also supported *I. parvidens*. The Baylor County sample was comprised almost exclusively of hybrid animals (15 of 16), while purported hybrids comprised the minority in Haskell (1 of 4), Knox (2 of 5), and Throckmorton (3 of 12) counties.

DISCUSSION

We propose that the thirteen-lined ground squirrel was the only regional *Ictidomys* during the late Pleistocene, occurring essentially throughout the higher plains of the western Kansan Province and sporadically over the contiguous Navahonian region of our study area. Extension into the Texan Province as far south as the Gulf Coast would have been a late Holocene (and perhaps very recent) phenomenon, as woodlands retreated eastward and human settlement further cleared the land. *Ictidomys tridecemlineatus* has a long and well-documented Pleistocene record across the Central Plains as far north as Wyoming and as far east as Pennsylvania (e.g., Kurten and Anderson 1980; Graham et al. 1987). The species has continually occupied essentially the western half of its modern South Plains distribution in Texas and Oklahoma (Johnson 1986; Dalquest and Schultz 1992; Smith and Cifelli 2000). More southerly extralimital populations in the vicinities of Carlsbad, New Mexico (Harris 1989) and El Paso, Texas (Van Devender et al. 1987a) vanished with the advent of regional mid-Holocene desertification, perhaps coincidentally with colonizations of the mountain parklands of New Mexico and Arizona at elevations as high as 2600 m (Bailey 1931). Eastern populations that extend as far south as the Houston vicinity on the Texas Gulf Coast were first noted by Bailey (1905) and probably originated via immigration along the emerging parklands and prairie corridors of the modern Texan Province as the eastern woodlands

retreated eastward. The extent to which settlement and land clearing practices facilitated this southern dispersal is uncertain.

Alternatively, the fossil record for the Rio Grande squirrel is problematic. There are no Pleistocene examples from Mexico for either *I. parvidens* or *I. mexicanus* (Arroyo-Cabrales and Polaco 2003), and few, if any, reliable records exist for *I. parvidens* from any of a series of Pleistocene faunas within the present range of this sciurid (Graham 1987, Van Devender 1987a, and Stangl et al. 1994 for west Texas; Harris 1987, 1989 for southeastern New Mexico). The original basis for a presumed Pleistocene presence of *I. parvidens* in north-central Texas is an isolated tooth initially identified as either *Spermophilus mexicanus* (= *I. parvidens*) or *U. richardsonii* (Dalquest 1965), but later assigned after reexamination to *U. elegans* (Dalquest and Schultz 1992). The other oft-cited Pleistocene record for *I. parvidens* is an isolated tooth of earliest Holocene age (ca. 9,000 YBP; Dalquest et al. 1969) from Schultz Cave on the southwestern Edwards Plateau, which Dalquest and Schultz (1992) later noted was indistinguishable from either *I. parvidens* or *U. richardsonii*. Since these earlier reports, both *I. parvidens* and *I. tridecemlineatus* were recorded with *U. richardsonii/elegans* from the same Pleistocene and early Holocene sediments of the southern Texas Panhandle that also contained such mesic grassland/

savanna taxa as *Microtus* and *Synaptomys* (Johnson 1986). Against both historical and ecological contexts, these latter Panhandle materials attributed to the Rio Grande ground squirrel appear incongruous and warrant reexamination.

The mid-Holocene warm cycle seems to coincide with the invasion from the Tamaulipan Province of Mexico by *I. parvidens* and its advancement westward along the Rio Grande and Pecos River valleys towards the western limits of its present range. The species first appears in a series of southwestern Balconian cave sediments and rock shelters dating 3-6,000 YBP (for summary, see Graham 1987). These sites are proximal to where Chihuahuan, Balconian, and Tamaulipan provinces converge and were inhabited by Paleo-Indians, suggesting the animals were brought into the sites as food items.

Baird (1857) recorded *I. parvidens* from along and on either side of the Rio Grande and north along the Gulf Coast to Corpus Christi, suggesting to him that the northern limits of this "Rio Grande squirrel" were largely coincidental with the river. His misstatement that the species occurred as far west along the river as Fort Bliss (vicinity of El Paso, a locality more than 200 km west of any known record for the species in Texas or New Mexico) was doubtless in reference to his reported specimen of *I. tridecemlineatus* from a now extirpated population from Fort Thorn of that vicinity. The species today occurs along the Rio Grande no farther than the eastern boundary of Big Bend National Park of Brewster County (Borrell and Bryant 1942; Schmidly 1977) and no farther west in the Chihuahuan Province of Texas than the Davis Mountains of Jeff Davis County (Blair 1940) and Apache Mountains of Culberson County (Dalquest and Stangl 1986; Stangl et al. 1994).

