Chuanling Li

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Dynamics of Late Quaternary Mammal Population Inferred from Geostatistical Study of the Faunmap Database and Its Implications for Conservation

Betreuender: Univ.-Prof. Dr. Dr. h.c. mult. Paul Müller
Berichterstattender: Dr. Martin Paulus
Berichterstattender: Univ.-Prof. Dr. Dr. h.c. mult. Paul Müller

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INTRODUCTION

In 1997, I obtained a scholarship from the Chinese Government to study in Germany. From September 1997 to July 1998, I attended Beijing Language and Cultural University to learn German. During this period, I received several invitations from Germany, one of which was from Dr. Paul Mueller, who was then the director of the Institute of Biogeography at the University of Saarland. My technical specialization is Quaternary mammals. I studied Zoology from 1984 to 1988 and earned my bachelor's degree in the Department of Biology, Lanzhou University. I studied Quaternary Geology since 1988 at the Department of Geology, Northwest University and earned my masters degree in 1991. I then worked at Northwest University and spent 6 years studying mammalian fossils from the karst caves of the Qinling Mountains. The study area is located in northern China, within the Palaeoarctic region. Most of the mammalian fossil taxa found in Qinling now are found only in the southern China, and are commonly considered to be elements of the Oriental region (Li, 1992, 1995, 1996a, 1996b, 1998a, 1998b, 2000; Xue, 1998, 1999a, 1999b). This research experience aroused my interests in biogeography. I found, on the one hand, without biogeographical and evolutionary ecological theories and models to analyze and explain the paleobiological data, fossils are only a pile of broken bones and teeth; they are not empirical representatives of once living animals that had particular ecological requirements and biogeographic histories. On the other hand, without the deep insight of the temporal and spatial changes of the Arealsystems of these organisms, it is difficult to understand our current environmental problems such as the rapid disappearance of biodiversity and to protect the natural resources more efficiently. My research motto became: “The past is the key to the current”. The research field that adopts this motto could link past events to current problems, and seems to me to be very important and interesting. This background indicates why I selected Biogeography, not a paleontological institute or a museum as the next station of my academic career.

In October 1998, I came to the University of Saarland as a visiting scholar. Soon after my arrival at Saarbrücken, Dr. Mueller gave me a copy of the book “Pleistocene Mammals of North America” (Kurten, B., Anderson, E. 1980). One week later he drove me to the University of Trier to attend his lecture. On the way he asked me what caused the extinction at the end of the Pleistocene in North America. I told him Martin’s Overkill theory, which I had learned from Kurten and Anderson's book. “I know Martin’s theory, but what are your own ideas about this extinction?” He asked. That question has shaped the direction of my later research. I am

Chinese and not familiar with the palaeontological and archaeological data of North American. In the University of Saarland and later in the University of Trier, it is also very difficulty to find these data. How can I overcome this problem? An electronic database of the Late Quaternary mammals, if one existed, would be the best solution of this problem. I soon found the Faunmap database at the Illinois State Museum web site. After I had downloaded the database to my computer, I met several major obstacles, because I do not know how to manipulate and analyze the database. To analyze the Faunmap database, one needs not only an understanding of the Paradox database and statistics, but also how to use GIS. This is not easy for a palaeontologist. It took me more than a year to clear these barriers.

Another similar database-- the European Quaternary Mammal database (EUQUAM) -- was found on the website of the University of Bonn, but it is much more simple than Faunmap. I appreciate the Faunmap database for its rapidly providing comprehensive and detailed information that researchers require. But there no such database in China, so the first idea that I had for my doctoral work was to build a similar database for my own country. But I soon found it would be very difficult to do so. There is very little information on absolute ages for many palaeontological and archaeological sites, which are critical to the analytical utility of this kind of database. EUQUAM also lacks absolute chronological data. It has taken 14 experts more than 4 years to build the Faunmap database, and 3 people 3 years to construct EUQUAM. Faunmap is a very comprehensive database, but analysis of Faunmap is still in the beginning, its full implications have not been explored. It may be wise to know its function, advantages and disadvantages before a new similar database is constructed. How can this kind of database be used to solve our current ecological, biogeographical and environmental problems? Which shortages of this kind database should be overcome in the future? What should palaeontologists and zooarchaeologis take into consideration in their future excavation and research in order to provide more valuable information? My purposes here are to try to answer these questions and to build connections between ecology, biogeography and paleontology.

This dissertation is divided into 6 chapters. Chapter one concerns how to use historical data to study the evolution (the origin, development, formation and dynamics) of Arealsystems, the requirements of historical data and the introduction of the Faunmap Database. Chapter two focuses on how to use the fossil data in Faunmap to study the Refugium Stage (the first stage) of the evolution of Arealsystems. By exploring "where did mammals live during the Last Glacial period?", 7 Refugia in North America are identified, 5 of which coincide with De Lattin's dispersal centers recognized by biogeographical methods using data on modern distributions. Chapter three concerns how to explore the internal structure of Arealsystems by analyzing the fossil data with ecological and biogeographical models. Some spatial patterns and historical processes are found. Chapter four focuses on one of the patterns, which could be tested by the observations of Lewis and Clark during their expedition in 1805-1806. This pattern is called Lewis and Clark’s pattern. The historical process of Lewis and Clark’s pattern may well explain the 200-year-old puzzle noted by modern ecologists and biogeographers -- “Why were big game then abundant on the east side rare on the west side of the Rocky Mountains? ” (Moore, 2002). The evolution of Arealsystems of relevant mammals are described in detail in this chapter. Chapter five focuses on another pattern, called Bayham’s pattern. This pattern can be tested by the model of Late Holocene resource intensification first described by Frank E. Bayham. The historical process creating the Bayham pattern will challenge the classic explanation of the Late Holocene resource intensification. Chapter six concludes that fossil data, though possible evolutionary changes and biases in preservation might exist, provide reasonably accurate and voluble information for the study of current ecological and biogeographical problems, for wildlife management and effective conservation. Suggestions are given for paleontologists and zooarchaeologists regarding how to provide more valuable information in their future excavation and research for other disciplines.

Space is not available to identify all the people who in some way influenced this work, but I must mention a few whose cooperation was indispensable. I express my deepest gratitude to Prof. Dr. rer. nat. Dr. h. c. mult. Paul Müller for his giving me this chance, for his support and encouragement, for his patience and understanding, Prof. Xiangxi Xue (Department of Geology, Northwest University, China), Prof. Zaiping Yu (director of Department of Geology, Northwest University, China), Prof. Sun Yong (President of Northwest University, China) for their collaboration, Dr. R. Lee Lyman (Department of Anthropology, University of Missouri-Columbia, USA), Dr. Peter D. Moore (Division of Life Sciences, King’s College, England) for their kind help. I thank the Faunmap Working Group (under the direction of Dr. Russell W. Graham, Denver Museum of Natural History, USA) and Illinois State Museum for the construction and free use of the Faunmap database, Dr. E. Schroeder (Illinois State Museum, USA), Dr. B. Weis (Denver Museum of Natural History, USA) for explaining some fields of the database, Prof. Robert Fisher and Dan Cole (Smithsonian Institute, USA) for providing the electrical distribution maps of North American Mammals, Dr. Nicolas Ray (Department of Anthropology and Ecology, University of Geneva. Switzerland) for sending me the vegetation map of the Last Glacial. I must also acknowledge the invaluable help provided by Ms. Anne Hemmes in English correction, Dr. Löhr Hartwig (Landesmuseum, Trier) in literature, Mrs.

Rebbeca Retzlaf in GIS, Mr. Schay in calculation with Excell, Elle Ortwin and R. Klein in computer assistance. Mega-thanks are due to all those tolerant folks and friends with whom I am in daily contact; for without them, simply, none of this would be worth doing.

