BIOGEOGRAPHIC RELATIONSHIPS OF POCKET GOPHERS

(*Geomys breviceps* AND *Geomys bursarius*)

IN THE SOUTHEASTERN PORTION

OF THEIR RANGES

DISSERTATION

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This research utilized population genetic analyses (protein starch-gel electrophoresis and DNA sequencing of the cytochrome *b* mtDNA gene), host-parasite specificity (lice coevolution), remote sensing of satellite data, and geographic information systems (GIS) to characterize newly discovered populations of pocket gophers (genus: *Geomys*) in Arkansas. These populations are isolated and occur in seemingly unsuitable habitat in the Ozark Mountains of Arkansas.

Analyses of electrophoretic and ectoparasite data suggested the populations in the Ozark Mountains represented isolates allied to *Geomys bursarius*, a species not known to occur in Arkansas. Comparison of mitochondrial DNA sequence data of the cytochrome *b* gene with that of other taxa and morphometric analyses confirmed that these populations are most closely allied to *G. bursarius* occurring to the north in Missouri. Moreover, these mtDNA sequence analyses indicated a degree of differentiation typical of that between other subspecies of pocket gophers. Therefore, these populations represent a distinct genetic entity in an intermediate stage of speciation and should be designated as a new subspecies, *Geomys bursarius ozarkensis*. Molecular clock analysis

revealed a time of lineage divergence for this new subspecies as approximately 511,000 YBP.

Due to the isolated nature and limited distribution of this subspecies, an evaluation of critical habitat needs was initiated. Remote sensing and GIS technologies were used to identify and describe suitable habitat. Computerized classification of satellite imagery of suitable vegetation, intergrated with ancillary digital information on soil associations, roads, and water systems, revealed that human activity had played a positive role in the establishment and dispersal of pocket gophers in this area.

This research represents an initial combination of classical systematic tools with remote sensing and GIS to investigate biogeographic patterns and evolution. This project establishes a framework for using an interdisciplinary approach to studying organisms with limited distributions, determining evolutionary status, and providing recommendations for conservation.

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CHAPTER I

INTRODUCTION

The relationship of the earth's history to the biotic distribution of organisms in space and time is the cornerstone of biogeography. Historically, biologists have utilized range maps, population genetics and/or morphology, and an organism's ecology and natural history to describe the biogeographical patterns observed for a particular species. However, modern biologists are rarely satisfied with the mere description of these patterns, opting for a delineation of environmental factors that are deterministic or limiting to the species being studied or to the elucidation of historical factors that have influenced the variation within the range of a taxon. Two contemporary tools, modern molecular techniques and remote sensing/GIS, have been used independently to aid the resurgence of biogeography.

Recent molecular techniques (DNA sequencing and RFLP analysis) for identifying phylogenetic relationships have given new insight into the historical biogeography of organisms. Riddle and Honeycutt (1990), successfully utilized mitochondrial DNA to assess biogeographic patterns of grasshopper mice (*Onychomys* sp.) in the western U. S. Also,Wilson and Choate (1997) investigated the taxonomic status and biogeography of southern bog lemmings (*Synaptomys cooperi*) on the central Great Plains (see also studies on tortoises, Lamb et al. 1989; Stellar sea lions, Bickham et al., 1996; Neartic Pikas, Hafner and Sullivan, 1995; pocket mice, Riddle, 1995).

Remote sensing and GIS (geographic information systems) analyses have allowed multiple environmental, biotic, and abiotic factors such as elevation, vegetation, soil, land use, geology, and precipitation to be analyzed simultaneously. The precedence for using satellite imagery and GIS for ecologically related applications includes recent studies on the quality of wetlands habitat for waterfowl (Work et al., 1976) predicting snow melt and nesting success of lesser Snow Geese (Kerbes and Moore, 1975), identifying potential habitat for reindeer and moose (Laperriere et al., 1980; George and Scorup, 1981), habitat utilization by kangaroos in Australia (Hill and Kelly, 1987), and characterization of habitats of endangered avian species in Texas (Shaw, 1990). Research combining both molecular and GIS techniques can provide valuable information in the analysis of an organism's historical biogeography.

Refuge Hypothesis

The prevailing explanation for the observed distributional patterns of several tropical, neotropical, and temperate organisms relates in some way to the "Refuge Hypothesis." According to this hypothesis (as summarized by Mayr and O'Hara, 1986), climate and vegetional upheavals during Pleistocene glaciation events fragmented the previously continuous ranges of many species into isolated refugia allowing for speciation. This line of thinking is not novel; it actually predates the publication of Darwin's *On The Origin of the Species by Means of Natural Selection...* in 1859. It first was proposed by Edward Forbes in 1846 as a means to explain the distributional patterns of plants in Europe. Darwin, (1958) reached the same conclusion independently but never made use of the refuge hypothesis as a means to explain speciation on continents.

More recently, authors have revived the refuge theory, indicating that, during times of advancing ice sheets, multiple refuge sites provided isolation that contributed to speciation of temperate zone populations surviving in isolated refugia of suitable habitats (Mayr, 1963).

As it became clear that glaciation events could produce drastic changes in the distribution of vegetation in tropical, subtropical and temperate regions, various authors argued that isolation by vegetational barriers could have been as effective as isolation by physical barriers (Hamilton, 1976; Snow, 1978; Brown et al. 1974; and others). Periods of reduced rainfall are believed to have led to the creation of temporary refugia partitioned out of previously continous habitats, creating floral islands separated by wide belts of savannah. The faunal components were isolated in these island refugia, which gave them the opportunity for speciation. With the return of more mesic conditions, habitat islands expanded simultaneously with the shrinking of savannahs and allowed for range expansions of speciated groups. This process has been implicated in the establishment of many current ranges, e.g. birds of Africa (Hall and Moreau, 1970; Snow, 1978) South America (Haffer, 1974) Australia (Keast, 1961) Australian anurans (Roberts and Maxson, 1985) and others.

Kilpatrick and Zimmerman (1976) utilized the "Refuge hypothesis" to explain the pronounced genetic discontinuities found within the eucinal mouse *Peromyscus pectoralis*. This rodent is a habitat specialist, occurring sympatrically in southcentral Texas with *P. attwateri*. Kilpatrick and Zimmerman (1976) describe a Pleistocene distribution of *P. pectoralis* which was contracted to three regions before population expansion and secondary contact. These hypothesized locations of refuge sites were concordant with character shifts and subspecific ranges as mapped by Schmidly (1972) into three geographic population groups: the Edwards Plateau, the Mexican Plateau, and tropical habitats of Tamaulipas.

Study Animal

Fossorial rodents provide an interesting and useful model system for the study of biogeography. Adaptations to fossorial life have been shown to contribute to population subdivision and establishment of local genetic forms (Nevo 1982; Zimmerman and Gayden, 1981). Some of these adaptations include low vagility, specific habitat requirements, disjunct populations, aggressive territoriality, and increased female biased sex ratios. Due to these characteristics, many species of fossorial rodents are polytypic, with several discrete genetic entities having been identified across their ranges.

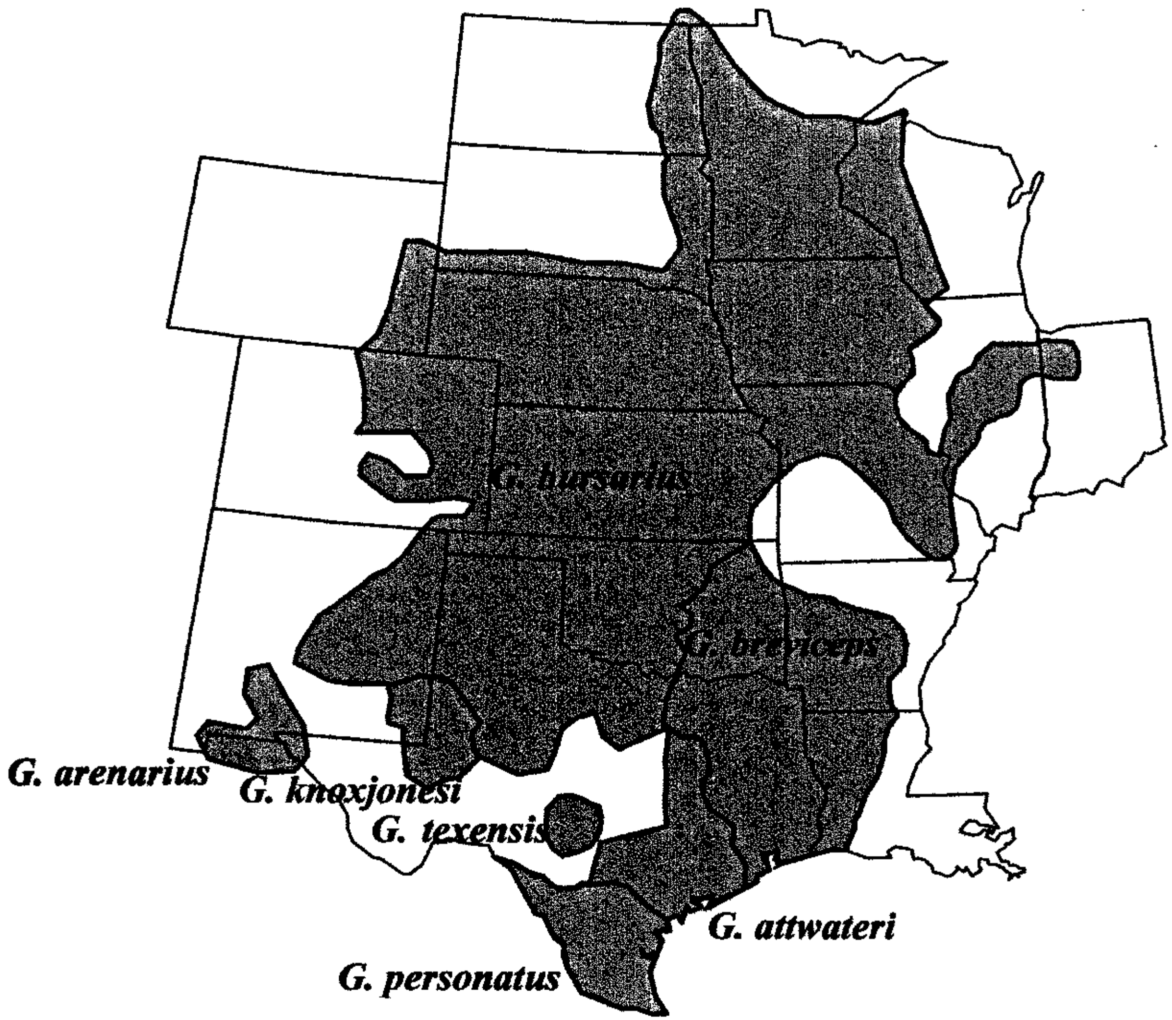
Pocket gophers represent a highly polytypic taxon of mammals with approximately 30 species and more than 300 subspecies described in North America (Hall, 1981). Pocket gophers are small fossorial rodents suitably adapted for a burrowing existance. They possess thick bodies, small heads, short necks, highly developed shoulders and forearms with long claws, and fur-lined cheek pouches that give pocket gophers their common name. Other specializations include, but are not limited to, small eyes with eyelids that close tightly to prevent even fine sand from entering, small ears with valves that can exclude soil while digging, and furred lips that extend behind the incisors to preclude soil from entering the mouth while digging. Three genera of pocket gophers occur in North America, the western pocket gopher (*Thomomys*), the yellow-faced pocket gopher (*Cratogeomys*), and the eastern pocket gopher (*Geomys*).

The genus *Geomys* occupies suitable habitats on the plains and prairies of the central United States (Fig 1). Suitable habitats include open unforested areas such as pastures, fields, prairies, and mowed areas with sparse to no trees present. Pocket gophers create a closed burrow or tunnel system in soils suitable for digging. Preferred soils are usually light textured and are highly porous and drain well. This subterranean lifestyle has much influence on the biology and evolution of pocket gophers.

Nevo (1982) summarizes the characteristics of the subterranean ecotope as being: 1) relatively simple, stable, specialized, and predictable; 2) poor in productivity and carrying capacity; 3) buffered against massive predation; 4) discontinous in spatial structure; and 5) essentially fine grained - a mosiac of unequally distributed sparse resources in both space and time. These characteristics result in populations of organisms that are highly specialized, exhibit high levels of interspecific and intraspecific competition, and occur as isolated subpopulations.

The current distribution of pocket gophers in the western hemisphere has been attributed by most authors to glacial advances and retreats. Davis (1986) discusses the range of the extant and fossil *Geomys* as being, in large measure, overlapped by regions covered by glacial advances during the Nebraskan, Kansan, Illinoian, and Wisconsin ice ages. For example, Russell (1968) discussed the evolution of pocket gophers and attributed the isolation and speciation of the *Geomys pinetus* lineage in the extreme southern U.S. to the Illionoian glaciation and subsequent post glaciation.

Figure 1. Range of *Geomys* spp. in the central United States



During the height of the glacial maxima, regions of the continent of North American were highly disparate. The vast majority of the northern portion was covered with ice, with the southern portion bearing extensively altered floral and faunal components, as well as more expansive terrestrial habitats due to the drop in sea level. Also, the present day western deserts supported a rich savannah ecology with extensive grasslands dotted with pines (Flint, 1971). During these times of glacial fluctuations, massive extinction and recolonization events must have occurred. Due to their limited dispersal capabilities, it is likely that the ranges of pocket gophers were altered dramatically. As the glaciers receded, pocket gophers were able to move northward advancing into areas of suitable habitat.

Much fossil evidence supports this glacial hypothesis as a directing factor in the distribution of these organisms. For example, Parmalee and Klippel (1981) describe *Geomys bursaurius illinoisensis* in central Tennessee during the Wisconsin glaciation. However, their present day range is limited to the prairie peninsula of Illinois and Indiana much farther to the north. Also, the isolation of *Geomys pinetus* into Georgia and Florida has been traced to the Irvingtonian age, approximately 2 MYBP (Wilkinson 1984).

The present study was undertaken with the following goals, to determine the systematic identity, range, and status of the newly discovered isolated populations in north central Arkansas; to establish a GIS model to characterize the habitat, determine habitat availability, and establish important large-scale biotic and abiotic factors important to the taxon in this region; and to investigate evolutionary divergence and processes which have led to the isolation of these populations and to establish biogeographic patterns of pocket gopher distributions in Arkansas.

CHAPTER II

A SECOND SPECIES OF POCKET GOPHER IN ARKANSAS

Introduction

Pocket gophers of the genus *Geomys* (Rodentia: Geomyidae) occurring in Arkansas were referred to as *G. bursarius dutcheri* by Sealander (1979). Who reported the species occurring in the West Gulf Coastal Plain, Ouachita Mountains division of the Interior Highlands, and the extreme western portion of the Ozark Mountains, but absent or scarce in the Mississippi alluvial plain. Subsequent systematic revisions within *Geomys* elevated various taxa to specific rank, including populations now referred to as *G. breviceps* in eastern Texas, Oklahoma, northern Louisiana, and southern Arkansas (Bohlin and Zimmerman, 1982). On the basis of morphology, Heaney and Timm (1983) tentatively reported that a single taxon of pocket gopher (*G. breviceps sagittalis*) occurs in Arkansas and expressed the need for more research to be done in this area. The occurrence of an isolated population of pocket gophers in northcentral Arkansas accentuates this point and also leads to problems associated with taxonomic assessment of species that exist in patchy environments. Because of the geographic proximity of these populations, it is unclear whether these represent *G. breviceps*, *G. bursarius*, or a new cryptic taxon.