One of the military expeditions relied upon by Baird (1857) for specimens was led by Capt. Randolph Marcy, a noted naturalist. He made no mention of any ground squirrels in his detailed notes (Marcy 1856) as he traversed a horizontal figure-8 trail (as mapped by Neighbors 1954) through the central two-thirds of our study area in the Rolling Plains of north-central Texas. The slow and leisurely travel afforded by horseback and wagon from mid-July to mid-August 1854 by Marcy was certainly conducive to observations of the diurnal

fauna, and it is difficult to believe that detection by sighting of animals or the sound of the squirrels' alarm calls would have escaped his notice.

Modern (post-1900) Zoogeography of Ictidomys.—Vernon Bailey's (1905) treatment of Texas mammals reflected extensive and systematic collecting across most of the state. Excepting the eastern and western extremities of Texas, his described range for *I. parvidens* (extrapolated in Fig. 1a from his account) and figured range of *I. tridecemlineatus* (incorporated into Fig. 1b) suggested that one or the other species occurred everywhere in our study area of the South Plains but the northern mesquite savanna—the region traversed by Marcy (1856). These distributions proposed by Bailey (1905) were little altered in portrayals of the species' ranges by Howell (1938), Taylor and Davis (1947), and as recently as Davis (1974). Absence of either species of *Ictidomys* from the northern mesquite savanna of the Rolling Plains therefore does not appear to be artifactual. It was not until the mid-1900s (Blair 1954; Dalquest 1968) that the appreciable expansion of the two species across north-central Texas was first documented—*I. parvidens* towards the north and east, and progression towards the conjoining of eastern and western populations of *I. tridecemlineatus* in northcentral Texas. We have yet to find any superficial evidence in Texas or southwestern Oklahoma for morphological intergradation in our study area between the pale western populations (*I. t. arenicola*) and their darker counterparts (*I. t. texensis*) to the east (Blair 1939; Dalquest et al. 1990; Stangl et al. 1992). Much of the rugged terrain proximal to the Caprock Escarpment, and extensively sandy areas in parts of the eastern Texas Panhandle, clearly prevents colonization by either species of *Ictidomys*.

We judge that contact of the ranges and subsequent sympatry of the two species was achieved sometime in the mid-1900s, and that the sporadic distribution of populations, and perhaps some degree of localized habitat segregation, continue to ensure that hybridization remains a localized phenomenon within this zone of sympatry. Perhaps inspired by a broad zone of mapped sympatry between *I. parvidens* and *I. tridecemlineatus* (Hall 1981), Earl Zimmerman, Gus Cothran, and colleagues (Zimmerman and Cothran 1976; Cothran et al. 1977; Cothran 1982, 1983; Cothran and Honeycutt 1984) proceeded to define the

nature and extent of hybridization between the two taxa at the morphological, genetic, and karyotypic levels. Among their findings are that hybridization is a localized phenomenon, that the two species did not coexist at any site, and that hybrid individuals were noted only among populations of *I. parvidens*.

Range expansion of *I. parvidens* to the north and east across the mesquite savanna of Texas from at least late 1960s to early 1970s has been dramatic, but more than two decades have elapsed since Cothran's (1983, 1984) efforts and this study, and little has changed. Hybridization remains a localized phenomenon in our study area, and mostly centered in Baylor County. Further encroachment westward into the Chihuahuan Province seems unlikely, given the markedly arid and rugged desert terrain in Texas and New Mexico. County records for *I. parvidens* reported herein (Jones, Shackelford, Stonewall, and Throckmorton counties of Texas) might represent further expansion of the species, although we recognize that this region has historically been neglected by collectors. The regional status of the Rio Grande squirrel is presently secure.