Finally, but not the least of appreciation, is especially given to my wife Xingliang Liu for her understanding, selfless support and constant encouragement, to my 6 year old daughter Yueling Li for her joyful laughter and my 8 month old son De Yang Li for his beautiful noisy cry, which accompanied the growth of my dissertation. This work was made possible by the financial aid of Biogeographie, Fachbereich 6, Universitaet Trier, and a scholarship from the Chinese government.

CHAPTER 1. HISTORICAL DATA AND THE EVOLUTION OF AREALSYSTEMS

1. 1 THE ROLES OF A PALAEONTOLOGIST IN BIOGEOGRAPHY AND ECOLOGY

It is already clear that palaeontologists can play a critical role in palaeobiogeography. But what can a palaeontologist contribute to biogeography? This question is not difficult to be answered in theory from the central task of biogeography. "… The central point of biogeography is the explanation of the stucture, function, history, and indicatory significance of Arealsystems of a species" (Müller, 1981). Ecologists and biogeographers may have an advantage in the sound and detailed descriptions of the shape, size, location, function, and structure of Arealsystems, while palaeontologists can get the upper hand in the explanation of its history, namely the evolution of Arealsystems. Palaeontologists, zooarchaelogists and paleoecologists have sound knowledge of the past flora and fauna and are familiar with the past environmental and climatic changes. They can study population changes over long time periods, which cannot be readily studied by modern ecologists and biogeographers (Van Valen, 1969, Deevey, 1969, Watts, 1973). So the advantage would lay definitely with them if they can not only manipulate efficiently large amounts of high qualitative historical data but also have concepts about modern biogeography.

Brown has also pointed out the significance of the studies of fossil records in biogeography: "Too often ecological biogeographers have ignored the influences of past environments and phylogenetic constraints on current distributions. Too often historical biogeographers have focused so exclusively on phylogenetic history that they ignored the influence of past and present environments. Too often both ecological and phylogenetic biogeographers have ignored the insights into past distributions and environments that can only come from studies of the fossil record. A synthetic perspective that incorporates information from phylogenetic reconstructions, the fossil record, and ecological studies will provide a more complete understanding of the processes that shaped geographical distributions" (Brown, 1996). Lyman has demonstrated the relevance of zooarchaeological data to modern wildlife management (Lyman, 1996)

The word "history" is often used in two different and sometimes confusing ways by biogeographers, ecologists and eolutionary biologists. There is the history of place: the changes in geology, climate, and other environmental factors that are extrinsic to particular organisms. Then there is the history of lineage: the changes in the intrinsic characteristics of organisms that have been inherited from their ancestors (Brown, 1995, 1996). Fossils and subfossils are best records of the history of lineage. Therefore historical data may include any biological, geological, and climatic information. Ancient DNA from fossil and subfossil will be another import historical data, and will play a critical role in the study of population gentics. Here the historical data mainly refer to the mammalian fossil or subfossil data from palaeontological or archaeological sites, the related geological and climatic information, and also archaeological data since the appearance of *Homo sapians*.

This dissertation develops a rationale of how to use historical data to solve biogeographical and ecological problems. It is argued that large amounts of historical data of high quality could be used to document the evolutionary processes of Arealsystems, to identify refugium, to show when the current shape and size of Areals come into being, to assist biogeographers to find the "hot spots" of the Arealsystem of a species (the area with a much higher population density than other areas within the range) and to find biogeographical patterns and historical processes, some of which can be tested by ecologists and biogeographers through the use of current data.

1. 2 The Arealsystem: for Ecologists, Biogeographers and Palaeontologists

Traditionally there has been little communication between ecology, biogeography and paleontology because of the vastly different spatial and temporal scales on which these disciplines studied. Ecologists have been concerned primarily with the regulation of abundance and distribution of species at local spatial and short time scales. Biogeographers have locused on the influence of contemporary and historic factors on species distribution at regional to global spatial scales. Paleontologists have studied changes in the composition of assemblages of speices over geological time scales. However, several authors have attempted to make connections between the patterns and processes that occur on vastly different spatial and temporal scales (see Jablonski, 1986, 1987, Ricklefs and Latham, 1992, Davis, 1986, Graham, 1986, Betancourt *et al.*, 1991). This interaction is important because the perspectives common to one discipline can introduce original insights to related disciplines (Enquist, 1995).

The analysis of the Arealsystem may provide another common platform for the communication between ecology, biogeography and paleontology (Fig. 2). The geographic range of a species, in the simplest meaning, is the area “occupied” by a given species, or simply “range” or “area” (Rapoport, 1982) or “Areal” in German (Müller, 1981), which may be the basic unit of biogeograohy. Species ranges are often not as uniform and static as the solid blots on maps suggest. Population density, for example, varies widely over the range, as well as from year to year. Most biogeographic research studies the structure and dynamics of Areals: their sizes, shapes, boundaries, overlaps, and locations. Ecologists are concerned with differences in habitats preferences, geographical and population genetical patterns, physiological and morphological properties in particular regions, so they consider only a portion of the range of one or more species. The comparative and quantitative studies of Areals will show the spatial variation in abundance or in other ecological parameters such as aggregation of individuals or habitat preference within the range, and then spatial patterns may be discerned. However, ecological biogeographers tend to explain distribution patterns with ecological processes, while historical biogeographers consider unique phylogenetic and distributional histories as the cause of the patterns.

Figure 2 shows that this could also be a fertile area for palaeontologists, zooarchaelogists and paleoecologists. They use historical data (fossils, subfossils, ancient DNA) to study the past distribution of extant species, detecting (inducing) patterns and evolutionary processes that produce the patterns. Here we temporarily call this unique study area “evolutionary biogeography”. Data from fossils and subfossils must be treated with caution because of possible evolutionary changes and biases in preservation (Enquist, 1995). However, this kind of possible taphonomic bias have been so exaggerated that ecologists, biogeographers and even paleontologists themselves have doubts about the value of data from fossilized individuals, populations and communities. Our study shows that patterns detected by analysis of fossil and subfossil data can be tested by ecologists and historical biogeographers using current data. This is another evidence that fossils and subfossils can provide reasonably accurate information for the analysis of Arealsystems. But it must be here pointed out that evoltionary biogeography is not historical biogeography. Historical biogeographers use current data, not historical data to deduce the history of place, history of lineage and historical processes that have produced the patterns of distribution, although the historical processes found by historical biogeographers may be the same as the evolutionary processes identified by evolutionary biogeographers. Evolutionary biogeography is also not paleobiogeography, for its main focus is on the past distribution of extant species within a relative short period of time (of the last 40,000 years, essentially the limits of radiocarbon dating). How fossil and subfossil data could be used to study the evolution of Arealsystems will be explained in the next section.