A major problem in determining the accurate distributions for cryptic species of *Geomys* is the lack of diagnostic characters for skins and skulls preserved in most collections. Discrimination between cryptic species of *Geomys* has been accomplished using several techniques, including morphology, karyology, allozyme electrophoresis, ectoparasitic analysis, and restriction endonuclease mapping of mitochondrial DNA and ribosomal DNA. Cothran and Zimmerman (1985) found that G. brevicens and *G. bursarius* from the vicinity of Norman, Oklahoma, were fixed for alternate alleles at two structural gene loci (Ldh-1 and Mdh-2) and fixed for alternate alleles on a regional basis at two additional loci (Idh-1, 6-Pgd-1). Bohlin and Zimmerman (1982) found that the two species were fixed for alternate alleles at another locus, alcohol dehydrogenase (Adh-1). Heaney and Timm (1983) effectively used analysis of mensural characters and coevolving lice (genus *Geomydoecus*) to differentiate species of *Geomys*. Most recently, Davis (1986) used mitochondrial and ribosomal DNA to examine evolutionary relationships among eight species of *Geomys*.

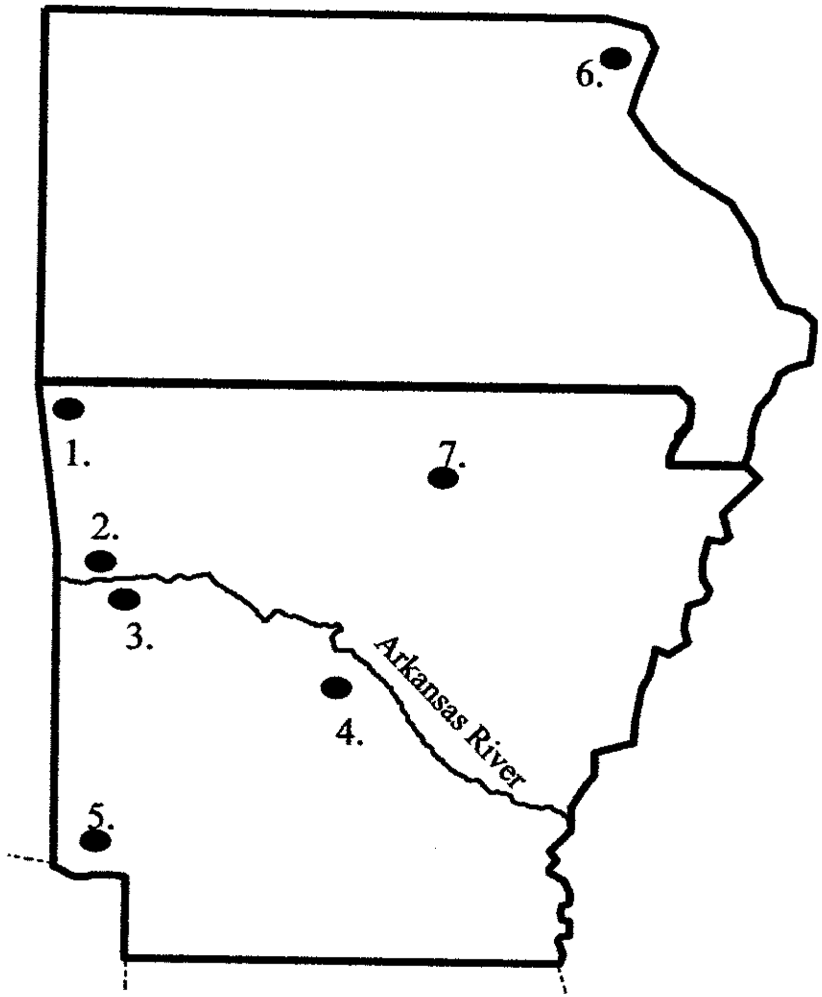
Based solely on the morphological analysis by Heaney and Timm (1983), Sealander and Heidt (1990) reported *G. breviceps sagittalis* to be the only species of pocket gopher occurring in Arkansas. The analysis of mammals of Arkansas by Sealander and Heidt (1990) included specimens of pocket gophers collected in the early 1980s from north-central Arkansas in the Ozark Mountains (Izard and Stone counties). These localities were separated by approximately 150 km from known populations to the north in Missouri and to the south and west in the remainder of Arkansas. The purpose of this study is to establish the relationships of pocket gophers from Izard Co. to populations *G. bursarius* from the north in Missouri and *G. breviceps* to the south and west.

Materials and Methods

Pocket gophers of the genus *Geomys* were collected from six localities in Arkansas and one locality in east-central Missouri. Localities (Fig. 2) were as follows: *Geomys breviceps*: Arkansas, 1.--City Golf Course, Silom Springs, Benton Co. (n = 4), 2.--Hwy 64, Alma, Crawford Co. (n = 5), 3.--10 miles S Ozark, Franklin Co. (n = 8), 4.--Intersection Hilldale and Hilltop Rd., Saline Co. (n = 10), 5.--3.0 miles NW Alleene, Little River Co. (n = 20). *Geomys bursarius*: Missouri, 6.--vicinity St. Louis, St. Louis Co. (n = 13). *Geomys* sp.: Arkansas, 7.--3 miles W Melbourne, Izard Co. (n = 13).

Samples of liver and muscle were removed and stored at -80°C. Immediately prior to electrophoresis, tissues were thawed and homogenized in double-distilled water. Starch gels were prepared as 12% suspensions of hydrolysed starch (1.25:1; Sigma Chemical Company, St. Louis, Missouri; Electrostarch Co., Madison, Wisconsin). Electrophoretic techniques followed those of Selander et al. (1971) and Bohlin and Zimmerman (1982). Allozymic variation encoded by 17 presumptive loci was examined by horizontal starch gel electrophoresis. Loci assayed included: isocitrate dehydrogenase (Idh-1, Idh-2, EC 1.1.1.42), L-lactate dehydrogenase (Ldh-1, Ldh-2, EC 1.1.1.27), malate dehydrogenase (Mdh-2, EC 1.1.1.37), phosphogluconate dehydrogenase (Pgdh-1, EC 1.1.1.44), malate dehydrogenase (Nadp+) (Mdhp-1, EC 1.1.1.40), phosphoglucomutase (Pgm-1, EC 5.4.2.2), superoxide dismutase (Sod-1, 1.15.1.1), glucose-6-phosphate isomerase (Gpi, EC 5.3.1.9), glycerol-3-phosphate dehydrogenase

Figure 2. Trapping localities of pocket gophers (*Geomsy*) in Arkansas and Missouri.



(G3pdh, EC 1.1.1.8), peptidase A (Pep-A, EC 3.4.13.18), sorbitol dehydrogenase (Sdh-1, 1.1.1.14), xanthine dehydrogenase (Xdh-1, EC 1.1.1.204), cytosol aminopeptidase (Cap-1, EC 3.4.11.1), alcohol dehydrogenase (Adh-1, EC 1.1.1.1), and aspartate aminotransferase (Aat-1, EC 2.6.1.1).

Pocket gopher chewing lice (*Geomydoecus*) have been shown to be species-specific and, in some cases, subspecies-specific (Heaney and Timm, 1983). From eight to 20 lice were collected from pocket gophers from each of the seven localities. Each specimen was keyed to species based mainly on genitalia and antennae morphology as established by Timm and Price (1980). All specimens were deposited in the Vertebrate Museum at the University of Arkansas at Little Rock.

Results and Discussion

Of the 17 loci examined, two (Mdh-2 and Adh-1) used to differentiate *G. bursarius* and *G. breviceps* in Oklahoma and Texas by Bohlin and Zimmerman (1982) and Cothran and Zimmerman (1985) exhibited fixed alternate alleles between the populations of *G. breviceps* from Arkansas and *G. bursarius* from Missouri. The Ldh-1 locus, consistently diagnostic for *G. breviceps* and *G. bursarius* in previous studies, did not exhibit fixed alternate alleles between *G. breviceps* from Arkansas and *G. bursarius* from Missouri. Specimens from Izard Co. were fixed for the same alleles at the Mdh-2 and Adh-1 loci as that of *G. bursarius* from St. Louis Co., Missouri. The fact that the Ldh-1 locus did not differ between *G. breviceps* and *G. bursarius* in our study probably reflects regional differences in genetic differentiation noted in previous studies of *Geomys* by Cothran and Zimmerman (1985).

Heaney and Timm (1983), determined that the chewing lice *Geomydoecus ewingi* occur on *G. breviceps*, while *Geomydoecus spickai* occurs exclusively on *G. bursarius missouriensis*. Species-specificity of lice identified from our known specimens of *G. breviceps sagittalis* and *G. bursarius missouriensis* agreed with the findings of Heaney and Timm (1983). Lice found on the Izard Co. specimens were identified as *G. spickai,* based on males having genitalia sacs with six spines and a thumb-like projection on the posterior margin of the antennal scape. Females were identified based on the number of complete loops (≤ 2) on the genital chamber sacs. These findings also establish a range extension for *G. spickai.*

Based on the allozyme data and identification of chewing louse, pocket gophers inhabiting Izard Co. are allied with *G. bursarius* to the north in Missouri rather than to the more widespread species in the state, *G. breviceps*. Therefore, two species of pocket gophers occur in Arkansas.

The taxonomic position of the Izard Co. population is unclear. Heaney and Timm (1983) suggested that *G. bursarius*, (which they considered *G. lutescens*) from Missouri may have, at one time, occurred as far south as Pulaski Co., in central Arkansas. I feel a plausible explanation for the distribution of pocket gophers in this region would be that there was a chain of populations from the current range of *G. bursarius* in eastern Missouri extending southwestward into central Arkansas. Localized extinctions may have resulted in the current distributions.

To compound the argument, Heaney and Timm (1983) reported that a population of pocket gophers occurring in southeastern Missouri, was morphologically most similar to what is currently recognized as *G. bursarius major*. These specimens were also distinct morphologically from the more widespread pocket gophers in Missouri, *G. bursarius missouriensis*. The status of this population is questionable, and several attempts to locate them have met with no success. We believe, as did McLaughlin (1958), that these populations are now extinct. It should be noted, however, that convergence in morphology among pocket gopher populations has been shown to be greatly influenced by soil composition and texture (Hendricksen, 1972; Wilkins and Swearingen, 1990), perhaps accounting for the similarity of these specimens to those of *G. bursarius major* to the west.

If other populations do exist in the Ozark Mountains, there is the potential for contact between *G. bursarius* and *G. breviceps*. Hybridization between cryptic species of *Geomys* occurs with resultant viable offspring (Tucker and Schmidly, 1981; Bohlin and Zimmerman, 1982; Dowler, 1982; Cothran and Zimmerman, 1985; Jones et al., 1995). Alternately, if this population is indeed relictual, then its taxonomic status and biogeographic origin merit additional investigation. The overall population dynamics and evolutionary status of this population should also be determined for conservation and management considerations.

We thank Mr. and Mrs. Y. D. Whitehurst for permission and assistance in trapping specimens on their property. J. A. Peppers, M. R. Ingraham, J. Smith, R. M. Pitts, and D. J. Gentry assisted in trapping efforts. Chewing lice identification was assisted by J. C. Abbott and R. J. Currie. R. E. Cook, P. D. Sudman, and an anonymous reviewer made helpful comments on earlier drafts of this manuscript. This research was sponsored, in part, by a Sigma Xi Grant to D. A. Elrod.

CHAPTER III

DISTRIBUTION OF BAIRD'S POCKET GOPHER (*Geomys breviceps*) IN ARKANSAS; WITH ADDITIONAL COUNTY RECORDS

Introduction

Pocket gophers, genus *Geomys*, are small (173-357 mm) fossorial rodents suitably adapted for a burrowing existence. The genus possesses: strongly clawed front legs, tiny eyes, round small ears, and external fur-lined cheek pouches. *Geomys* sp. range from southern Manitoba, Canada across the central United States to Texas and eastward to the Mississippi river in the south and into Indiana in the north. Also, two disjunct species occur: one, *Geomys pinetus* in the extreme southeastern United States, and the other, *Geomys tropicalis* along the northeastern coast of Mexico.

Heaney and Timm (1983), using morphology and ectoparasite data, tentatively reported only one species of pocket gopher (*Geomys breviceps*) inhabiting Arkansas and expressed the need for more research to be done in this area. Based on this, Sealander and Heidt (1990) reported one species, *G. breviceps,* to occur in the state exclusively. They reported the distribution of pocket gophers in Arkansas to include the West Gulf Coastal Plain, the Ouachita Mountains, and the western and southern portions of the Ozark mountains.

Recently, Elrod et al. (1996) reported that pocket gophers in one population in Izard county were actually the plains pocket gopher (*Geomys bursarius*) rather than *G. breviceps* as previously thought. The presence of *G. bursarius* rather than *G. breviceps* in this county greatly altered the geographic distribution of *G. breviceps* in Arkansas as depicted by Sealander and Heidt (1990). The purpose of this study was to investigate the biogeographical distributions and describe new county records for *G. breviceps* in Arkansas.

Materials and Methods

During vehicle surveys (from March 1995 to November 1996) of 27 counties, pocket gopher mounds (dirt deposited at the surface, excavated during tunneling) were observed and pocket gophers were collected using Victor gopher traps (Woodstream Corp, Lititz, PA). Traps were checked approximately every two hours to insure tissue quality. Voucher specimens were prepared, and tissues (liver and muscle) were removed and stored at -80°C for subsequent allozymic analysis. All specimens were deposited in the Vertebrate Museum at the University of Arkansas at Little Rock.

Taxonomic identification was accomplished following the horizontal starch gel electrophoresis techniques of Bohlin and Zimmerman (1982) and Elrod et al. (in press). Specifically, the fixed alternate alleles malate dehydrogenase (Nadp+)(Mdhp-1, EC 1.1.1.40) and alcohol dehydrogenase (Adh-1, E.C. 1.1.1.1) which have been shown to be diagnostic in Arkansas for *G. bursarius* and *G. breviceps* were examined (Elrod et al., in press). Also, the species-specific chewing lice (genus *Geomydoecus*) of pocket gophers were evaluated based on morphological criteria established by Timm and Price (1980).

The recent review of the literature and specimen records from 22 museums by Sealander and Heidt (1990) provided the data base from which the biogeographic distributions of *Geomys* in Arkansas were investigated.