Schmidly (2004) first called attention to declining numbers of the thirteen-lined ground squirrel in north Texas, attributing this trend to habitat degradation. This

would not seem to apply to such artificial habitat afforded by cemeteries, where we noted the extirpation of two substantial populations of *I. tridecemlineatus* sampled earlier by Cothran. First is Vernon of Wilbarger County, which is presently unoccupied by any ground squirrels, although we collected *I. tridecemlineatus* from Lockett, less than 10 km to the south—a locality from where Dalquest (1968) once reported a specimen of *I. parvidens*. Second is Matador of Motley County, which is presently occupied by *I. parvidens*. We judge this latter case an example of opportunistic colonization by the Rio Grande squirrel following a complete extirpation of *I. tridecemlineatus*, as there is no morphological evidence of any residual hybridization that might be expected following active displacement of one species by the other. We cannot ascertain if these extirpations are natural phenomena (e.g., epizootic event) or if they are even related. However, control efforts on the parts of groundskeepers are suspect, and such populations are certainly vulnerable to control methods. At least two golf courses within our study area actively control ground squirrels on their grounds, although most attitudes we encountered in Texas ranged from protective to indifference. Nevertheless, we concur with Schmidly's (2004) concern about the conservation status of *I. tridecemlineatus*.

SUMMARY AND CONCLUSIONS

Our interpretations of the literature and findings reported herein suggest that western populations of *Ictidomys tridecemlineatus arenicola* have likely occupied the Navahonian and western Kansas provinces since the late Pleistocene. The mid-Holocene shift towards a warmer and more arid environment opened an avenue to the Gulf Coast via the Texan Province for *I. t. texensis*. If further facilitated by human habitat modification (e.g., agricultural practices, transportation routes), then arrival of this eastern subspecies in the vicinity of Houston, Texas, may even be an historical event of the late 1800s or earliest 1900s. Morphological intergradation between the two subspecific taxa in the Rolling Plains of the eastern Kansan has yet to be demonstrated either in Texas (Dalquest et al. 1990; Schmidly 2004) or in Oklahoma (Stangl et al. 1992).

The same Holocene climate shift that permitted access of *I. tridecemlineatus* to the Gulf Coast may also be responsible for dispersal of *I. parvidens* beyond the Rio Grande and into the southern Rolling Plains. Subsequent range expansion of the Rio Grande squirrel to the north and east may also have been facilitated by human activity, and the contact and subsequent hybridization with eastern populations of *I. tridecemlineatus* may have occurred no earlier than the mid-1900s, as first postulated by Cothran (1982).

The range of *I. tridecemlineatus* appears to be stable at present, although extirpation of at least two populations in our study area suggest that Schmidly's (2004) call to monitor the species seems warranted. Conversely, our collecting records suggest that the Rio

Grande squirrel has experienced some territorial gains since the late 1900s (e.g., northernmost record for the species in Motley County, new county records for five north-central Texas counties).

Hybridization between the two *Ictidomys* is ongoing, and hybrid individuals presently constitute almost the entire population in sampled areas of Baylor County, Texas. Lesser degrees of hybridization were noted in contiguous counties of Haskell, Knox, and Throckmorton. However, we note that the observed range in variation for hybrid individuals of determining characters (e.g., color, body dimensions, hind foot size) supports Cothran's (1982, 1983) findings of allozymic F_1 s, F_2 s, and backcross individuals, and genetic introgression practically guarantees that our subjective determination of hybrid individuals is conservative.

Ictidomys occupying natural settings tend to be elusive and sporadically distributed, but the two spe-

cies are conspicuous and often abundant and readily collected where they exploit modified circumstances (e.g., cemeteries, parks, golf courses, school campuses). Such behavior certainly facilitates observations and collections for future studies, to include: 1) monitoring of the conservation status of *I. tridecemlineatus*; 2) determining both the full geographic extent of hybridization between the two species; 3) documentation of any intergradation between eastern and western components of *I. tridecemlineatus*; 4) accuracy of our methods for hybrid determination; and 5) determination of genetic distances between populations at both specific and subspecific levels as objective measures of introgression or chronological sequences of events (e.g., times of origin, divergence, or convergence). Some of these investigations will require sophisticated and more sensitive genetic tools, but such preliminary morphological assessments as ours can provide both testable hypotheses and avenues for future study.