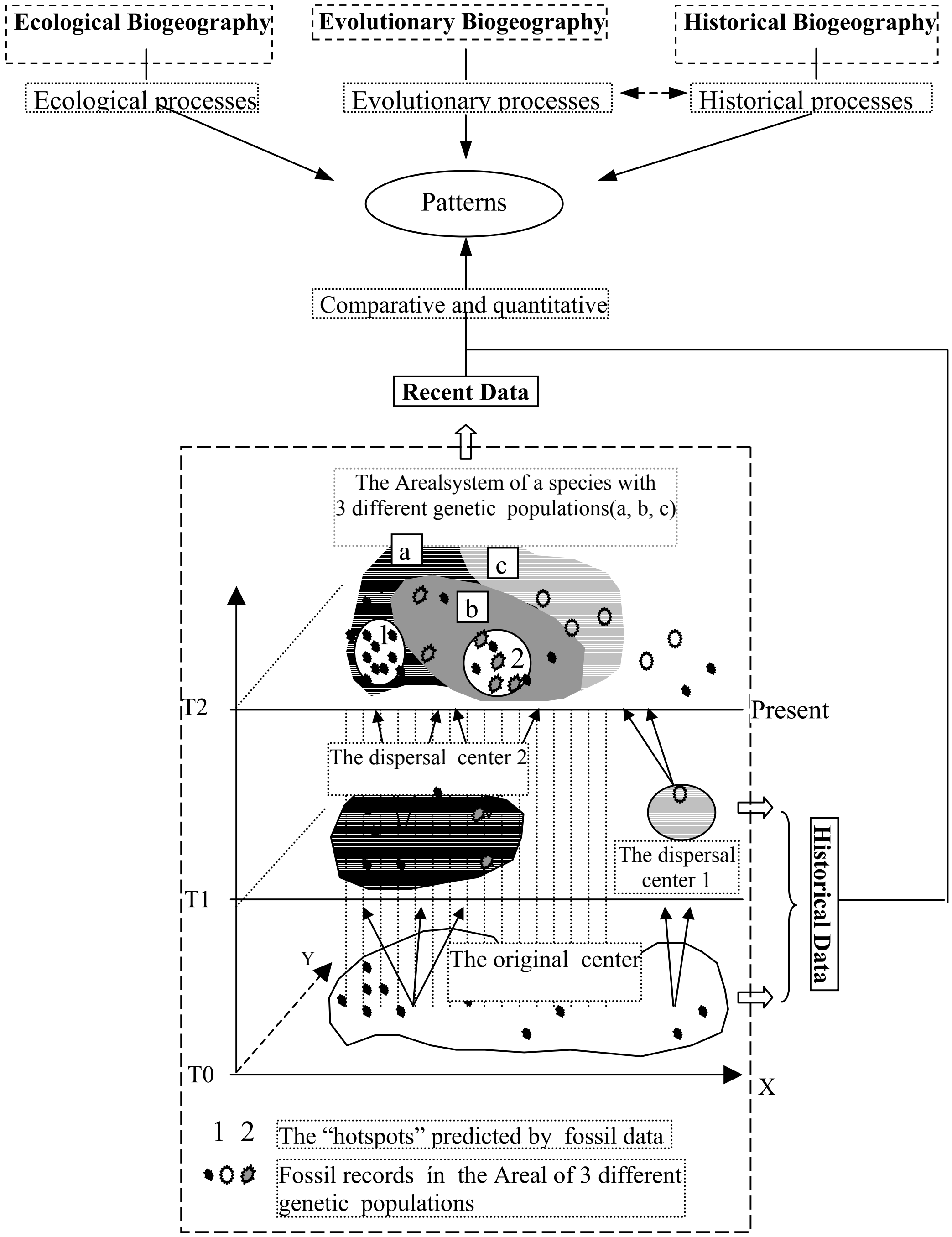


Fig. 1 The model of a synthetic (spatial and temporal) analysis of Arealsystem of a species, showing the evolutionary process of the Arealsystem, which may be revealed by comparative and quantitative analysis of historical data.

The theories about the evolution of Arealsystems have been proposed by De Lattin (1957,1959, 1967) and further advanced by Mueller, P. (1972, 1973, 1981), which can be briefly shown in Fig. 1. The original center in period T0 was split into two dispersal centers in period T1, which can be indicated by the past distribution of fossil records in period T0 and T1 separately. This also expresses Mueller's idea that the centre of origin can become widely separated from the centre of dispersal (Mueller, 1972). The current Areal is plesiochor to dispersal centre 1 and the original centre, but is apochor to dispersal centre 2. It also shows that the “hot spots” within the range could be predicted by fossil records. The ancient DNA abstracted from fossils and subfossils can play an important role in the future population genetics. The difficulty of identification of fragmental fossil and subfossil materials will be solved to some extent by the analysis of ancient DNA, which will in turn facilitate the study of the relationship between different genetic populations.

Considering the long history of biogeography and the central place of the Arealsystem in biogeography, it is surprizing that most comparative and quantitative studies of the characteristics of ranges have been done within the last 25 years (Brown, 1995). Such studies have been greatly facilitated by advances in computer technology: scanners, digitizers, GIS, large computerized database and advances in mathematical and simulation modeling. However, the studies of the evolution of Arealsystems are still in their theory stage. Ecologists and biogeographers can study the temporal changes of Areals only for a short period. Most standardized biological surveys (e.g. the North American Breeding Bird Survey and Butter Survey) can provide detailed data for, at maximum, the past 20 years. This has prevented ecologists and biogeographers from the practical study of the evolution of Arealsystems. In this dissertation we will show that a great advance could be made by implication of large paleontological database.

1. 3 THE EVOLUTION OF AREALSYSTEMS

The Arealsystem of a species has its own shape, size, location, and boundary. But when did the current shape, size, location, and boundary of the Areal come into being? The human acitivities have large effects on the current Areals of many species. So their current Areals may not reflect their natural distributions. What are their natural primitive distributions? Or how greatly have human activities changed their distributions? How did Areals respond to climate change, for example, the current global warming? Each species may have its own unique answer, or for many species there exists a common pattern. The study of the evolution or history of Arealsystems can give us answers. From the questions that it can answer we can already perceive the practical and theoretical significance of the study.

The evolution of Arealsystem concerns the origin (the original center), development (expansion from the original or dispersal center), formation (in a relatively stable stage), dynamics (shift, contract or vanish) of Areals, which can be in a natural process or under human influences.

Over the last two centuries, a lot of fossil records of mammals have been collected. Mammal fossils are one of the best materials to document the evolutionary process of Arealsystems. Pollen can be transmited by wind widely from one area to another area. So the location in which fossil pollen were found may not be the location where the represented plants lived. Taphonomic studies show, however, that mammal remains that are of high socioeconomic value to humans may have been transported more than 20 km away, whereas mammal remains of low socioeconomic value have probably not been transported far (<5km) (Lyman, 1995). These deviations are not significant and thus could be ignored. The locations where mammal fossils were found could well present their past distribution. The principle of how fossil records can reveal the evolution of Arealsystems has been showed in Fig 1. Each record has it own dates (relative or absolute). With the functions of GIS, fossil records in past periods T0 and T1 can be seperated from those of period T2 (present). Then the past distribution of the species in periods T0, T1 and T2 can be reconstructed. The preconditions of exact reconstruction of past distribution are: First, fossil records must be plenty enough in time and space to document the changes. Second, fossil records must have relative exact dates. Comparing the past distributions in the different periods, the origin, development and dynamics of the Arealsystem will clearly be shown.