Results

Of the 27 counties surveyed, no evidence of pocket gophers were observed (mounds of earth) or collected from the following 14 counties: Arkansas, Conway, Cross, Garland, Montgomery, Lonoke, Perry, Pope, St. Francis, Stone, Van Buren, White, Woodruff, and Yell. Pocket gophers collected from the remaining 13 counties were subjected to allozyme electrophoresis and it was determined that the Mdhp-2 and Adh-1 loci were consistent with the findings of Elrod et al. (1996) for *Geomys breviceps*. The ectoparasite analysis was concordant with the allozyme analysis, and it was concluded that pocket gophers analyzed in this study were *G. breviceps*. Therefore, 13 new county records are established for *G. breviceps* in Arkansas. Localities and sample sizes are as follows:

Ashley County, 5 miles North of Crossett, n = 4

Calhoun County, 3.5 miles West of Hampton, n = 1;

Cleburne County, Junction of Hwy 25 and Hwy 5, n = 5;

Crawford County, 0.5 miles East of the Junction of Hwy 64 and 71, n = 5;

Faulkner County, Levee-Arkansas River, 10 miles West of Lake Conway, n = 2;

Hot Springs County, 8 miles Northeast Malvern, n = 1;

Lincoln County, 3.1 miles North of Yorktown, n = 2

Logan County, 10 miles South of Paris, n = 5;

Pike County, 1 miles East of Kirby, n = 2

Polk County, Grannis, on Hwy 71, n = 2

Prairie County, 2 miles South of Hickory Plains, n = 1

Scott County, 1 mile East of Mansfield, n = 4; 0.5 miles West of Abbott. n = 1

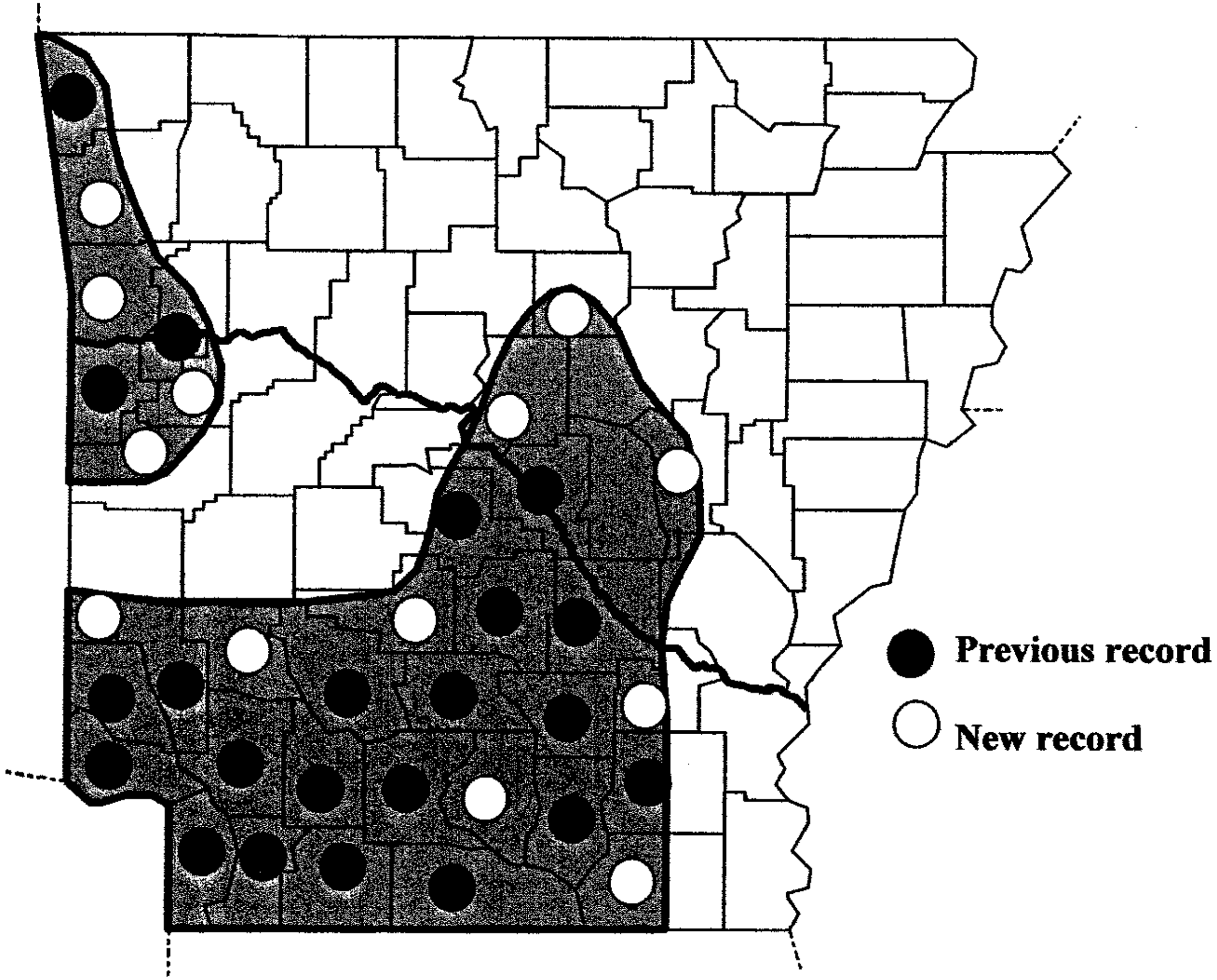
Washington County, Farmington, on Hwy 16, n = 1

Discussion

In light of these new county records, a conservative range for *G. breviceps* in Arkansas is presented in Fig. 3. To date, *G. breviceps* has been found to occur in four of the five major physiographic regions (Ozark Mountains, Ouachita Mountains, West Gulf Coastal Plain, and the Mississippi Alluvial Plain) within Arkansas. The species has yet to be collected from Crowley's Ridge.

Of the four physiographic regions *G. breviceps* occupies, it is most common in the West Gulf Coastal Plain, where it occurs in all counties. It is rare in the Mississippi Alluvial Plain being found only in Prairie County located in the Grand Prairie subdivision. In the Ozark and Ouachita Mountains (with the exception of the Arkansas River Valley), pocket gophers are fairly uncommon. Pocket gopher populations in these areas appear to exist primarily in scattered islands of suitable habitat. These islands are often associated with old creek and river beds where deposits of sand are located. Also, loamy well-drained soils where erosion has been minimal on mountain sides and tops appear to be utilized. Apparently as long as a corridor for dispersal exists into suitable habitat colonization has occurred.

Figure 3. Current known distribution of Baird's pocket gopher, *Geomys breviceps*, in Arkansas



A gap in *G. breviceps*' distribution within Arkansas occurs in the Ouachita mountains and runs northeastward to the Arkansas River (Fig. 3). This area apparently separates *G. breviceps* into two distinct groupings (western and south-central). The separation between the groupings has been extensively surveyed for pocket gophers; however, none has been located to date.

Based on fossil remains, current pocket gopher distributions have been attributed to past glaciation events (Russell, 1968). These glacials and interglacials allowed pocket gopher populations to advance and withdraw periodically. It is thought that *G. bursarius* and *G. breviceps* arose from a common ancestor (Russell, 1968; Davis, 1986). Heaney and Timm (1983) suggest that the split between the *G. bursarius* and *G. breviceps* ancestors occurred during the Kansan glaciation with speciation of the *G. breviceps* group occurring at some later time. Thus, glacial events would have had an impact on the speciation of *G. breviceps* and would have had a major influence on present day distributions of *G. breviceps*.

In addition to or as a result of glacial history, the current proposed distribution of *G. breviceps* in Arkansas can best be explained by two colonization events. One invasion must have had a combined source from Louisiana and east Texas populations. These populations moved into the Gulf Coastal Plain via northern expansions from Louisiana and northeastern expansions from East Texas, and moved upward through suitable habitat into the Ouachita Mountains. Another invasion came from Oklahoma eastward into the Ouachita and Ozark Mountains (particularly the Arkansas River Valley) of

Arkansas. Based on available information (Russell, 1968), these invasions probably occurred after the Wisconsin glaciation.

Recent colonization events appear to have occurred north of the Arkansas river in the central portion of the state. The route of colonization is uncertain even though it has been surveyed extensively. It should be noted that a contact zone between *G. breviceps* and *G. bursarius* is being approached in the Ozark mountains. At present, known populations of both species are separated by a distance of approximately 50 km and a mountain range. Populations of both species, are found in close proximity to the White River, a potential corridor to dispersal.

If in the future, populations are identified from the area located along the Arkansas River (linking the two groups of *G. breviceps*), genetic investigations will need to be conducted in order to determine relatedness of the populations. In addition, because pocket gophers seem to have colonized suitable habitat which may be isolated, we feel that more localities will be discovered which will likely alter the proposed distribution presented herein.

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CHAPTER IV

MITOCHONDRIAL DNA SEQUENCE AND MORPHOLOGICAL ANALYSES OF A NEW SUBSPECIES OF POCKET GOPHER (GENUS *Geomys*) FROM THE OZARK MOUNTAINS OF ARKANSAS

Introduction

Eastern pocket gophers of the genus *Geomys* are represented by nine extant species ranging primarily throughout the Great Plains of the central United States. Seven of these species occur east of the front range of the Rocky Mountains from southern Manitoba to southern Texas and eastward to the Mississippi River, extending across this river in a narrow band through Illinois and into northwestern Indiana (Bohlin and Zimmerman, 1991; Cothran and Zimmerman, 1985; Hall, 1981). Two species, *G. tropicalis* and *G. pinetis*, occur as disjunct isolates in coastal areas of the Mexican state of Tamaulipas and in the southeastern states of Alabama, Georgia, and Florida, respectively (Hall, 1981).

The distribution of eastern pocket gophers over this large geographic area reveals a mosaic of multiple, fragmented populations due primarily to their specialized habitat requirements. They may occur in a wide variety of grassy habitats, but prefer deep, loose-textured soils (Miller, 1964). The low vagility of pocket gophers leads to restricted gene flow and small effective population sizes, contributing to increased opportunities for stochastic events such as genetic drift and bottlenecks which genetically structure local demes (Nevo, 1979, 1982; Patton and Feder, 1978, 1981; Patton and Yang, 1977; Penney and Zimmerman, 1976; Zimmerman, 1988; Zimmerman and Gayden, 1981). These attributes result in spatial subdivision, local extinctions, and recolonizations, features characteristic of metapopulations (Levins, 1970).

One polytypic species of *Geomys*, the plains pocket gopher, *G. bursarius* occurs over much of the Great Plains from Manitoba, Canada, to Texas. A second species, *G. breviceps*, has a more restricted distribution in eastern Texas and Oklahoma and northern Louisiana and, until recently, was the only species of pocket gopher thought to occur in Arkansas. Utilizing allozyme electrophoresis and ectoparasite analysis, Elrod et al., (1996) determined that relictual, isolated populations of pocket gophers occurring in the Ozark Mountains of north central Arkansas were most closely allied to *G. bursarius* and not to the more widespread species in the state, *G. breviceps*. These populations appear to be isolated by approximately 150 km from the range of *G. bursarius* to the north in Missouri. The present study was undertaken to establish the taxonomic status of the relictual populations of *G. bursarius* in the Ozark mountains of Arkansas. Nucleotide sequences of the mitochondrial cytochrome *b* gene and morphologic variation were assessed among populations of the isolates in the Ozark Mountains, several subspecies of *G. bursarius*, and *G. breviceps* to determine the extent to which geographic isolation has contributed to genomic modification and to ascertain the biogeographic history of these unique populations.

Materials and Methods

Pocket gophers were collected using Victor gopher traps (Woodstream Corp, Lititz, PA) which were checked approximately every two hours to insure tissue quality. Voucher specimens were prepared and tissues (liver and muscle) removed and stored at -80°C for subsequent allozymic and DNA analysis. All specimens were deposited in the Vertebrate Museum at the University of Arkansas at Little Rock.

For the morphological analysis, specimens collected for this study, as well as specimens from the Vertebrate Museum at the University of Arkansas at Little Rock and the Texas Cooperative Wildlife Collection, Texas A&M University were examined. Twelve morphometric measurements were recorded from 97 known G. breviceps from Arkansas, 75 *G. bursarius missouriensis* from near St. Louis, Missouri, and 35 from the Ozark populations from Izard County, Arkansas. Measurements were taken with digital calipers to the nearest 0.01 mm. Each skull was assigned to one of four age classes following the criteria established by Hendricksen, 1972. After variation due to age class and sexual dimorphism (older males having secondary sexual characteristics becoming rugose with increased age) were removed, sample sizes allowed only the use of adult females in morphometric analyses. Univariate and multivariate biometric routines were employed to analyze the character set. Discriminant function analysis and principal components analysis were performed using Statistical Analysis Systems (SAS).

Genomic DNA was obtained from liver tissues following the technique of Hillis et al. (1990). Polymerase chain reaction was utilized to amplify the entire cytochrome *b* gene utilizing modified *Thermus aquaticus* DNA polymerase (Promega, Madison, WI) (Saiki et al., 1986, 1988). Initial amplifications were performed using two primers (L14735, 5'-TGAAAAACCATCGTTGTTAATTCAACT-3' and H15906, 5'-CATCTCCGGTTTA CAAGACCTAAGTAAT-3') designed to anneal within the t-RNA genes flanking the mitochondrial cytochrome b gene. These primers are modifications of those listed by Irwin et al. (1991) and were engineered by P. D. Sudman specifically for use with geomid DNA. Additional primers were used in subsequent amplifications and/or sequencing reactions included: H15149 (5'-AAACTGCAGCC CCTCAGAATGATATTTGTCCTCA-3'), L15049 (5'-GCCTGTACATCCACTCGGAC GAGG-3'), H15915 (5'-AACTGCAGTCATCTCCGGTTTACAAGAC-3'), L15408 (5'-CAGATTGCGGCAAAGTACCATTCCA-3'), L15513 (5'-CTAGGAGACCCTGACA ACTA-3'), and H15275 (5'-GGAGGAAGTGCAGGGCGAAGAATCG-3') (Irwin et al., 1991; Edwards et al. 1991). L and H refer to the 3' position of each primer with reference to human mitochondrial DNA light and heavy strands, respectively (Anderson et al., 1981).

Primers L14735 and H15906 were used in double-stranded PCR amplifications in 50 µl reactions volumes. Each reaction included 3 µl of each primer(10 µM), 2 µl of MgCl2 (25 mM), 6µl of deoxynucleoside-triphosphate mixture (dATP, dGTP, dCTP, and dTTP, 1 µM each), 5 µl of 10 X Taq buffer, and 1.25 units of Taq DNA polymerase. PCR was performed with the following thermal cycling procedures: initial denaturation at 94oC for 2 minutes followed by 35 cycles of 94°C - one minute, 56°C - one minute, 72°C - two minutes and a final 72°C extension for 10 minutes. Reaction success was assessed by electrophoresis of 5 µl of product on a 1% agarose gel, staining with ethidium bromide, and viewing under UV light.

Single-stranded DNA was generated from five µl of the double-stranded product in 100 µl reaction volumes. Asymmetric PCR reactions using only one primer were performed under the same conditions as above for symmetric reactions. Twenty-five thermal cycles were performed following the same procedure as that of the last cycles of the symmetric reactions.

Purification of single-stranded product was accomplished prior to sequencing and concentrated to 25 µl using Ultrafree-MC 30,000 NMWL filters (Millipore Corp., Bedford, MA). Sequencing reactions were performed on 7µl of the resulting single-stranded template using T7 DNA polymerase (Sequenase version 2.0, Unites States Biochemical, Cleveland, OH) following standard dideoxy chain-termination protocols (Sanger et al., 1977).

Phylogenetic analyses were conducted using version 3.5c of Phylip (Phylogeny Inference Package, Felsenstein, 1993) and version 1.01 of Mega (Molecular Evolutionary Genetic Analysis, Kumar et al., 1993) with *G. pineatus* designated as the outgroup *a priori*. Tree-building procedures using the entire data set included maximum parsimony and maximum-likelihood. Distance estimations were assessed using the Kimura two-parameter model (Kimura, 1980). Molecular clock analyses were performed on 3rd position of codons and used a 10:1 transition:transversion ratio (Irwin et al., 1991) and asssuming a 10% change per 1 million years.

Results

The sequence of 1140 base pairs of the cytochrome b gene of mtDNA was compared among the ten taxa and the Ozark population of *Geomys*. Excluding the outgroup, *G. pinetis*, there were 262 variable characters resolved. Of these, 120 were found to be phylogenetically informative. Of the variable characters, 47 (19.65%) occurred at the first position of codons, nine (4.21%) occurred at the second position, and 206 (76.14%) occurred at the third position. Of the 120 phylogenetically informative characters, 19 (15.57%), 2 (1.79%), and 99 (82.63%) occurred at the first, second, and third codon positions, respectively. The total nucleotide variability represented 31 variable amino acids in the cytochrome b sequence which is 379 amino acids in length. Variable amino acids (denoted parenthetically in Appendix I) are distributed throughout the gene.