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APPENDIX

Following is a list of north-central Texas localities and Midwestern State University (MWSU) catalog numbers for 149 specimens of *Ictidomys* collected during a 31-county survey from 2004 to 2007, and three laboratory-generated F₁ animals. Soft tissues (liver, heart, kidney, muscle) of each specimen are deposited with the Museum of Texas Tech University.

Ictidomys parvidens (n = 86).—Baylor Co.: Seymour Masonic Cemetery, 1 (MWSU 22327). Cottle Co.: Paducah Cemetery, 6 (MWSU 22336-22339, 22464, 22465). Dickens Co.: Dickens Cemetery, 2 (MWSU 22458, 22463); Spur Cemetery, 4 (MWSU 22383-22386). Fisher Co.: Rotan Cemetery, 2 (MWSU 22340, 22341). Garza Co.: Post Cemetery, 6 (MWSU 22419, 22420, 22422-22424, 22426). Haskell Co.: Haskell, 3 (MWSU 22282-22284). Jones Co.: Stamford Cemetery, 3 (MWSU 22346-22348); Hamilton Cemetery, 4 (MWSU 22342-22345); Anson, 1 (22349); 1 mi E of Anson, 10 (MWSU 22350-22354, 22363-22367). Kent Co.: Clairemont Fairground, 3 (MWSU 22421, 22427, 22428). King Co.: Guthrie High School campus, 2 (MWSU 22456, 22457); 11.8 mi. N, 18.3 mi. W Benjamin, 1 (MWSU 22571). Knox Co.: Goree Cemetery, 3 (MWSU 22370-22372); Benjamin Cemetery, 4 (MWSU 22390, 22434-22436); Truscott Cemetery, 1 (MWSU 22560); 4.0 mi. W Truscott, 1 (MWSU 22570). Motley Co.: Matador Cemetery, 6 (MWSU 22381, 22382, 22459, 22460, 22466, 22467). Stonewall Co.: Aspermont Cemetery, 4 (MWSU 22406-22409); City of Aspermont, 2 (MWSU 22410, 22411). Shackelford Co.: Albany, 3 (MWSU 22374-22376); Albany Cemetery, 4 (MWSU 22373, 22403, 22404, 22415). Throckmorton Co.: Throckmorton Cemetery, 10 (MWSU 22261, 22262, 22285, 22291, 22355-22359, 22793).

Ictidomys tridecemlineatus (n = 42).—Archer Co.: Windthorst, 4 (MWSU 22437-22439, 22443); Megargel Cemetery, 2 (MWSU 22441, 22442). Crosby Co.: Ralls Cemetery, 3 (MWSU 22425, 22432, 22433). Floyd Co.: Floydada Cemetery, 3 (MWSU 22429-22431). Hardeman Co.: Quanah Cemetery, 4 (MWSU 22308-22311). Wichita Co.: Kiwanis Park, Wichita Falls, 6 (MWSU 22312-22314, 22316, 22319, 22516); Electra Cemetery, 7 (MWSU 22301-22307); River Creek Golf Course, 10 mi SE Burkburnett, 4 (MWSU 22321, 22322, 22323, 22324); Burkburnett Cemetery, 4 (MWSU 22317-22320); Memorial Stadium, Wichita Falls, 2 (MWSU 22325, 22326). Wilbarger Co.: 0.4 mi NE Lockett, 3 (MWSU 22790, 22794, 22795).

Purported hybrids (n = 21).—Baylor Co.: Seymour Masonic Cemetery, 11 (MWSU 22328-22335, 22413, 22414); Seymour Catholic Cemetery, 1 (MWSU 22440); Old Seymour Cemetery, 1 (MWSU 22412); Salt Creek Golf Course, Seymour, 2 (MWSU 22788, 22789). Haskell Co.: Haskell Cemetery, 1 (MWSU 22284). Knox Co.: Goree Cemetery, 2 (MWSU 22371, 22372). Throckmorton Co.: Throckmorton Cemetery, 3 (MWSU 22286, 22287, 22360).

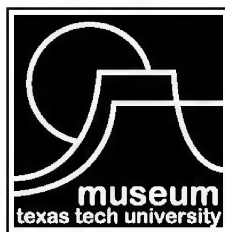
Laboratory-bred F₁ animals (n = 3).—Off-spring of female *I. parvidens* from Albany (Shackelford Co.) and male *I. tridecemlineatus* from Wichita Falls (Wichita Co.) (MWSU 22564-22566).

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