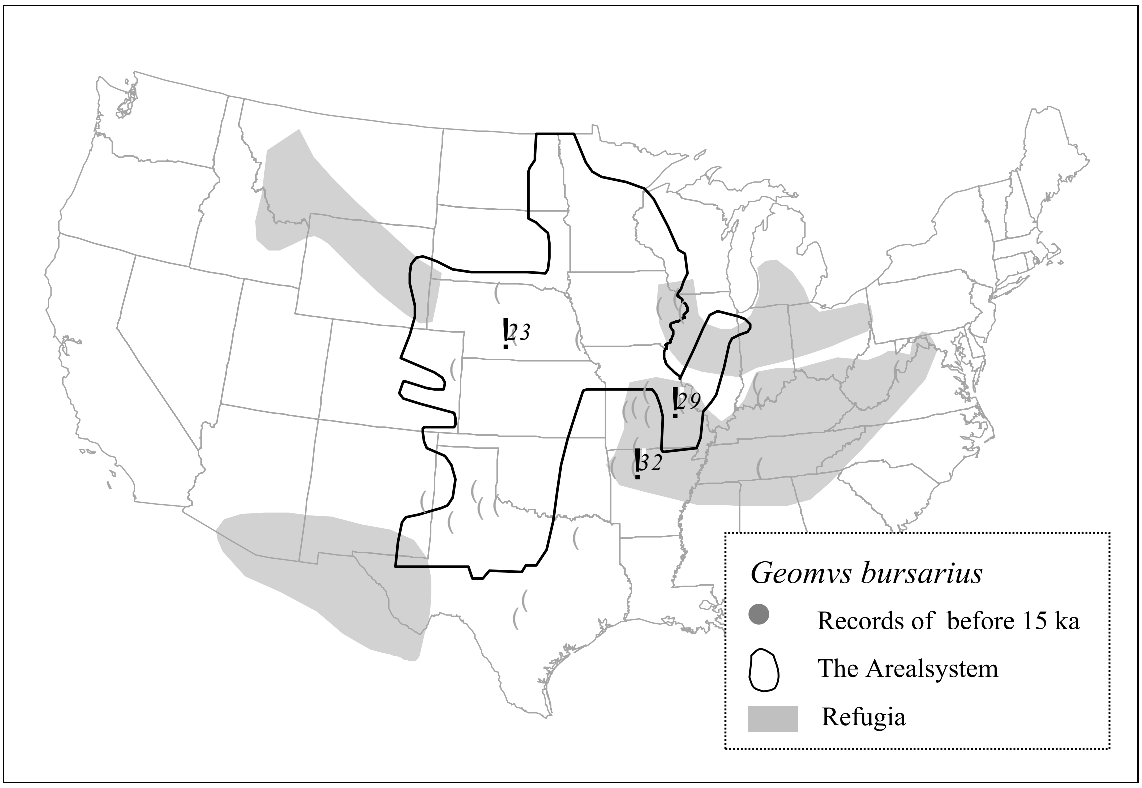


Fig. 2 The Past Distribution of Geomys bursarius before 15 ka

By the analysis of over 70 species (with records more than 100) it is found that the evolutionary process of Arealsystems can be divided into 6 stages. This process of many mammals will be described in detail later. Here we take the evolution of the Arealsystem of *Geomys bursarius* for example:

Refugium stage: before 15 ka, many species distributed only or mainly in refugium or dispersal centres. Comparing to its current Areal, the past distribution of *Geomys bursarius* in this stage was more easterly and southerly, mainly living in the Appalachia Center (Fig. 2, this will be discussed in next chapter). The numbers in the squares are the records with the highest MNIs of this period, which reflect the “hot spots” of this period (this will be discussed in chapter 3).

Dispersal stage: From 15 ka to about 8 ka, as it became warm and the ice sheet receded, most species started to migrated from their refugium to other areas in different directions, northward, southward, eastward or westward. The ranges of most species expanded and was often much larger than that in the former stage. Many species might still live in their refugia, while others might have disappeared from their refugia or some parts of their refugia. The gray arrow in Fig. 3 shows the dispersal direction of Plain Pocket Gopher, while the white arrow shows it disappeared gradually from Appalachia Centre. But the positions with the highest MNIs in this stage did not change a lot from before.

Developing stage: From about 8000 years ago to about 3000 years ago, the shape, size, location and boundary of most Areals had become very similar to that of the current ranges. From Fig. 4 it can be seen that Plain Pocket Gopher had dissapeared from the eastern area of its refugium, and expanded northwards further. As it migrated northward, the hot spots might start to appear in the northern part of its range.

Transitional stage: From 3000 years ago to 1000 years ago, the shape, size, location and boundary may not change a lot from that of the developing stage, but internal structure within the ranges of many species could change significantly. For example, the hot spots of many species might shift from one area to another. The white arrow in Fig. 4, 5 shows the shift of hot spots from its original area to new northerly area.

Primitive stage: From 1000 years ago to 500 years ago, the ranges in this stage may reflect the natural distributions of many species. Not only the shape, location, boundary but also the internal structure of most species ranges might be the same as that of the next stage, and the size often reached its maximum in this stage, when their ranges were not altered by human activities.

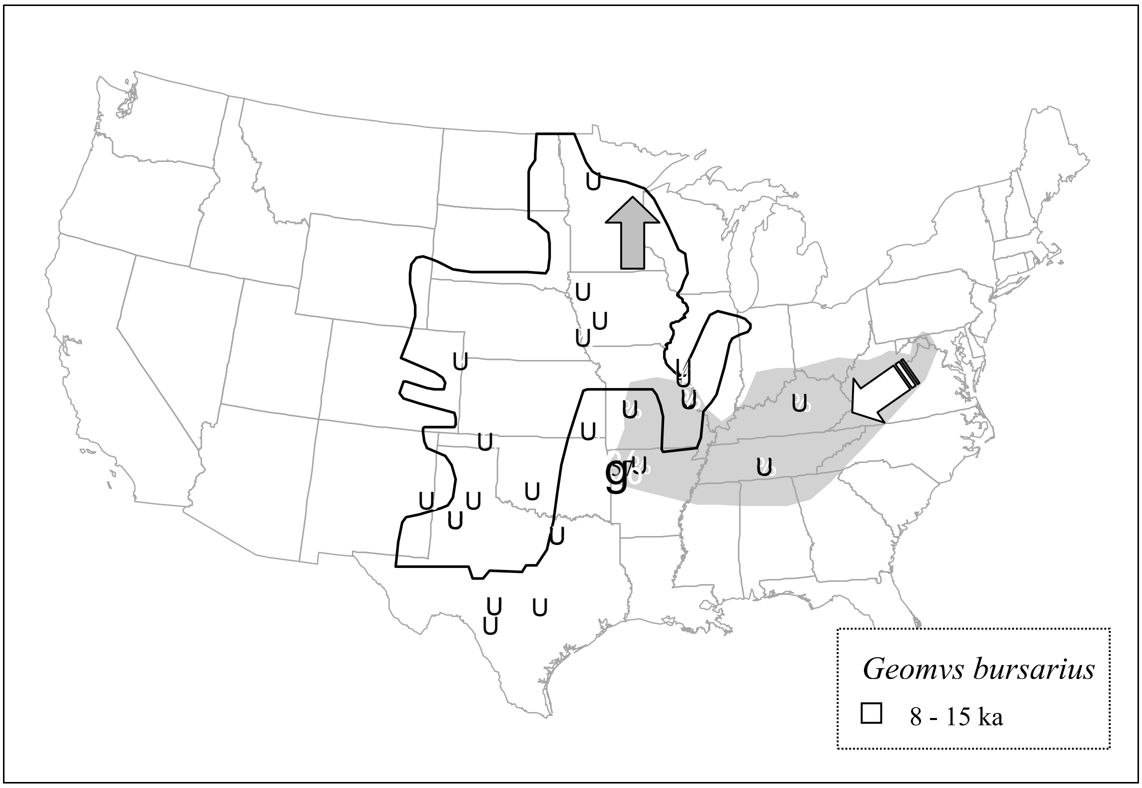


Fig. 3 The Past Distribution of *Geomys bursarius* during 8 – 15 ka

Human disturbing stage: The last 500 years. For many species, their ranges may have not any changes from the premitive stage. But for many other species, their Areals may be changed in their boundaries, shapes, sizes and even internal structures due to the influences of human activities. For these species, the current range may not reflect their natural distribution, which can only be found in the primitive stage. This should be paid attention to when man watches the Areal of a species. Comparing the natural distribution of *Geomys bursarius* during 0,5 – 1 ka with its current Areal, it can be found that intensive land uses have caused a large contract of its primitive range (the gray arrows in Fig. 5 shows where the contract happend and their directions). However, these may have not changed its internal structures. The northwestern Iowa may be this gopher's hot spot (where had the highest MNIs of 331).