The number of nucleotide substitutions between the Ozark population and *G. breviceps* was 148, while the mean number of substitutions between this population and eight subspecies of *G. bursarius* was 69. The least number of nucleotide substitutions for all pairwise combinations of the Ozark population and the ten taxa of *Geomys* occurred with *G. bursarius missouriensis*, 42. Transition to transversion ratios ranged from 2.18 between the Ozark population and *G. pinetis* to 16.00 between *G. bursarius major* and *G. bursarius illinoiensis* (Table 1). The largest ratio, indicating greater similarity in genomes, determined for the Ozark population and other subspecies of *Geomys* was with *G. bursarius missouriensis* (5.000).

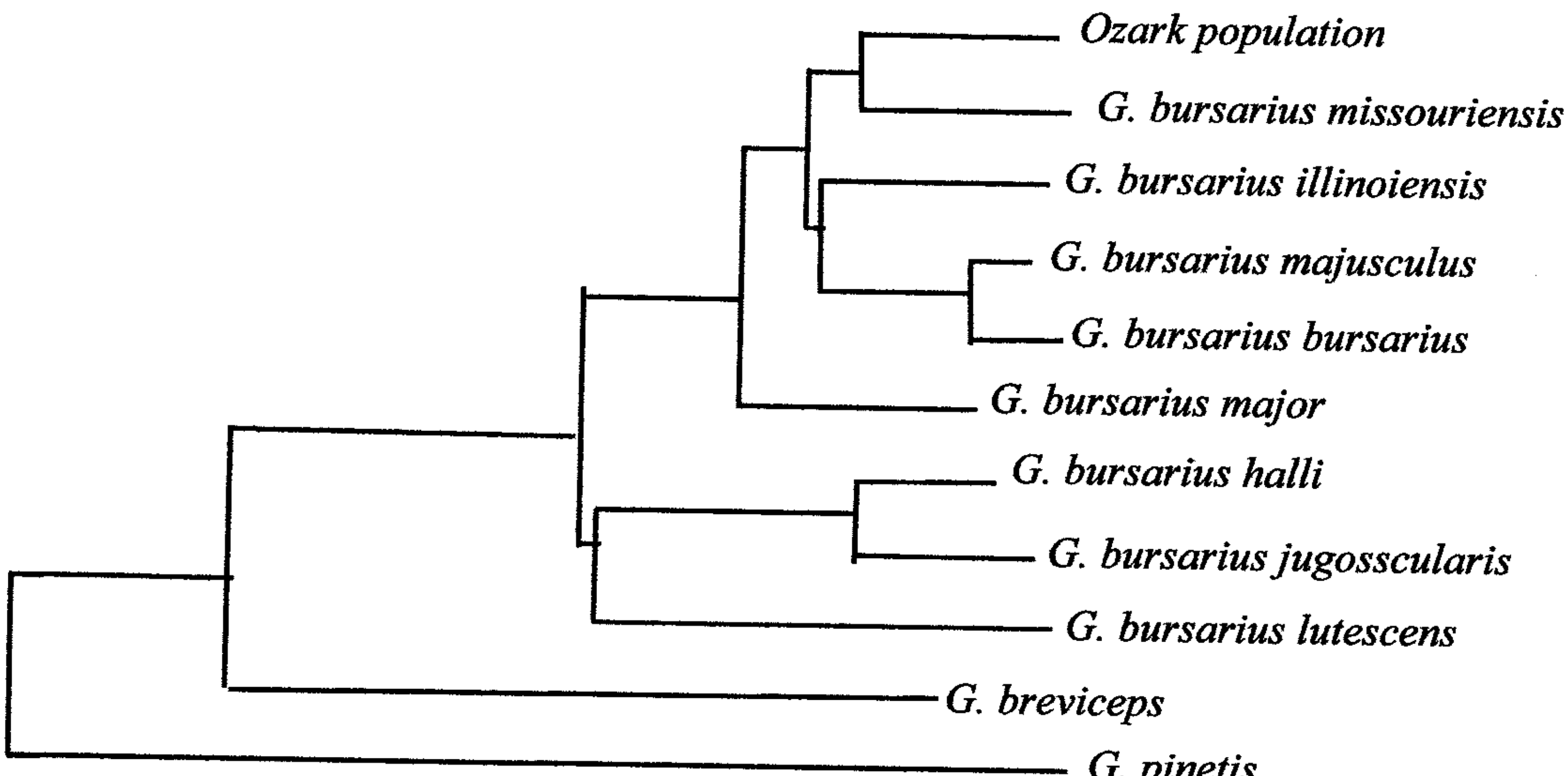
The Kimura-2 parameter distance between the Ozark population and *G. breviceps* was 0.146 (Table 1), while the mean distance between the Ozark populations and eight subspecies of *G. bursarius* was 0.060, with a range of from 0.038 to 0.087. The greatest similarity between the Ozark population and subspecies of *G. bursarius* was with *G. bursarius missouriensis*, 0.038. Genetic distance between the Ozark population and *G. b. missouriensis* was comparable to or greater than those in the matrix for pairwise combinations of other subspecies of *G. bursarius*, including *G. b. majusculus* / *G. b. illinoensis* (0.038), *G. b. halli* / *G. b. jugossicularis* (0.0288), and *G. b. majusculus* / *G. b. major* (0.013). The mean distance between *G. breviceps* and the eight recognized subspecies of *Geomys* was 0.142, while that among the subspecies of *Geomys* was 0.065.

Irrespective of which tree-building algorhythm was used, all trees produced resulted in identical topologies (Fig 4). The cladistic analysis using Kimura 2-parameter distance with all nucleotide changes and using *G.pinetis* as an outgroup resulted in a tree with *G. breviceps* being the most distant taxon and two major clades comprised of the remaining *G. bursarius* taxa. Of these major clades, one included *G. b. lutescens*, *G. b. jugossicularis*, and *G. b. halli* as sister taxa, and a second was comprised of the population from the Ozark Mountains and *G. b. missouriensis*, *G. b. illinoienisis*, *G. b. majusculus*, *G. b. bursarius*, and *G. b. major*. Within this major clade, *G. b. major* was the most divergent taxon, with *G. b. majusculus*, *G. b. bursarius*, and *G. b. illinoiensis*

Table 1. Kimura-2 parameter distances (above) and transition to transversion ratios (below) based on analysis of nucleotide sequence differences for the cytochrome *b* gene of mtDNA for pairwise combinations of 11 taxa of pocket gophers, genus *Geomys*. Taxa abbreviations are as follows: Gpin - *G. pinetus*, Gbrev - *G. breviceps*, Gbmaj - *G. bursarius major*, Gbill - *G. bursarius illinoiensis*, Gbjug - *G. bursarius juggossicularis*, Gbbur - G. bursarius bursarius, Gbmjs - *G. bursarius majusculus*, Gbhal - *G. bursarius halli*, Gbmis - *G. bursarius missouriensis*, Gblut - *G. bursarius lutescens*, Ozark - Ozark populations.

Taxon	Gpin	Gbrev	Gbmaj	Gbill	Gbjug	Gbbur	Gbmjs	Gbhal	Gbmis	Gblut	Ozark
Gpin	--	0.1890	0.1908	0.2031	0.1977	0.2006	0.2028	0.1981	0.1993	0.2064	0.1938
Gbrev	2.796	--	0.1370	0.1471	0.1426	0.1457	0.1437	0.1362	0.1418	0.1393	0.1458
Gbmaj	2.481	3.242	--	0.0467	0.0766	0.0505	0.0476	0.0738	0.0583	0.0821	0.0523
Gbill	2.600	3.382	16.000	--	0.0930	0.0410	0.0381	0.0859	0.0467	0.0912	0.0437
Gbjug	2.345	3.394	4.125	4.765	--	0.0857	0.0828	0.0288	0.0881	0.0849	0.0866
Gbbur	2.564	3.111	10.000	10.250	4.353	--	0.0133	0.0829	0.0485	0.0910	0.0474
Gbmjs	2.474	3.294	9.400	9.500	4.867	2.750	--	0.0799	0.0448	0.0901	0.0418
Gbhal	2.527	3.633	5.077	5.500	9.667	5.286	5.917	--	0.0811	0.0779	0.0817
Gbmis	2.545	3.800	11.600	11.750	6.154	7.833	11.250	7.600	--	0.0822	0.0381
Gblut	2.466	3.303	7.700	6.385	5.429	5.400	6.308	6.545	8.667	--	0.0889
Ozark	2.183	3.229	4.700	4.333	3.600	3.727	4.111	4.118	5.000	4.875	--

Figure 4. Cladogram derived from Kimura 2-parameter distance with all nucleotide changes included.



Each— is approximately equal to a distance of 0.00166

grouping in a common clade. The Ozark population were placed as a sister taxon to *G. b. missouriensis* within this major clade.

Morphological analysis of adult female pocket gophers included three specific groups: *G. breviceps*, *G. bursarius missouriensis* and the individuals from the Ozark Mountains in Arkansas. Based on univariate biometric routines, a general trend in character means was apparent. Specimens of *G. breviceps* had lowest means for all characters with the exception of least interorbital width, while the samples of *G. bursarius missouriensis* had the largest character means with the exception of least interorbital width. The Ozark populations had character means that were consistently intermediate between those of the two known groups. Results of a Student-Neuman-Kuels multiple range test ($\propto = 0.05$) on means of 14 cranial measurements illustrating these trends are presented in Table 2. *G. breviceps*, *G. bursarius missouriensis*, and the Ozark populations differed significantly for 11 of the 14 measurements. For two of the remaining measurements, zygomatic breadth and first molar width, the Ozark populations did not differ significantly from *G. bursarius missouriensis*. For braincase width, the Ozark populations did not differ significantly from *G. breviceps* or *G. bursarius missouriensis*.

Principal components were extracted to summarize character variation among groups. Loadings, which indicate the correlation of characters with the first three principal components, are given in Table 3 and represent a cumulative 86.5 % of the total inter-locality phenetic variation. Principal component I represented 71.5% of the variation and is essentially a size factor with no high correlations. The second principal component represented 8.5% of the variation, with high positive loadings for least intorbital width and braincase width. Principal component III represented 6.6% of the variation with high positive loadings for least intorbital width and high negative loadings for braincase width. Construction of 95% confidence ellipses around the means for

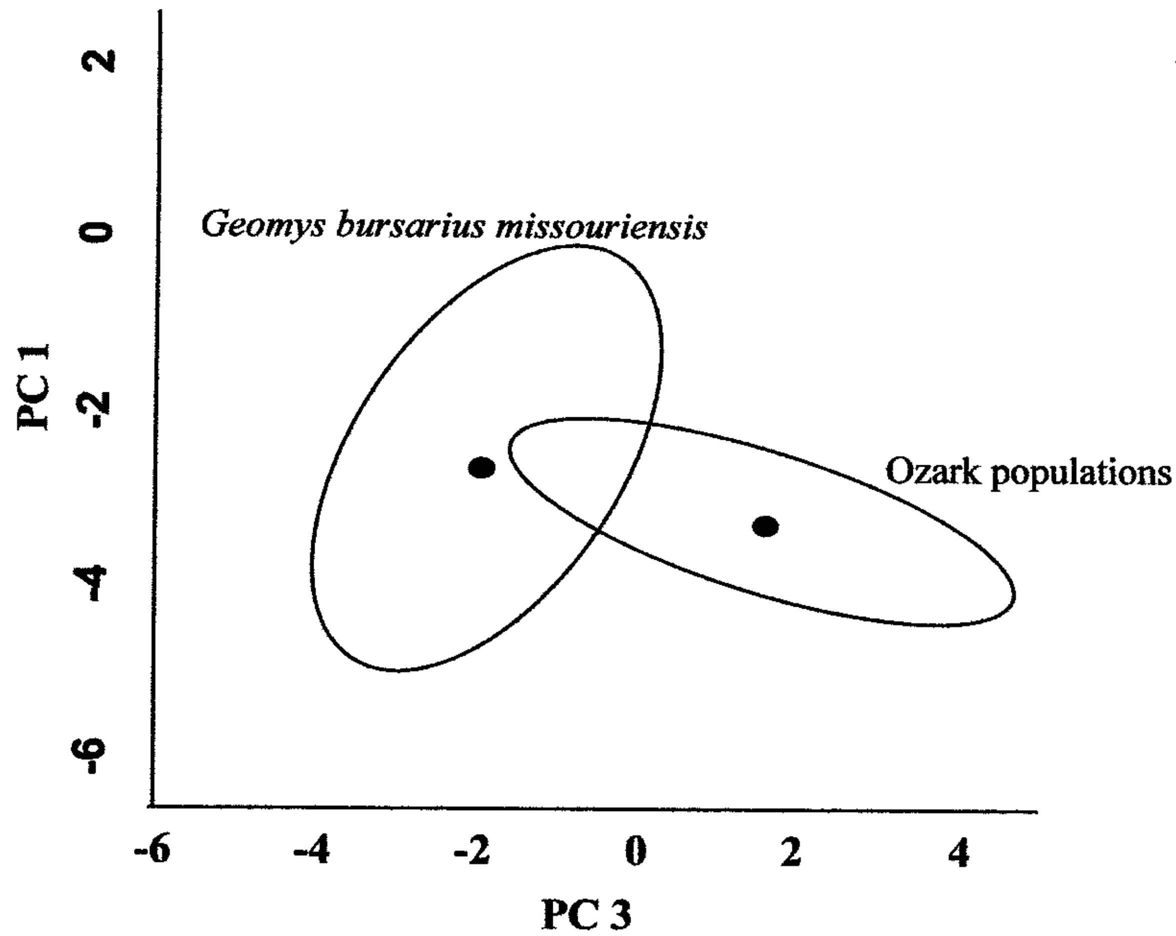
Table. 2 Results of Student-Neuman-Kuels multiple range test for 14 cranial measurements of pocket gophers of the genus *Geomys* from Arkansas and Missouri. Nonsignificant subsets ($\alpha = 0.05$) are shown by lines below taxa and character means.

Character	*G. breviceps*	*Ozark population*	*G. bursarius missouriensis*
Greatest skull length	40.12	42.76	44.91
Braincase width	17.72	18.23	18.62
Greatest skull depth	12.49	13.05	13.41
Condylobasal length	38.72	41.50	43.71
Basal length	36.88	39.40	41.55
Zygomatic breadth	24.05	24.50	27.03
Rostral width	8.41	8.84	9.35
Rostral height	6.70	7.20	7.58
Least interorbital width	6.77	6.26	6.02
First molar width	1.79	1.86	2.00
Posterior molar to anterior incisor length	25.11	26.07	28.32
Palatal length	22.88	24.50	25.77
Greatest optic foramen length	13.40	14.09	14.85
Mandibular length	26.27	27.79	29.77

Table 3. Loadings of characters on the first three principal components in an analysis of cranial morphology in *G. breviceps*, *G. bursarius missouriensis* and Ozark populations of pocket gophers.

Measurement	Principal Component I	Principal Component II	Principal Component III
Greatest skull length	0.306971	-0.000253	0.123150
Braincase width	0.125680	0.515275	-0.686636
Greatest skull depth	0.258356	0.206657	-0.215512
Condylobasal length	0.306967	-0.056542	0.089049
Basal length	0.304616	-0.074907	0.075228
Zygomatic Breadth	0.292560	-0.173777	-0.091171
Rostral width	0.258517	0.023015	0.274695
Rostral height	0.257888	0.151135	-0.054868
First molar width	0.252240	-0.028443	0.094836
Posterior molar to anterior incisor length	0.304055	-0.105312	0.086585
Palatal length	0.305986	-0.053343	0.102017
Least intorbital width	-0.012457	0.767986	0.557735
Greatest optic foramen length	0.278255	0.103465	-0.168573
Mandibular length	0.299990	-0.118971	-0.012931

Figure 5. Ninety-five percent confidence ellipses around means for characters in the principal components analysis for *Geomys bursarius missouriensis* and Ozark populations of pocket gophers.