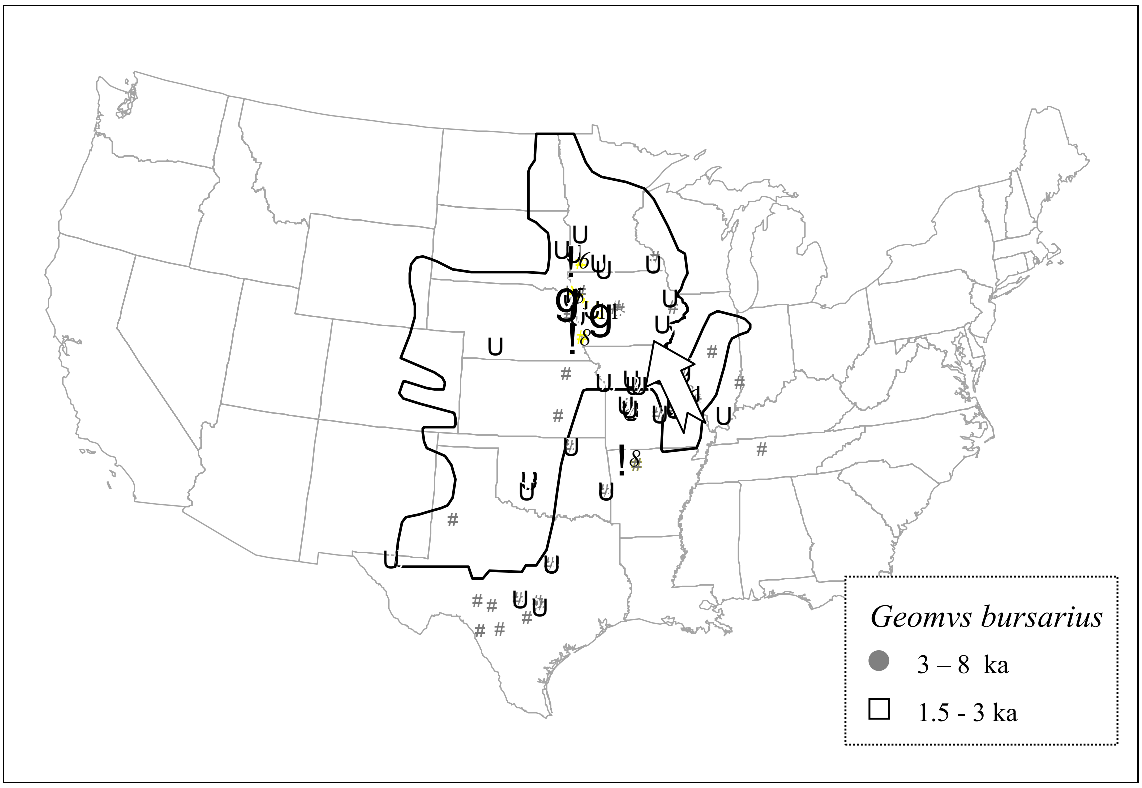


Fig. 4 The Past Distribution of *Geomys bursarius* during 8 ka and 1.5 ka

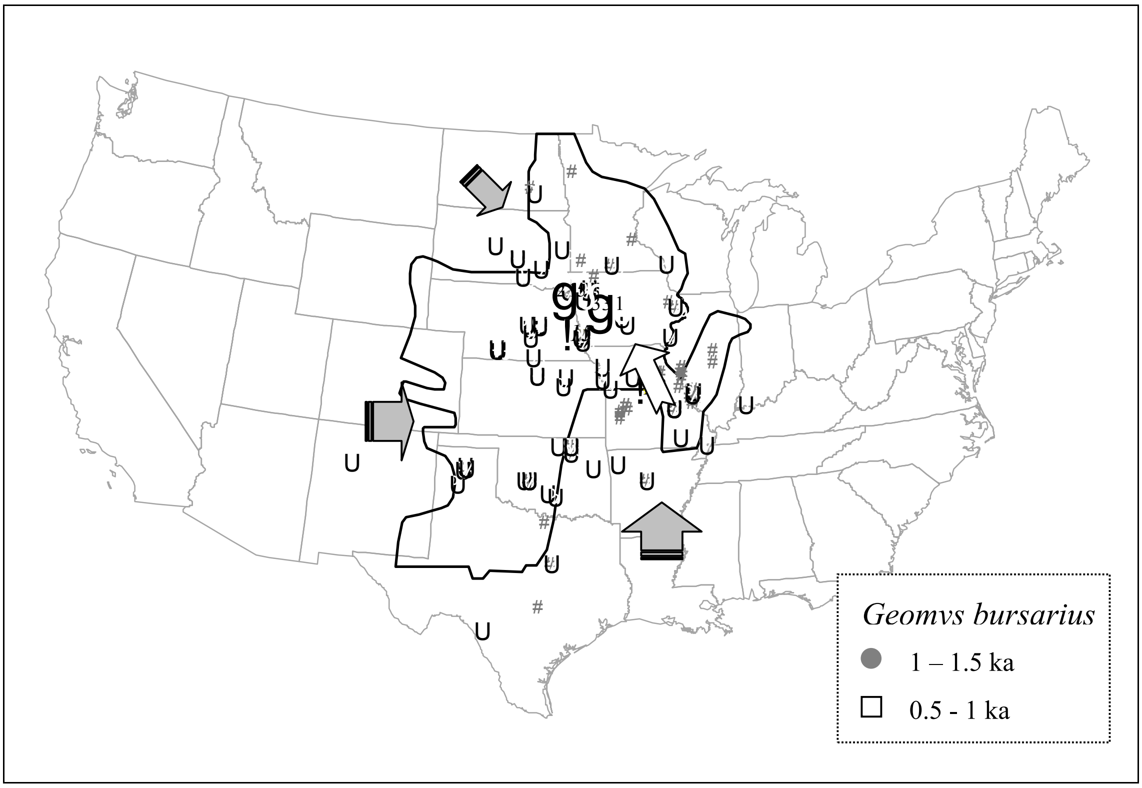


Fig. 5 The Past Distribution of *Geomys bursarius* during 1 – 1,5 ka and 0,5 – 1 ka

1. 4 MATERIAL AND METHOD: FAUNMAP

In this section we will check which information a fossil record contains, and introduce Faunmap, containing all fossil and subfossil data used in this work. Some important fields will be explained here.

Faunmap is an electronic database documenting the late Quaternary distribution of mammal species in the United States. It has been developed at the Illinois State Museum (ISM), co-directed by Dr. Russell W. Graham, formally of ISM and now at the Denver Museum of Natural History, and Dr. Ernest L. Lundelius, Jr. from the University of Texas at Austin. Data have been derived from scientific literature, including selected theses and contract reports published from 1860 to 1994. All references have been recorded in an electronic bibliography with more than 2500 citations. A network of 14 Regional Collaborators have assisted with data selection and validation. The building of this database had taken them 4 years. The primary purpose of this database is to investigate the evolution of mammalian communities. Specifically, with statistical techniques and mapping capabilities of a Geographic Information System (GIS), changes in the distributions of individual species and their effects upon mammal community composition can be documented for the late Quaternary. Understanding these processes will also facilitate paleoenvironmental reconstructions.

But analysis of Faunmap has not been fully explored. Two explanatory volumes have been published. The first volume describes the database structure, lists locality data for each site, and provides a bibliography of data sources. The second volume provides a systematic list of taxa, maps of site locations for seven time periods, and Late Quaternary distribution maps of selected mammal species (modern and extinct)(Faunmap Working Group, 1994a, b). The Faunmap has only been used to assess the evolution of mammalian communities in fluctuating environments. Maps illustrating changes in distributions of individual species document an individualistic response with species migrating in different directions, at different rates, and at different times (Graham, 1997).

Faunmap includes information on site names and numbers, locations, relative and absolute chronologies, cultural associations, depositional systems, taphonomic attributes, and mammal species from each site. It consists of Archival Database, Research Database and Lookup files. The Archival Database for Faunmap contains data derived directedly from the scientific literature with a minimal amount of change. Before these data could be used for any type of analysis, it was essential to create a Research Database, which would standardize taxonomy, establish a chronological framework, eliminate intrusive taxa, and remove temporally mixed faunal assemblage. In developing the Research Database, the Archival Database was passed through a filter of decision-making processes that can introduce various subjective biases. It woul be emphasized that the original data is preserved in the Archival Database, which can be used to create other Reseach Database (Fig. 6).

The Lookup files are tables used to define the codes in the database. For example, L_Bmodi is used to define the codes of bone modification in Faunal Table and Modification Table (Tab. 1.), and L_Prec is used to define the codes of precision in the Locality Table (Tab. 2.)

Archival Database: 10 Tables

LOCALITY Tatabase: 2937 records, and 17 fields:

Machine#	Site Name	Alternate Name	County	State/Province	Site#	Coded by	Date coded

Comment	Coding Update	Quadrangle	Precision	Quad Size	Latitude	Longitude	Altitude

Repository

Of 17 fields Precision has a lookup table (L_Prec), and Repository (L_Repos). Sites were subdivided into “Analysis Unit”, the smallest components of a site (e.g. excavation levels, microstratigraphy, cultural components, etc.), as defined in the published accounts.

ABSOLUTE Table: 4953 records and 12 fields:

Machine#	Analysis Unit	Age ID	Asociated Date	Standard Deviatin	Dating Method

Material Type	Lab	Date Position	Confidence	Rank	Taxon

And Dating Method, Material Type, Date Position have lookup tables of L_Abmeth, L_Matter L_Posdt and L_Confi respectively.

AGENT Table: 5353 records and 4 fields:

Machine#	Analysis Unit	Agent#	Agent

Agent has a lookup table (L_Agent).

AGE Table: 4953 records and 12 fields:

Machine#	Analysis Unit	Period	Epoch	Age	Land/Mammal Age	Oxygen isotope

Magnetochron	Minimum age	Min. age method	Maximum age	Max. age method

It has the following Lookup Tables: Period, L_Period, Epoch, L_Epoch, Age, L_Age, Min. age method, L_Methdt, Max. age method, L_Methdt.

COMMENT Table: 907 records and 5 fields:

Machine#	Analysis Unit	Taxon	Line#	Comment

CULTURE Table: 3920 records and 4 fields:

Machine#	Analysis Unit	Culture ID	Cultural Age

DEPOSIT Table: 4821 records and 7 fields:

Machine#	Analysis Unit	Recovery Method	Depositional System	Depositional environ	Facies	Mixing

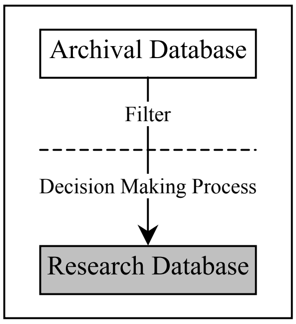


Fig. 6 The relationship between the Archival and the Research databases

Precision	Definition
QA	Quadrangle Approx.
QP	Quadrangle Precise
QC	Quadrangle County
E	Exact

Tab. 1 The Lookup Table of Precision (L_Prec.)

Bone modification	Definition
IM	Impact marks
SF	Spiral fracture
TF	Transverse fracture
LF	Longitudinal fracture
PO	Polish
BN	Burned
RG	Rodent gnawed
CG	Carnivore gnawed
W0	Weathered
W1	Weathering stage 1
W2	Weathering stage 2
W3	Weathering stage 3
W4	Weathering stage 4
W5	Weathering stage 5
AB	Abraded
MN	Mineralized
RE	Root etched
ET	Etched
PT	Pitted
FL	Flaked
ST	Striations
SM	Slice marks
SS	Scrape striations
SA	Shallow abrasions
HB	Human butchering
TP	Tooth punctures
DE	Decorated
BC	Bone color
PH	Pathology
AE	Artifact embedded
BT	Bone Tool
TM	Trampling

Tab. 2 The Lookup Table of Bone Modification (L_Bmodi)

The following fields have Lookup tables: Recovery Method, L_Recov; Depositional System, L_Desys; Depositional environ, L_Deen; Facies, L_Facies.

FAUNAL Table: 43851 records and 8 fields:

Machine#	Analysis Unit	Taxon id	ID confidence	MNI	NISP	Context	Modification

MNI is the Minimum Nmber of Individual, whose ecological meanings will be discussed in detail later. NISP means Number of Identified Speciemen. Modification indicates if there are any marks on the bones. It could be seen from Table 1 that there are 32 kinds of modification, 4 of which (Burned (BN), Human butchering (HB), Decorated (DE), and Bone Tool (BT) are connected with human's activities.

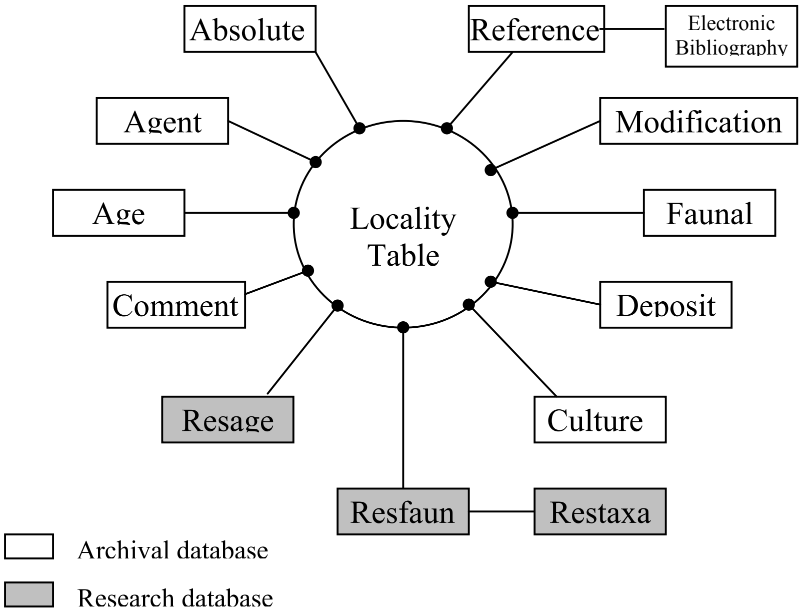


Fig. 7 The Structure of Faunmap (After Graham, 1994)

MODIFICATION Table: 2829 records and 4 fields:

Machine#	Analysis Unit	Modif. #	Modification

REFERENCE Table: 4270 records and 6 fields:

Machine#	Reference#	Bibnum	UID	Author	Year

Research Database: 3 Tables

RESAGE Table: 4953 records and11 fields:

Machine#	Analysis Unit	Site Name	State/Province	Epoch	Age	Minimum Age	Maximum Age	Resage	Rio	Site Type

RESFAUN Table: 43851 records and 9 fields:

Machine#	Analysis Unit	Taxon id	ID confidence	MNI	NISP	Context	Modification	Rio

RESTAXA Table: 704 records and 4 fields:

Taxon id	Research id	Revised Name	Common Name

Revised Name was defined by L_Taxa.