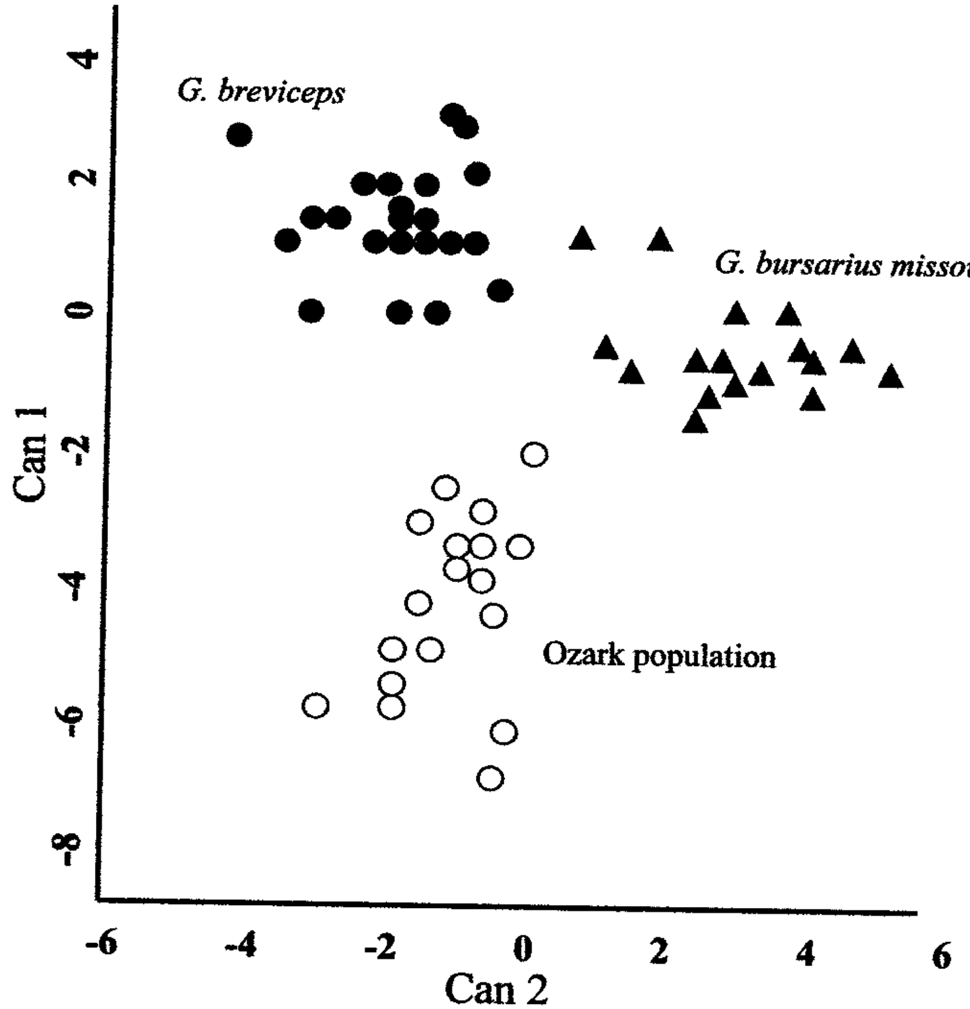


characters in the principal components analysis (Fig. 5) indicated little overlap in the ellipses with major differences between the orientation of the variation. Neither mean was included in 95% confidence ellipses of the alternate taxa.

Using *G. breviceps* from Arkansas and *G. bursarius missouriensis* as knowns and pocket gophers from the Ozark Mountains in Izard Co. as unknowns in a discriminant function analysis, all characters in combination were found to be useful discriminators, and all known *G. breviceps* and *G. bursarius missouriensis* were classified correctly. All specimens from the Ozark populations were classified with *G. bursarius missouriensis*. First molar width (1.33) and posterior molar to anterior incisor length (4.14) were the most positively weighted, and condylobasal length (-1.85) and palatal length (-2.88) were the most negatively weighted characters based on raw discriminant function coefficients of canonical I variables; rostral height (1.17) and posterior molar to anterior incisor length (1.25) were the most positively weighted, and palatal length (-1.65) and least interorbital width (-2.34) were the most negatively weighted characters of canonical II variables.

When treating each of the three groups, *G. breviceps* , *G. bursarius misouriensis*, and the Ozark populations, as known groups, all 13 characters were useful discriminators. The plot of canonical dicriminant functions (Fig. 6) demonstrates complete separation between groupings, with the Ozark specimens defined clearly as a separate entity. Zygomatic breadth (1.21) and posterior molar to anterior incisor length (4.14) were the most positively weighted, and condylobasal length (-1.86) and palatal length (-2.90) were the most negatively weighted characters based on raw discriminant function coefficients of canonical I variables; greatest skull length (1.14) and posterior molar to anterior incisor length (1.51) were the most positively weighted, and palatal length (-1.87) and least interorbital width (-2.57) were the most negatively weighted characters of canonical II variables.

Figure 6. Plot of canonical discriminant functions with all groups designated as known entities.



Discussion

Numerous studies on the genus *Geomys* indicate that local populations differentiate under the influences of a variety of factors that relate to the biology of fossorial rodents. It has become abundantly clear that in *Geomys* the low degree of vagility resulting in isolation of populations, founder effects resulting in nonrandom samples of genomes from parental populations, and parameters of population dynamics such as low effective population sizes resulting in genetic drift have been manifested by high levels of genic divergence (Baker et al., 1989; Block and Zimmerman, 1991; Bohlin and Zimmerman, 1982; Cothran and Zimmerman, 1985; Davis, 1986), chromosomal variation (Baker, et al., 1989; Dowler, 1982; Honeycutt and Schmidly, 1979; Tucker and Schmidly, 1981) and morphological differentiation (Heany and Timm, 1983, 1985; Honeycutt and Schmidly, 1979; Hendrickson, 1972). More often than not, these differences are concomitant with reproductive isolation or are reflective of intermediate stages of speciation. It is not surprising, therefore, that differences between populations of *Geomys* isolated in the Ozark Mountains of northern Arkansas and populations of pocket gophers proximal to it have differentiated from some more widespread, ancestral form.

Based on allozyme similarities and conspecific chewing lice, Elrod et al. (1996) presented evidence that populations of *Geomys* in north-central Arkansas were allied with *G. bursarius missouriensis* to the north and not with the more widespread species in the state, *G. breviceps*. Analysis of nucleotide sequences of the cytochrome *b* gene of mtDNA for several subspecies of *G. bursarius* confirms this conclusion. The number of nucleotide substitutions and the Kimura-2 distance parameter between the Ozark populations and *G. breviceps* were 148 and 0.146, respectively, while these same measures between the Ozark populations and *G. bursarius missouriensis* were 42 nucleotide differences and a distance of 0.0381. These similarities resulted in the Ozark populations and *G. bursarius missouriensis* pairing as sister taxa in the cladogram, as well (Fig. 4). Based on evidence provided from this cladogram and considering the populations from the Ozark Mountains to represent a sister taxon to *G. b. missouriensis*, a maximum likelihood estimate of genetic distance was calculated based on 3rd position changes only and a 10:1 transition:transversion ratio (Irwin et al. 1991). This estimate indicates a lineage divergence for the Ozark populations and *G. bursarius missouriensis* of approximately 511,000 YBP (10.96 + 9.48/2 = 10.22/2 since both lineages were diverging).

The analysis of 14 skull measures provided a similar confirmation of the relationships of the Ozark populations with *G. bursarius missouriensis*. Univariate statistical analyses demonstrated significant differences between 13 of 14 means of cranial measurements of the Ozark populations and *G. breviceps*. Univariate analyses also demonstrated that the Ozark populations and *G. bursarius missouriensis* were significantly different in means of 11 of 14 cranial characters. Discriminant function analysis, utilizing *G. bursarius missouriensis* and *G. breviceps* as known taxa and the Ozark populations as unknowns, grouped all specimens from the Ozark populations with *G. bursarius missouriensis*.

Principal components analysis was able to separate the Ozark populations and *G. bursarius missouriensis*, with little overlap in confidence ellipses. Honeycutt and Schmidly (1979) indicated that size variation is described by axis I, and axis II was demonstrative of interspecific variation. Moreover, they indicated that intraspecific, and presumably subspecific, variation was explained by axis III. Although axis III typically represents less than 10% of the variation in morphometric studies, there is precedence from other investigations that have utilized variation represented by axis III to explain differentiation in pocket gophers (Honeycutt and Schmidly, 1979; Demastes and Hafner, 1991). Therefore, the utilization of the variation expressed by axes I and III in our principal components analysis to demonstrate morphological differentiation seems warranted. The degree of overlap between these populations in the principal components analysis, as reflected by ellipses of 95% confidence limits (Fig. 5), are comparable to or greater than differences observed among recognized subspecies of *G. bursarius* examined by Heaney and Timm (1983). These results can be contrasted to the analysis of Honeycutt and Schmidly (1979) who found greater similarities between local populations of *Geomys* in Texas. In that study, the degree of overlap in cranial morphology was extensive, and ellipses that reflected one standard deviation around the population means included the centroids of others in over half of the populations included in their study. Results of the principal components analysis are concordant with that of Heaney and Timm (1983), and differences in cranial morphology between Ozark populations and *G. bursarius missouriensis* are typical of comparisons between other subspecies of *Geomys*.

The lack of complete separation in the principal components analysis may reflect common gene arrays that impart similar cranial morphologies to the Ozark populations and *G. bursarius missouriensis* or convergence in morphology among pocket gophers that has been demonstrated to be influenced greatly by similarities in soil composition and texture (Hendrickson, 1972; Wilkins and Swearingen, 1990).

Collectively, similarities in allozymes, external parasites, nucleotide sequences of the cytochrome b gene of mtDNA, and cranial morphology indicate that the populations of *Geomys* isolated in the Ozark Mountains of northern Arkansas are most closely related to populations of *G. bursarius* to the north in Missouri. The biogeographic history of these populations, however, remains unclear.

The closest records of *G. bursarius* to those of the Ozark populations are from Williamsville and Hunter, Co., Missouri, ca. 150 km to the northeast. Several attempts by us and others (McLaughlin, 1958) to collect pocket gophers at these localities have met with no success, and McLaughlin (1958) concluded that this population is now extinct. Furthermore, extant *G. bursarius missouriensis* ranges over the northern half of Missouri and as far south as the area around St. Louis County. Therefore, the Ozark populations appear to be separated by a much greater distance from existing populations of *G. bursarius missouriensis* than that indicated from commonly used range maps i.e. Hall, (1981).

The populations of *G. bursarius* in the Ozark Mountains occur in deep, sandy soils of the flood plain of the White River in Izard Co. Two specimens collected over 10 yrs ago from immediately across the White River in Stone Co. have been documented, however extensive searching at this locality has not confirmed that this population exists currently. We assume at this time that the Ozark populations of *G. bursarius* reflect an isolated relict of a once widespread series of populations of eastern pocket gophers that ranged into this portion of the state from the north. Indeed, fossil remains of *G. bursarius* of Wisconsin glacial age have been found in cave deposits in Newton Co., Arkansas (Brown, 1908; Hay, 1924), ca. 120 km west of extant Ozark populations in Izard, Co. However our estimate of a divergence time of 511,000 YBP, based on cytochrome b nucleotide differences between the Ozark population and *G. bursarius missouriensis*, would indicate that these populations differentiated much earlier. Therefore, these populations appear to have remained isolated in suitable soils along the White River of what is recognized as the Salem Plateau of the interior highlands of Arkansas.

Collectively, the degree of genetic and morphological differentiation of the Ozark populations is typical to that for other subspecies of *G. bursarius*. For example, the amount of nucleotide sequence divergence between the Ozark populations and *G. bursarius missouriensis* (0.0381) is equivalent or greater to those between currently recognized subspecies such as *G. bursarius illinoiensis* and *G. bursarius majusculus*, (0.0381), *G. b. halli* and *G. bursarius jugossicularis* (0.0288), and *G. bursarius majusculus* and *G. bursarius bursarius* (0.133). Similarly, morphological differentiation is concordant with that between other subspecies of *G. bursarius* (Heaney and Timm, 1983). We conclude that, since these populations represent a discrete genetic entity and that their geographic isolation is indicative of incipient species or populations in an intermediate stage of the speciation process, it is not without precedence that they be recognized as a distinct subspecies of *G. bursarius*.

Geomys bursarius ozarkensis, new subspecies

Holotype.-- Adult male, skin (adult pelage) and skull, no. 5708; Vertebrate Museum, University of Arkansas Little Rock, obtained on 10 October 1996 by D. A. Elrod; from 3 mi. South Melbourne, Izard Co., Arkansas.

Distribution. -- Presently known from extreme southern Izard Co. and northeastern Stone Co, Arkansas.

Diagnosis. -- Size relatively smaller than *G. bursarius missouriensis* in most cranial measurements; pelage of dorsum blackish brown washed with black, that of the ventor gray washed ochraceous.

Description. -- The subspecies occurs only within narrow limits of northcentral Arkansas where it inhabits sandy, deep soils of the flood plain of the White River. The subspecies averages larger in cranial and external measurements than does *G. breviceps*, the other species of pocket gopher in the state. Although the subspecies can be distinguished from *G. breviceps* based on allozyme differences and a chewing louse (*Geomydoecus spickai*) that is specific to its sister taxon, *G. bursarius missouriensis* (Elrod et al., 1996), there are no morphological features other than size by which the subspecies differs from other species of pocket gophers in Arkansas. Similarly, *G. bursarius ozarkensis* differs from *G. bursarius missouriensis* only in size.

Measurements. --External and cranial measurements for the holotype are: Total length, 303 mm; length of tail, 72 mm; length of hind foot, 30 mm; ear from notch, 4 mm; Means for external measurements of the holotype and nine topotypes: total length - 258 mm, tail length - 66 mm; hind foot length - 31 mm; ear from notch - 4 mm; Means for external measurements of 18 allotypes: total length - 208 mm, tail length - 53 mm; hind foot length - 35 mm; ear from notch - 3 mm; Means for cranial measurements for 35 adult female specimens are provided in Table 2.

Etymology - The subspecies name is derived from the Ozark Mountains, the physiographic region to which it is restricted in northern Arkansas.

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Specimens Examined

Geomys bursarius missouriensis - Missouri: St. Louis Co.; 1.0 mi. Creve Coeur Lake.

Geomys bursarius illinoiensis - llinois: Madison Co., 1 mi. N, 2 mi. W Collinsville.

Geomys bursarius majusculus - Kansas: Riley Co.; 1 mi. E Manhatten Airport (Hwy K-18)

Geomys bursarius jugossicularis - Colorado: Fremont Co.; 3 mi. S, 4 mi. E Cannon City; 5190 ft.

Geomys bursarius bursarius - Iowa: Jasper Co.; 2.7 mi N Oakland Acres.

Geomys bursarius halli - Nebraska: Harlan Co.; 2 mi W Alma.

Geomys breviceps sagitallis - Louisiana: Vernon Par.; 2 mi. S, 3 mi. W Rosepine.

Geomys pinetis austinus - Florida: Polk Co.; 11.3 km N., 1.6 km W Lakeland.

Geomys bursarius ozarkensis - Arkansas: Izard Co.; 3 mi. S Melbourne.

CHAPTER V

HABITAT CHARACTERIZATION AND BIOGEOGRAPHIC AFFINITIES OF THE OZARK POCKET GOPHER (*Geomys bursarius ozarkensis*) USING REMOTE SENSING AND GIS TECHNOLOGIES

Introduction

The distribution of pocket gophers (Genus *Geomys*) has been well documented in Arkansas (Elrod et. al., 1996a,b). Of the five physiographic regions occurring within the state (Fig 6), pocket gophers occur in greatest abundance in the Gulf coastal plain, with all counties inhabited by pocket gophers, and in least abundance in the Ouachita and Ozark Mountains, where they persist in isolated areas of suitable habitat often associated with waterways (i.e. rivers, streams and creeks). Pocket gophers are seemingly absent from the Mississippi Delta and Crowley's Ridge physiographic regions (Elrod et al., 1996b).

Suitable habitat for pocket gophers has been reported as primarily open grasslands such as prairies, pastures, fallow fields, and, in urban areas, lawns and golf courses (Hansen and Beck, 1968) where the soils are deep, light in texture, and porous with good drainage (Miller, 1964). Soils that are continuously wet, of small particle size, or diffuse gas poorly are generally avoided (Davis et al. 1938, Davis 1940, Kennerly, 1964, Miller, 1964, and McNab 1966).

Recently, Elrod et. al. (1996a), identified isolated populations of pocket gophers occurring in the Ozark mountains of North-central Arkansas as being most closely related to the plains pocket gopher *Geomys bursarius* occurring to the north in Missouri. This extended the range of this species by approximately 150 km southward and marked a new species of pocket gopher inhabiting Arkansas. This resulted in two species of pocket gophers recognized as occurring in the state. Further analyzes of these populations, utilizing cranial morphology and mitochondrial sequencing of the cytochrome-*b* gene, identified this population as a distinct genetic entity that warranted recognition as a new subspecies within the *G. bursarius* group. The name assigned was *Geomys bursarius ozarkensis*, reflecting the geographic location of this distinct taxon.

G. b. ozarkensis exhibits some interesting biogeographic characteristics. After intensive investigation, the taxon has been documented to be restricted to the southwestern third of Izard County, Arkansas. This represents an extremely limited distribution for a subspecies. Additionally, this population is located in seemingly unsuitable pocket gopher habitat, the Ozark Mountains. Other populations of pocket gophers have been reported within close proximity in adjacent Stone County, Arkansas (Sealander and Heidt, 1990) and in Carter and Wayne Counties in southeastern Missouri (McLaughlin, 1958).

The Ozark Mountains are characterized by three plateaus, Springfield Plateau, Salem Plateau, and Boston Mountains. Izard County falls almost entirely within the Salem Plateau which is characterized as rough to rolling hills, with elevations averaging 380 m, with moderately steep to gently sloping upland contours and occasional outcrops of dolomite and sandstone (Sealander and Heidt, 1990;). The extreme southern portion of Izard County lies within the Springfield Plateau physiographic region. This plateau is higher in elevation than the Salem Plateau and has been dissected by numerous streams. These dissected areas are characterized by steep, V-shaped valleys that are moderately to gently sloping and are long and narrow with winding ridges. Limestone and sandstone outcrops are common.

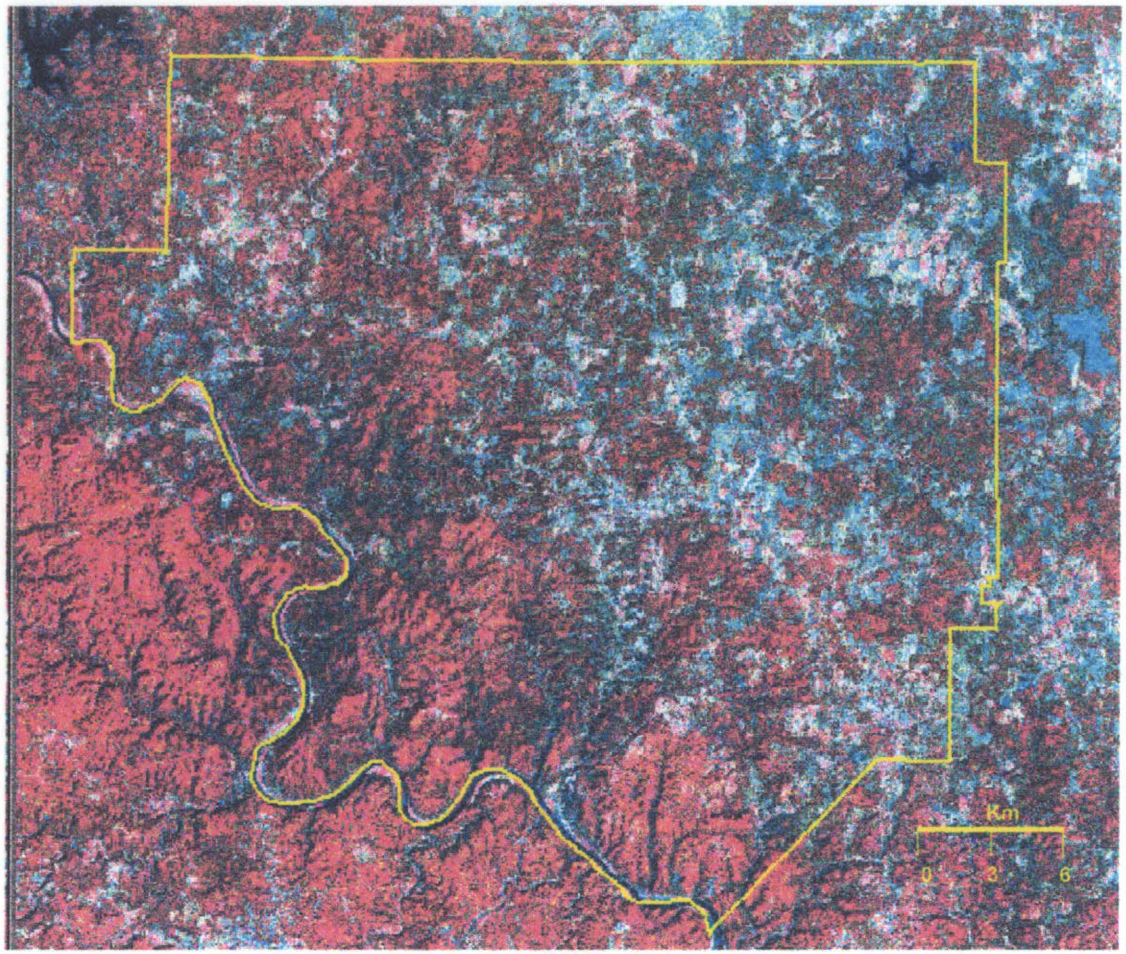
The purpose of this study was to characterize the habitat for *G. b. ozarkensis* within the current known range and based on this information, predict potential locations where other populations may occur within the area of study. Furthermore, information concerning the biogeographic history of this subspecies was investigated to ascertain patterns of dispersal for pocket gophers in Arkansas.

Due to the limited knowledge of the ecology and biogeography of this new subspecies, geographic information systems (GIS) and remote sensing technologies were utilized to examine its distributional affinities. Remote sensing and GIS technologies have been used extensively to elucidate ecological characteristics relating to a variety of biological properties of species including: modeling elk calving habitat in a prairie environment (Bian and West, 1997), modeling habitat suitability index for moose (Hepinstall et al., 1996), Florida scrub jay habitat for purposes of land-use management (Duncan, et al., 1995; Breininger, et al., 1991) modeling bobwhite quail habitat and the assessing the potential impact of Conservation Reserve Program lands (Roseberry et al., 1994) assessing crane habitat suitability (Herr and Queen, 1993) red squirrel habitat modeling using logistic multiple regression (Pereira and Itami, 1991) and habitat characterization for the Texas kangaroo rat (Shaw, 1989).

Materials and Methods

Landsat TM data (30-m X 30-m pixel size) was acquired for the Ozark Mountains (scene 24/35-- acquisition date 10-03-92)) in northern Arkansas and southern Missouri (Fig. 7). Using Earth Resources Data Analysis System (ERDAS) the image was rectified to provide spatial reference using the Universal Transverse Mercator (UTM) coordinate system and to correct error produced by changes in satellite altitude and attitude (roll, pitch, and yaw). Twenty five ground control points (GCPs) were extracted from 1:100,000 topographic maps of the area and were matched to recognizable features on the image. GCP coordinates contributing the greatest error were removed sequentially resulting in a final root mean square error (RMS) of 0.38 pixels, which was achieved with 16 GCP used in the rectification (Table 4).

Figure 7. Landsat TM raw image of Izard Co., Arkansas



Pixels values were replaced on the new coordinate system using the nearest neighbor algorithm, and, after rectification, resulting pixels were referenced not only by rows and columns but in relation to the UTM map projection system.

The image was classified using supervised and unsupervised routines into ten classes, pasture, pasture with sparse trees, hayfields, upland hardwood forest, bottomland hardwood forest, water, agriculture, roads, shrub land, and barren ground. This image was further reduced to a binary map of suitable and unsuitable vegetation for pocket gophers (Fig. 8). Accuracy of this binary map was assessed; for 58 random locations, all reported values (tested locations) of suitable and unsuitable habitat were found to be correct.

Ancillary data sources were used as coverages to aid in the determination of suitable habitat as well as potential habitat for *G. b. ozarkensis*. These data sources were as follows:

1) Transportation (Fig. 9) and surface water (Fig. 10) from U. S. Department of Commerce, Tiger files (1990 census) were examined as potential barriers to dispersal or corridors for organisms to disperse into areas of suitable habitat. Due to the linear nature of these land forms, organisms located are not residents of the habitat merely persisting while attempting to locate suitable habitat.

2) STATSGO (State Soil Geographic Database) was utilized to elucidate suitable soils. This soil association data, represents multiple groups of similar soil types and contains numerous characteristics (such as texture, depth to bed rock, percent sand, etc.), (Fig. 11).

3) Global positioning systems (GPS) were used to identify known pocket gopher locations. Only the center of areas > 100 m in size where pocket gophers occurred were used as locations. This eliminated accuracy problems which can be incurred due to error introduced by selective availability. These locations

Table 4. Ground Control Points used in Rectification Process

GCP	X coord	Y coord
1	591368	4028221
2	625861	4010797
3	534798	3974421
4	561985	3940927
5	537448	4016551
6	541297	4008379
7	551296	4028207
8	542809	3919689
9	553160	3924970
10	583711	3927325
11	613631	3953276
12	624509	3935572
13	630529	3974254
14	664081	3957351
15	624026	3906982
16	652049	3928383

Figure 8. Suitable vegetation derived from Landsat TM data with pocket gopher localities overlaid.

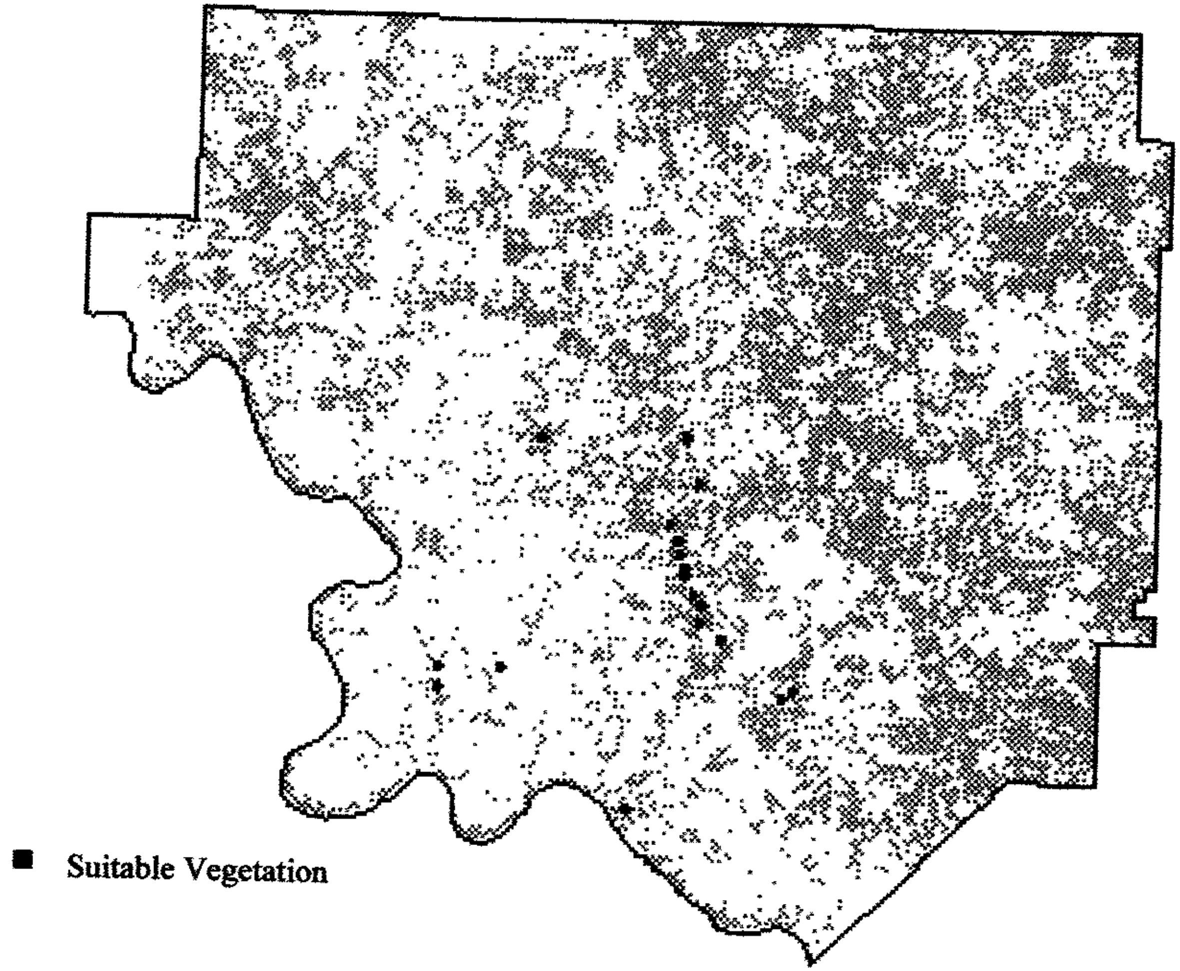


Figure 9. Relationship of roads within Izard county to pocket gopher locations.