Figure 7 describes the relationship between Paradox Tables in the Faunmap Database. The Locality Table is the master table, and the Locality Machine Number (MN) relates all other tables to it. Lines connecting boxes to the central circle represent this relationship. Each table can stand-alone or they can be related to any other table by Machine Number (MN) and Analysis Unit (AU). Lines along the circle connecting the nodes joining the tables to the circle represent the relationships between tables. The Reference Table is related to the Electronic Bibliography by BIBNUM and the Restaxa Table is related to the Resfaun Table by the Taxon Id code(TID).

1. 5 THE REQUIREMENTS OF FOSSIL AND SUBFOSSIL DATA FOR THEIR IMPLICATION IN BIOGEOGRAPHY

As mentioned above, to document the past distributions, fossil and subfossil data must satified some requirements: The locations in which fossils and subfossils were found could well reflect where the represented organisms lived; Plenty enough in time and space; Relatively exact dates; Correct identified. Here it will be shown that the data contained in Faunmap satifies well all of these requirements.

Faunmap contains data captured from 2919 well-dated paleontological and archaeological sites that contain mammalian remains (Fig. 8). From Fig. 8 it can be seen that these sites are relatively even distributed in most of the contiguous 48 states of USA except in North Carolina, South Carolina and Mississippi. This will ensure that the spatial pattern detected in the analysis may not be caused by sample errors. Fig. 9 shows the temporal distribution of all fossil records in Faunmap, with focus on sites during the last 40,000 years, i.e., 40 ka, or essentially the limits of radiocarbon dating. It can be seen from the curve that before 15 ka the number of fossil records found is very low and fluctuates irregularly, with an unusual high during 22-23 ka. Another unusual high number of fossil records can be found during 6-7 ka. However, the temporal distribution pattern has been showed in the curve: the more recent, the higher the number of fossil records found. The temporal distribution of most species fits to this pattern.

This pattern may reflect overall that this species has a stable or a growing population size. There are a few species, whose temporal distribution does not fit to this pattern: with much higher number of fossil records found in the past, but only few records near recent. This may not be caused by the sample errors, but may indicate that they have a decreasing population size. This curve also decides the cut of time slices in the analysis: the last 500 year, 0,5 - 1 ka, 1 - 1,5 ka, 1,5 - 3 ka, 3 – 8 ka, 8 – 15 ka and over 15 ka. This will make sure that the number

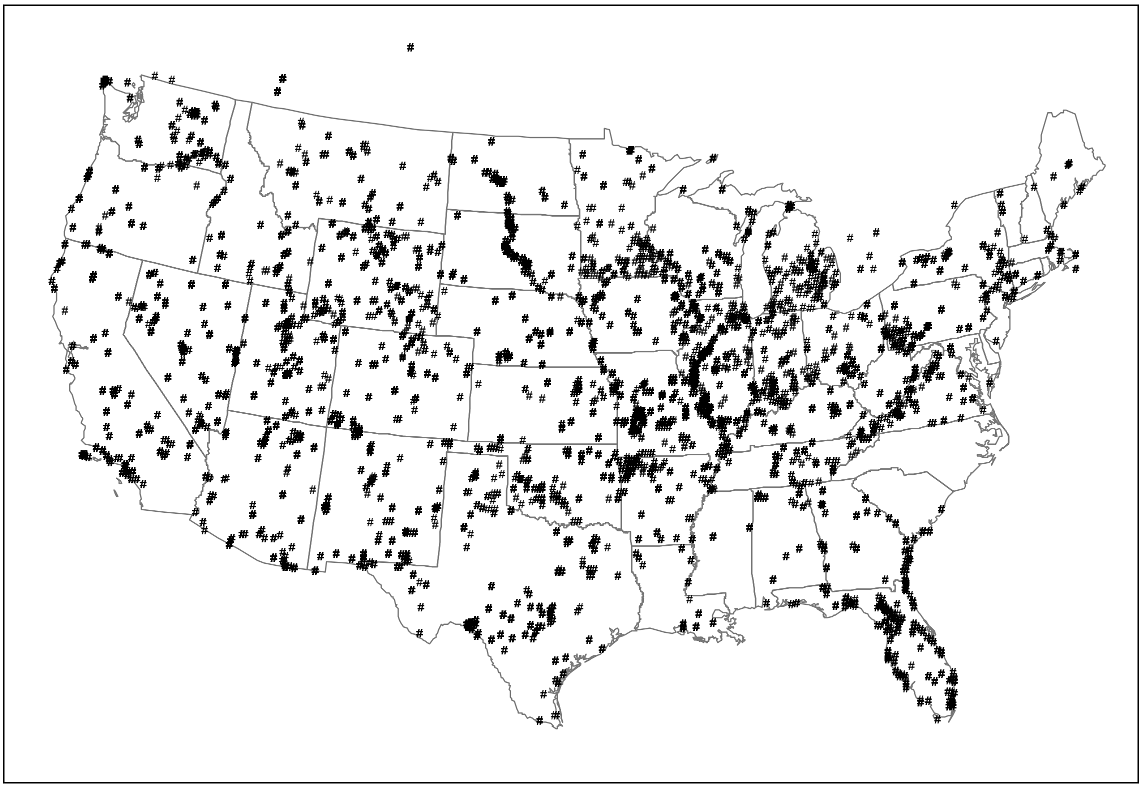


Fig. 8 The Distribution of all palaeontological and archaeological sites in Faunmap

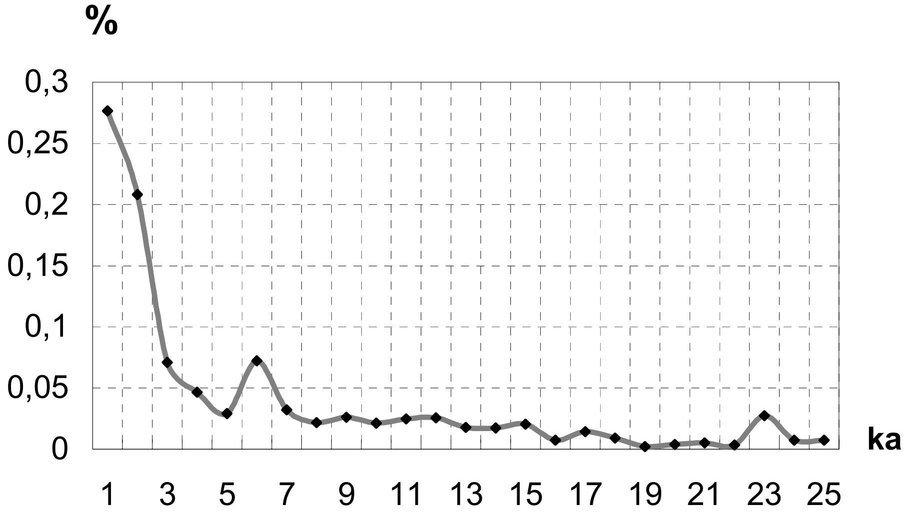


Fig. 9 The temporal distribution of all fossil records in Faunmap

of fossil and subfossil records falled equally into each time slice.

Only Research Database and LOCALITY Table were used in this analysis. From Archival Database to Research Database, American experts have made a filter of decision-making processes. But this will avoid decision-making by us, which may introduce more severe subject bias due to our limited expertise.