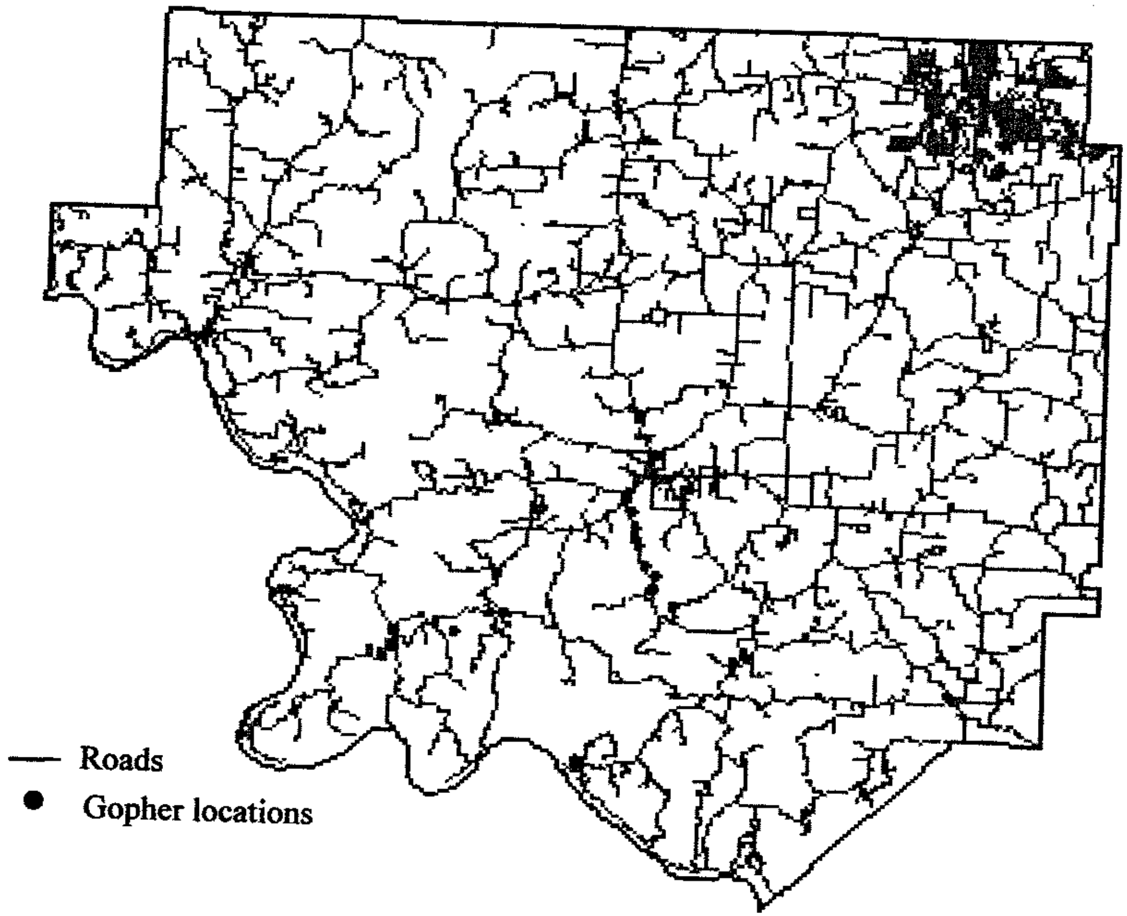
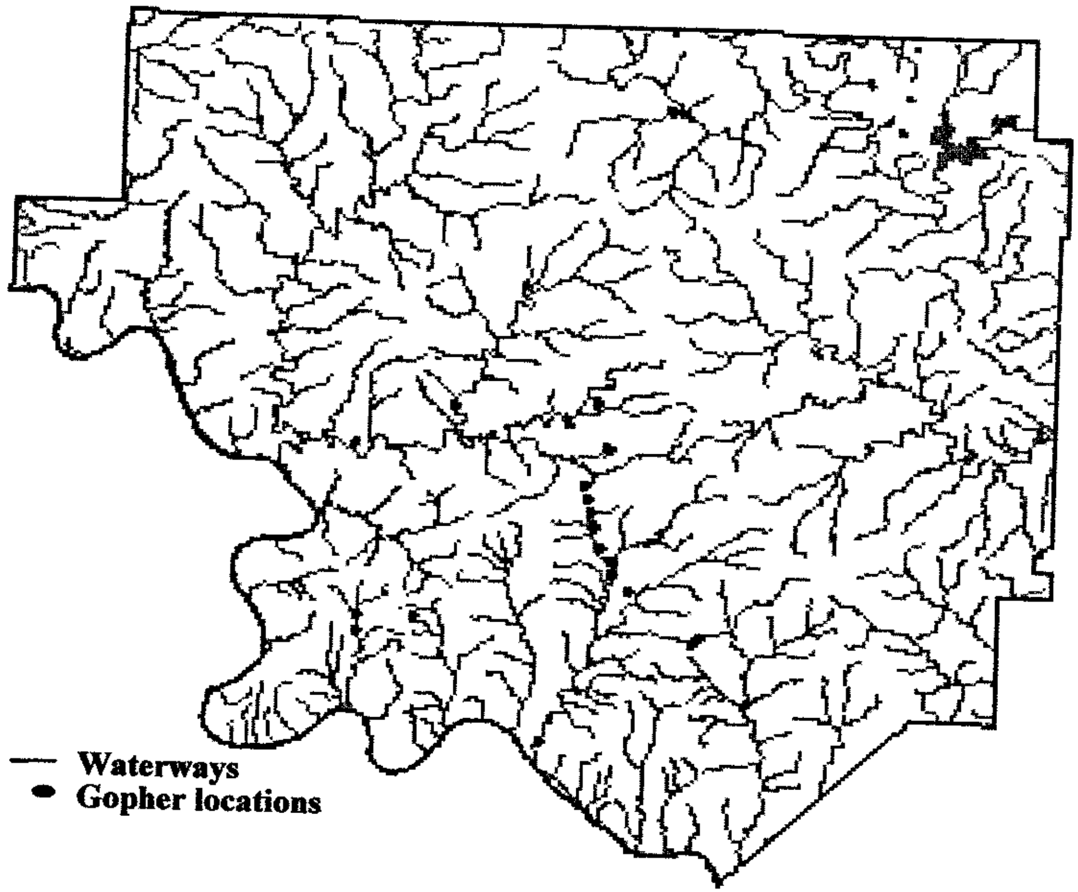


Figure 10. Relationship of waterways within Izard county to pocket gopher locations.



(Table 5) were overlaid onto multiple coverages in order to determine habitat characteristics.

All layers were visualized in ARCVIEW, and an overall map of all coverages within the study area was produced to reflect suitable habitat within Izard Co., Arkansas.

Results

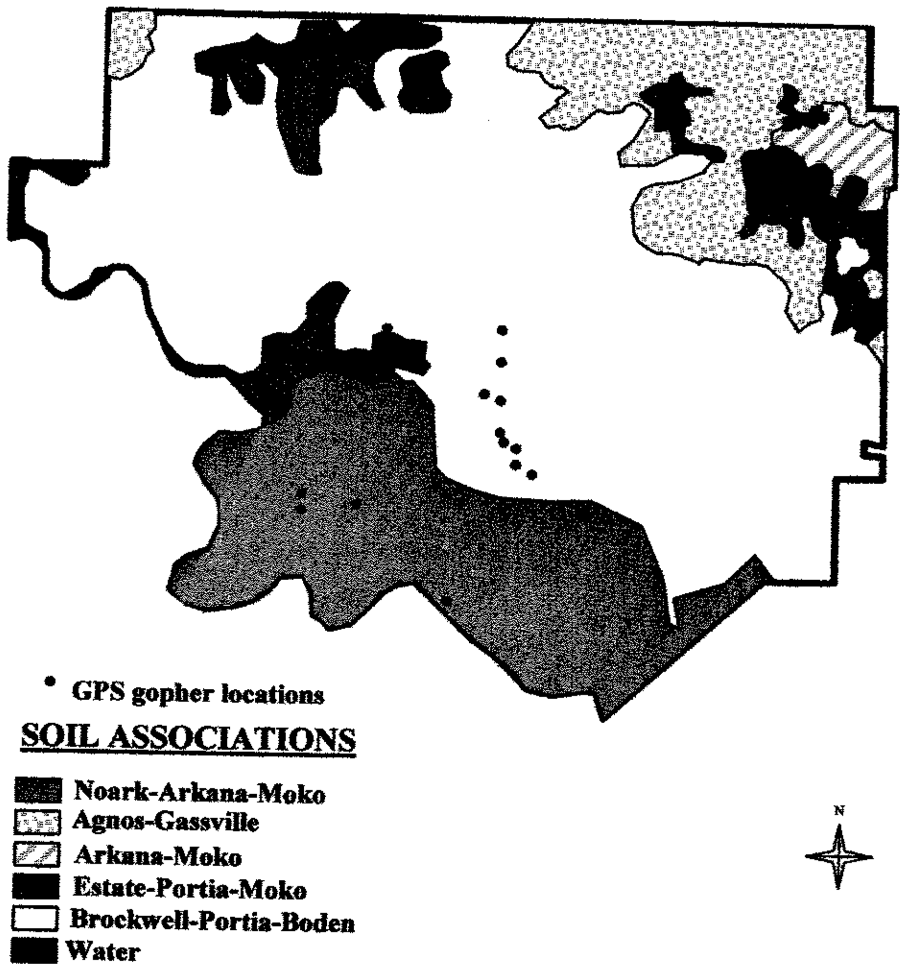
Utilizing remotely sensed data and ancillary digital data layers in a GIS model, certain factors determining the current, known distribution of *Geomys bursarius ozarkensis* in Izard Co., Arkansas were identified. The classified satellite image confirmed the Ozark mountains as being heavily forested in hardwoods and widely dispersed oak-pine forests with both mesic and xeric communities. The most common cover class would be characterized as mesic with differing combinations of hardwoods; southern red oak (*Quercus falcata)*, red oak (Quercus rubra), white oak (*Quercus alba*) together with hickories (*Carya spp.*), and less frequently, sugar maple (Acer saccharum), chinquapin oak (*Q. prinoides*), sweetgum (*Liquidamber styraciflua*), black walnut (*Juglans nigra*) and an occasional short-leaf pine (*Pinus echinata*). Another cover class (dry forest community) is found on xeric exposures, particularly on ridgetops and south- or west-facing slopes. Here, shortleaf pine dominates and in areas where bedrock is frequently at or near the surface red cedar (*Juniperus*) glades are common. Also, upland prairies are scattered through the Salem Plateau most notably in areas of claypans or shallow, rocky soils.

Within the Ozark mountains, Izard County represents an area of approximately 149,826 hectares. This includes 906 hectares of large water bodies. The southern and western portions of the county drain into the White River that forms the border of the county on the south and west. Major streams that flow into the White River include Piney, Mill, Wideman, Twin, Lyons, Hidden, and Lafferty Creeks and Rocky Bayou. The economy of the county is based on livestock and poultry production, tourism, retirement

Table 5. Global Positioning System localities for G. bursarius missouriensis in Izard County, Arkansas.

X-coordinate	Y-Coordinate
602804	3981937
598351	3991502
597759	3993513
597729	3993658
591294	3993426
595474	3976508
602376	3981652
599488	3984191
598545	3985071
598638	3985748
598188	3986305
597824	3987267
597737	3987517
597653	3988119
597541	3988803
597225	3989514
586897	3982806
589633	3982806
586891	3981894

Figure 11. Soil Associations of Izard County in relation to pocket gopher locations.

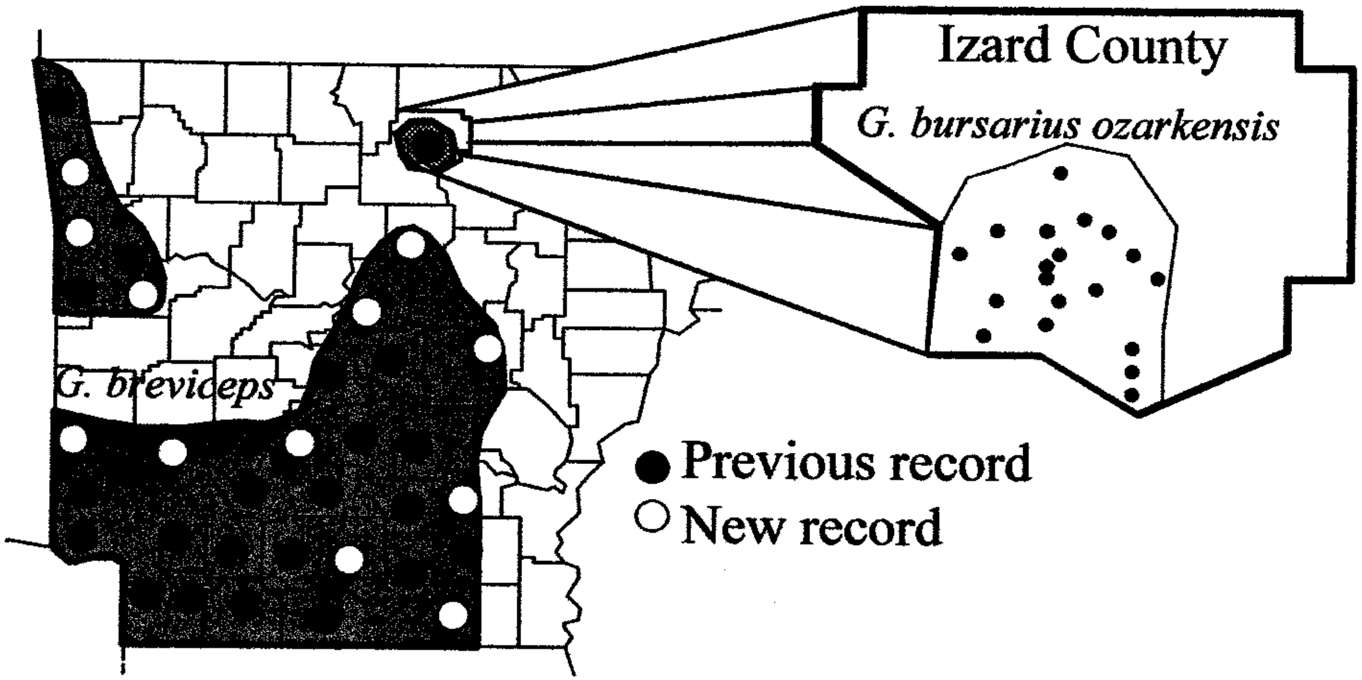


income, and timber production. Most farm income is derived from livestock, mainly beef cattle. Coverage of harvested crop land in the county is small, with main crops being hay, corn, small grains and vegetables. Most soils on the flood plains are poorly suited for cultivation. Nearly all cleared land is used for pasture and forage crops.

The distribution of the Ozark pocket gopher in the Ozark Mountains was establilshed based on extensive field surveys, in which every road was examined in a 30-km radius from the assumed distributional center of Ozark pocket gophers in Izard County. This area included all of Izard County and portions of Stone, Independence, Sharp, and Baxter Counties. From these surveys, the current, known distribution of *G. b. ozarkensis,* based on actual collections and direct observations, was identified as approximately the southwestern third of Izard Co., Arkansas (Fig 12).

Habitat characteristics for the Ozark pocket gopher were determined from GPS locations of pocket gopher populations identified from the field surveys in Izard County (Coordinates in Table 5). From these GPS positions for localities, *G. b. ozarkensis* was found to inhabit open areas often associated with pastureland, fields, mowed areas, and lawns in urban areas. Based on these locations and their incorporation onto the classified vegetation layer derived from satellite imagery, the resulting binary map of suitable and unsuitable vegetation for the Ozark pocket gophers produced a map illustrates the amount and distribution of suitable vegetation for pocket gophers in Izard County (Fig. 8). The amount of suitable vegetation for pocket gophers within Izard County was determined to be 56,675, hectares, with the remaining coverage (93,151 hectares) being unsuitable. Therefore, approximately one-third of the county is represented by suitable vegetation for pocket gophers. This paucity of vegetation suitable for pocket gophers is particularly evident in the southern third of Izard County where *G. b. ozarkensis* is known to occur.

Figure 12. Current known distribution of pocket gophers in Arkansas.



Suitable habitat for *G. b. ozarkensis* was further characterized by utilizing STATSGO soil associations. Izard County is comprised of seven distinct soil associations, and, of these, pocket gopher populations were found in three associations within Izard County, Noark-Arkana-Moko, Estate-Portia-Moko, and Brockwell-Portia-Boden (Fig. 10). These three soil associations comprise approximately 77% (115,366 hectares) of the soil associations in Izard County. Populations of Ozark pocket gophers occur most frequently in the Noark-Arkana-Moko soil association. This soil association is an upland soil group characterized as deep, moderately deep and shallow, gently sloping to steep, well drained, cherty and stony soils that form in residuum of cherty limestone and comprises 16% (23,972 hectares) of the soil associations within Izard County. Another soil association in which populations of pocket gophers occur is the Estate-Portia-Moko, with a total of 15% (22,474 hectares) and is characterized as occurring on uplands and being deep to shallow, gently sloping to steep, well drained, stony and loamy soils that formed in residuum or colluvium of interbedded sandstone and limestone and residuum of limestone or dolomite. The fewest pocket gopher locations were identified from the Brockwell-Portia-Boden soil association, which comprises the most common soil association for the county (46% or 68,920 hectares). This upland association is characterized by deep, gently sloping to steep, well drained, stony and loamy soils that formed in residuum of sandstone, residuum or colluvium that derived from interbedded sandstone and limestone, or residuum of sandstone and siltstone.

The distribution of the Ozark pocket gopher in Izard County can be characterized additionally as being in association with roadways and watercourses (streams, creeks, and rivers). This is especially evident in the southeastern portion of the distribution. It is likely that these streams afford corridors for dispersal by providing deposits of suitable, deep, sandy soils. Roads are well maintained in the area, and mowed roadsides appear to serve as corridors connecting areas of suitable habitat. It is unlikely that these roadside easements represent more than areas for dispersal and are occupied by pocket gophers for a relatively short amount of time.

Discussion

The necessary combination of ecological factors for supporting viable populations of *G. b. ozarkensis* in the Ozark Mountains was consistently determined to be comprised of open areas with herbaceous vegetation, and deep, sandy soils, often in association with stream courses. These parameters are similar to those reported for plains pocket gophers over much of their range in the central United States (Davis et al, 1938; Hansen and Morris, 1968; Kennerly, 1964; Miller, 1964).

Based on a model of suitable vegetation derived from Landsat TM data, within Izard County, Arkansas, there is a limited amount of suitable vegetation in which the Ozark pocket gopher can occur. Interestingly, *G. b. ozarkensis* is found in an area of Izard County with the least amount of suitable vegetation that also occurs in a highly fragmented distribution . Therefore, the current range of Ozark pocket gophers may reflect the lack of adequate corridors for dispersal into areas of suitable vegetation occurring more commonly and in larger expanses in the northern and eastern portions of the county . Additionally, other key components of suitable habitat may be absent or reduced suitability of intervening habitats may prevent pocket gophers from dispersing into areas to the north and east.

Pocket gophers were also identified in close proximity to waterways in Izard County. In Arkansas and Missouri, as is often the case, pocket gophers are found in association with water systems (Elrod, 1996b). As such, levees can provide suitable habitat for pocket gophers, and, within Arkansas and Missouri, high densities of pocket gophers were observed on levees of the Arkansas and Mississippi Rivers. Presumably these man-made structures have created suitable habitat for pocket gophers since they are constructed from adjacent soils, often sandy, river sediments, and are maintained in an open (mowed) state. However, there are no true levee systems associated with the White River in North Arkansas.

Although, open areas adjacent to river systems provide suitable habitat and corridors to dispersal, large, fast flowing rivers can act as barriers to dispersal for pocket gophers. Pocket gophers have been reported as vigorous swimmers in placid waters and have been known to cross more than 50 meters of water if allowed to touch bottom occasionally while swimming (Best and Hart, 1976). In Izard County, the association of pocket gophers to waterways is easily identified as being adjacent to the White River and along streams and creeks flowing southwardly into it (Fig 9).

G. b. ozarkensis was found to inhabit three distinct soil associations in Izard County. These three soil associations comprise a major portion of the county (77%). These associations are groupings representing multiple soil types. Each soil type possesses varying characteristics, of which many may not be suitable for pocket gophers. Based on analysis of detailed U. S. Soil Conservation Service soil survey maps, pocket gophers were identified to inhabit soils associated with streams and river systems. Currently, higher resolution digital data (SSURGO-Soil Survey Geographic Database) are unavailable for this area. Additionally, digitizing U. S. Soil Conservation Service maps introduces error, because the data were not ortho-rectified, polygons from adjacent maps often do not adjoin correctly, and landmarks for referencing are lacking due to nature of this heavily forested area. Thus, higher resolution data must be used to obtain a more detailed predictive model of pocket gopher distributions in this area.

The restricted distribution of *G. b. ozarkensis* in Izard county is not uncommon for pocket gopher taxa over portions of their ranges. Several species and subspecies of pocket gophers are found to inhabit discrete geographical regions, often of limited size. *Geomys texensis* has been identified from the central basin of the Edward's Plateau restricted to seven counties in cental Texas (Block and Zimmerman, 1991). *G. b. industrius* is confined to the Great Bend Prairie of south-central Kansas (Sudman et al., 1987). The Mer Rouge pocket gopher, *Geomys breviceps breviceps,* occurs exclusively in Morehouse Parish, Louisiana and represents the smallest distribution of a currently recognized subspecies of pocket gopher (Demastes and Hafner, 1991). The distribution of *G. b. missouriensis* extends from the vicinity of St. Louis, Missouri southward to within a few km of the Missouri-Arkansas border (McLaughlin, 1958). Two localities in southeastern Missouri, Hunter, Carter County, and Williamsville, Wayne County, were reported by McLaughlin (1958), but pocket gophers were not located on several subsequent expeditions in that area. It is of interest that the location in Hunter, Missouri represents the type locality for *G. b. missouriensis* and appears to no longer to sustain viable populations (McLaughlin, 1958; personal observation).

Based on indirect evidence, this distribution of *G. b. ozarkensis* in northern Arkansas appears to have been previously restricted to suitable soils and vegetation in the proximity of the White River. Increased human activity (land clearing and road construction) has not only created suitable areas for pocket gophers to inhabit but also has reduced large expanses of unsuitable habitat that no longer represent barriers to dispersal. Due to the topography of the Ozark Mountains and the propensity for humans to build close to waterways, this trend in clearing forested valleys will undoubtably increase. As pocket gopher densities increase within Izard County, dispersal into suitable habitat, albeit limited, should continue to occur. Nevertheless, the subspecies is highly localized currently in a fragmented habitat which is characterized by limited suitability for increases in density of present populations and expansion of its range is limited by few avenues for dispersal. Additional research is necessary determine its ecological status and to formulate potential strategies for conservation of this unique genetic entity.

CHAPTER VI

CONCLUSIONS AND SUMMARY

Currently, the distribution of pocket gophers in the central United States appears to be concordant with the prairie vegetational region, as described by Wright (1971), with certain taxa of pocket gophers occurring as isolated populations located in areas of suitable grassland habitats imbedded in eastern hardwood forest (*G. bursarius ozarkensis, G. breviceps)*, coniferous/hardwood forests of the southeast and Gulf coastal plain (*G. attwateri, G. pinetus)*, and shrubland of Texas and north Mexico (*G. personatus, G. tropicalis, G. arenarius, G. texensis)*. Undoubtedly, this distribution has been shaped by past climatic changes and represents a temporary snapshot in a dynamic process of climatic/vegetational change.

Changes in vegetation, as well as climate, are central to the concept of the refuge hypothesis. Upon initial analysis, vegetational changes associated with Pleistocene glaciation events appear to have played a more important role than have climatic changes in creating geographic isolation for genetic differentiation in many organisms that are habitat specialists, including pocket gophers. However, based on the current ranges of pocket gophers and their distribution in areas of extreme temperature differences, occurring from Manitoba, Canada to northern Mexico (Hall, 1981), climatic factors appear to be of less importance to the biogeography of pocket gophers than do vegetational changes. Nevertheless, due to the interaction and cause and effect relationship of climate to vegetation over large regions, climatic factors play an equally important role. With this in mind, reconstruction of vegetational changes during and following glaciation, along with fossil evidence and our current knowledge of the systematic relationships of pocket gophers, a reasonable hypothesis of past trends in systematic relationships of pocket gophers, a reasonable hypothesis of past trends in pocket gopher biogeography can be formulated to explain the current distribution in the context of the refugium hypothesis for *G. bursarius ozarkensis*.

The distribution of relictual pocket gopher populations has long been explained as being due primarily to glacial advances, retreats, and deposits. Davis (1986) discussed the ranges of the extant and fossil species of *Geomys*, in large measure, as having been covered by glacial advances during the successive Nebraskan, Kansan, Illinoian, and Wisconsin ice ages. These glacial events have been hypothesized as the mechanism for the isolation of *Geomys pinetus* in Florida as discussed in Russell's (1968) work on the evolution of pocket gophers. Davis (1986) agreed with this hypothesis to explain the current distribution of *G. pinetus* in the southeastern U. S. concluding that pocket gophers were able to disperse eastward during the Pleistocene when soil conditions were suitable for range expansion of pocket gophers into this region. Davis (1986) also reviewed the impact of glaciers on changing regional soil patterns due to sand deposition left from glacial retreats, as well as, wind blown depositions from these deposits. The current distribution of *G. bursarius illinoiensis* in wind deposited loess along the southern and eastern margins of the Illinois and Kankakee Rivers from the Wisconsin glacial retreat represents an example of the latter.

The distribution of pocket gophers during and following glaciation events is uncertain. However, fossil remains of *Geomys* during the Pleistocene provides evidence of past biogeographic patterns that supports the plausibility of invoking the refuge hypothesis to explain the current distribution of *G. bursarius ozarkensis*.

The fossil evidence of late Pleistocene populations of pocket gophers in Tennessee and Kentucky indicate this region was a part a southeastern refugium for certain populations of *Geomys* other than *G. pinetus*. Based on the occurrence of late Pleistocene fossils of *G. bursarius illinoiensis* in the Nashville basin of central Tennessee

(Parmalee and Klippel, 1981) and other fossil remains of *Geomys* identified from northern Arkansas (Newton County), north-central and southwestern Kentucky (Guilday et al., 1971; Guilday and Parmalee, 1979), and Middle Tennessee (Guilday, 1977), it appears likely that a once widespread ancestral form of the plains pocket gopher ranged across the southcentral states from the Ozark highlands to the western foothills of the Appalachian Mountains.

These locations of pocket gopher remains in Arkansas, Tennessee, and Kentucky, as well as other prairie species such as the Prairie Chicken (*Tympanuchus cupido*) and the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), led Parmalee and Klippel (1981) to suggest that drier conditions than those of present day and well-established and extensive prairies or open parklands occurred throughout the region. Presently, pocket gophers do not occur in Tennessee, Kentucky, and Mississippi, and G. pineatus occurs only in the extreme southern portions of Alabama and Georgia, as well as Florida (Hall, 1981).

The fossil remains identified by Parmalee and Klippel (1981) as *G. b. illionoisensis* in Tennessee are of direct importance in explaining the occurrence of a relictual population of a genetically distinct *G. bursarius* isolated in the Ozark Mountains of northern Arkansas. Based on similarities in cytochrome-*b* nucleotide sequences, *G. b. illionoisensis* was found to be a sister taxon to *G. b. ozarkensis* (see Fig 4). These data provide strong support for a southeastern refugium for a portion of the ancestral clade of *G. bursarius* during the Pleistocene.

The degree of differentiation observed between the Ozark population of plains pocket gophers and its closest sister taxon, *G. bursarius missouriensis,* is more than sufficient to recognize this unique genetic entity as a distinct subspecies. Also, the estimate of time since divergence from its common ancestor places was determined from cytochrome-*b* nucleotide sequence divergence to be ca. 500,000 ybp. The amount of sequence divergence is similar to values found for *G. bursarius missouriensis* and *G. bursarius illinoensis* (P. D. Sudman, personal communication). This places the approximate time for divergence of these closely related taxa, *G. bursarius ozarkensis, G. bursarius missouriensis,* and *G. bursarius illinoensis* as approximating the Kansan glacial.

Davis (1986) illustrates the extent of the four most recent glaciation events, and the Kansan glaciation marked the most southern extent of the four major ice sheets into the central United States. Additionally, the refugium occurred in close proximity to the Mississippi River. Thus, an obvious explanation for the current geographic distributions of the *G. bursarius ozarkensis/missouriensis/illinoiensis* clade would involve a refugium for the ancestral form to *G. b. ozarkensis, G. b. missouriensis* and *G. b. illinoiensis* in the southeastern Unites States in close proximity to the Mississippi River. As the Kansan ice sheet retreated, pocket gophers began a northward expansion into areas of suitable habitat. The Mississippi River isolated ancestral populations in eastern and western groups. The eastern group moved northward along the Mississippi River and up the eastern and southern margin of the Illinois River in Illinois and into relict prairies in Indiana differentiating into *G. bursarius illinoiensis.* The western group followed the glacial retreat northward in a similar fashion, leaving relictual isolates behind in the Ozark Mountains, with geographic isolation contributing to genetic differentiation of *G. bursarius ozarkensis*. Finally, northward movement and eventual isolation of populations in southeastern Missouri resulted in divergence of *G. bursarius missouriensis*. The range of this subspecies is parapatric with that of *G. bursarius illionoensis* but separated from the latter by the Mississippi River (Hall, 1981). Based on the distribution of fossil evidence, estimates of divergence time from molecular data, and current distributions of distinct genetic entities, this scenario represents the most parsimonious hypothesis for the historical biogeography of these sister taxa.

Another species of pocket gopher whose range extends to within 150 km of *G. bursarius ozarkensis* is *G. breviceps*. This species occurs from eastern Texas and Oklahoma, to northern Louisiana and southern and western Arkansas (Bohlin and Zimmerman, 1982). *G. breviceps* currently has no known fossil history, therefore historical inferences relating to the biogeography of this species can be derived only from current distributional trends.

In Arkansas, this species occurs in open habitats across the southern oak pine belt and is separated from a second group of populations in the northwestern portion of the state by the Ouachita Mountains. Evidence from ribosomal DNA (Davis, 1986) indicate a close relationship between species of pocket gophers occurring in southeastern Texas and northern Mexico, *G. attwateri, G. personatus,* and *G. tropicalis*, and allozyme analyses (Block and Zimmerman, 1991) would indicate that *G. breviceps* is a sister taxon to *G. attwateri* and *G. personatus*. These four taxa may have speciated from a single lineage, originating from a southern refugium perhaps in south Texas or northern Mexico. With the expansion of range of *G. breviceps* northward, Elrod et al. (1996) hypothesized two colonization events for *G. breviceps* into Arkansas, one group derived from populations in Louisiana to the south and another entering northwestern Arkansas around the Ouachita Mountains from populations in Oklahoma. The ranges of the two species, *G. breviceps* and *G. bursarius ozarkensis*, approach one another in northern Arkansas, however, genetic analysis and known ecological distributional data have provided no evidence of contact between the two.

The current rekindling of interest in understanding biodiversity of organisms has made studies such as this one an endeavor that supports the importance of incorporating a diverse array of data into a framework that provides a basis for understanding species distributions. For one, the distributions of species are not static, they expand and contract both a long and short term basis. Species distributions are dynamic, and, in

North America and Europe, Pleistocene glacial advances and retreats have influenced expansions and contractions of animal and plant ranges, resulting in the present day ranges being much different than in the past. All of this does not consider the impact that human activity has had on changing the biota of a region, for example, clearing of land in the eastern U.S. has allowed the expansion of coyotes into the New England states within historical times. Similarly, it is not known how clearing of land and construction of transportation corridors may be influencing range expansions of the plains pocket gopher. Whatever the cause for changes in distributions of plants and animals, there are consequences not only to other species in the community but genetic changes, some adaptive and others induced by stochastic events (founder effect and genetic drift) or mating structure intrinsic to a species (inbreeding, outbreeding, polygamy, monogamy). These parameters of populations must be understood in light of biogeographic diversity or uniqueness of a population. Placing these population parameters into a context of having adapted to a set of habitat characteristics and, in turn, relying on past distributions as a basis for understanding current distribution to form an underlying basis for describing the dynamics of biodiversity. This study has attempted to take all of these factors into account for the Ozark pocket gopher, dispersal of pocket gophers from a refugium into previously unoccupied habitat, genetic differentiation under isolation, current habitat preferences, and the distribution of preferred habitat within the Ozark Mountains, in order to construct a reasonable scenario of the biogeographic position of this distinct entity and important component of grassland communities in the central U.S.

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