CHAPTER 2 GLACIAL REFUGIA AND DE LATTIN'S DISPERSAL CENTRES

2. 1 INTRODUCTION

The Last Glacial is the most recent geological event, which had a large effect on the distribution of flora and fauna. As the drop of temperature, the climate and vegetation zone were forced to shift southward, many mammals went either to extinct, or their Areals became significantly narrower, and in some cases fragmental. The famous Glacial Refugia Theory was proposed to explain the distributional changes. Glacial refugia are areas, which had warm climate due to its special geographical positions during the glacial time. They had often diverse ecological conditions, and thus could still provide suitable environment for the survival of many species. Much more species tended to concentrate in the glacial refugia than in other regions. As a result, glacial refugia can now be recongnized biogeographically by its richness in species and endemic species (De Lattin, 1967, p. 321).

The glacial refugia can be identified by the analysis of dispersal centre. Four glacial refugia had been recognized in North America: the American Pacific Refugium, the American Atlantic Refugium, the Mexico Refugium, and the Alaska Refugium (Reinig, 1937). The dispersal centres represent areas where fauna and flora were preserved during regressive phases (De Lattin, 1957, 1967), which can be worked out by plotting the breeding ranges of species and subspecies on a map of the region under investigation, the individual ranges overlap in "areas of congruence" or "nuclear areas". The regions where an unusually large number of ranges overlap were called dispersal centres. Sixteen dispersal centres had been identified in North America (De Lattin, 1957, 1967).

However, many people do not believe glacial refugia. Ecological or historical factors or both might have caused the richness in species and endemic species in a region. The dispersal centres worked out this way above may be or may not be the glacial refugium, because many species, especially the arctic apecies, do now no longer live in their refugia due to their long migration after the glacial time. Some considered that the dispersal centres may not be connected with the glacial time or even with the Pleistocene (Mueller, 1973). In addition, the distributional data used by De Lattin might be very different from the most current data (Wilson, 1993). This may be caused by the changes of taxonomic status, the distributional changes of the last 50 years due to human activities, or the inexact distributional data that was used. So it is necessary to examine these dispersal centres in North America by using the most current distributional data. In fact, the dispersal centres identified by De Lattin in Europe have been further tested by analysis of genetic population structures (see Schmitt, 2002 and references therein).

Fossil data may be one of the best materials to test the glacial refugia theory and the dispersal centers. The principle is simple: If a region is considered to be a refugium for its abundance in species and endemic species, these species should have distributed purely in or primarily in this region during the glacial period, which could be identified by where their fossil records of this period left. If these species and endemic species also left their fossils purely or primarily in this region, it is definitely a refugium. If the fossil records of these species were found in other areas, the richness in species and endemic species in this region should be resulted from other ecolgical and historical factors.

In this chapter, by analysis of the fossil data of 479 species contained in the Faunmap database with ArcView 3.3, 7 glacial refugia are recognized in North America, some of which are the same or almost the same as the dispersal centres or refugia found by Reinig (1937) and De Lattin (1957, 1967). And many dispersal centres defined by De Lattin (1957, 1967) may not be refugia. Two new refugia are recongnized: the Great Lake and the Rocky Mountain Refugium.

1. 2 METHODS AND MATERIALS

In this section, the methods of using fossil data of the Faunmap database to detect glacial refugia will be introduced here by an example: Woodchuck (*Marmota monax*), and its refugium. *Marmota monax* is a large marmot. Its Areal extend from Alaska and British Columbia south to northern Idaho, east through most of southern Canada, and south to eastern Kansas, northern Alabama, and Virginia (Fig. 10b). The distribution of fossil records is almost the same as the Areal in North America, with only a few scattering out of the range in Montana, South Dakota and Nebraska (Fig. 10). Where did this marmot live during the glacial age? To answer this question, Fossil records older than 15 ka (mean age) were seperated from others, which concentrated only in the Appalachian area (Fig. 10a). This indicates that this marmot only lived in the Appalachia area of the glacial time. But this area cannot be called a glacial refugium unless other species have the same pattern.

The past distributions of 479 species (4742 records in total) before 15 ka overlapped each other with ArcView 3.3, and it is found that not only woodchuck but also about 21 other species distributed only in this area during this regressive period (See results and discussion). Many other species mainly distributed here with only a few records found in other areas, while others occurred here with only a few records in this area. Therefore this area was considered to be a glacial refugium, namely the Appalachia Refugium. Species with their fossil records during the glacial time only in one refugium are called monocentric species, and Species with their fossils in more than one refugium during the glacial time are called polycentric species.

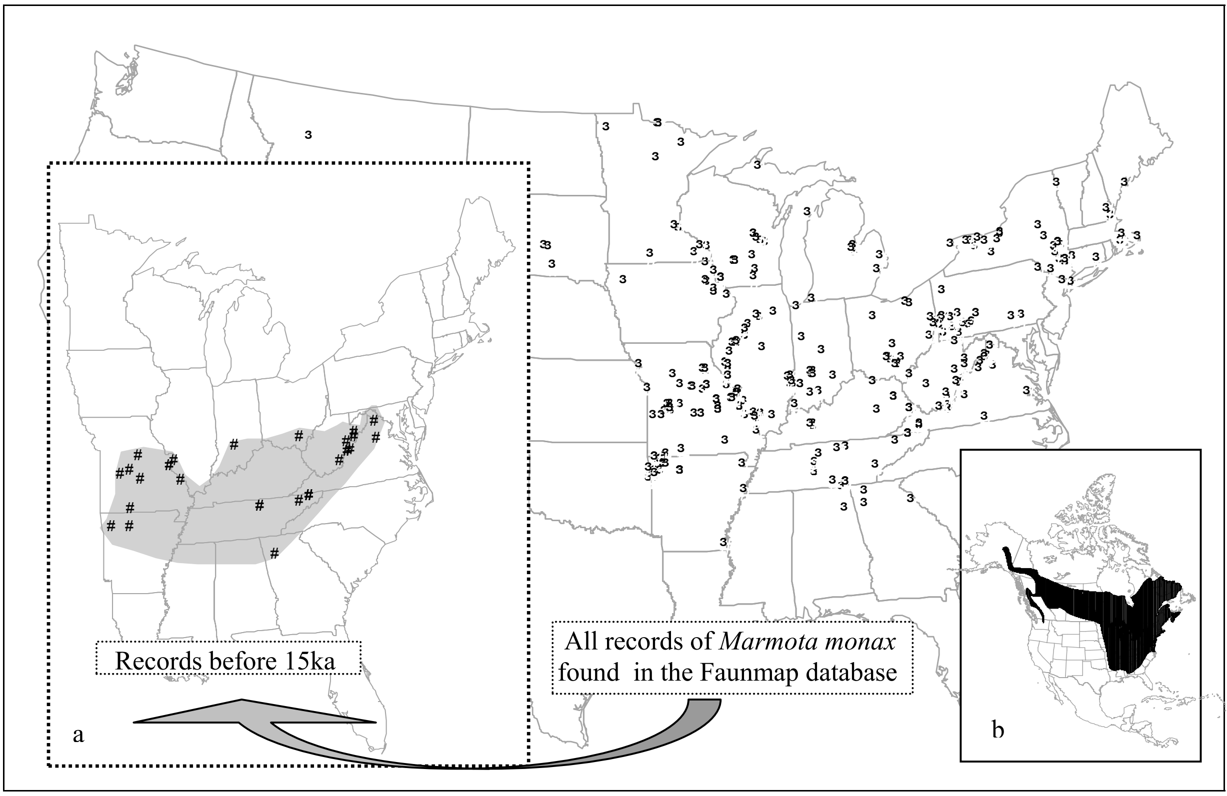


Fig. 10 The Methods of Using Fossil Data to Detect Glacial Refugium

Woodchunk's current Areal is plesichor to its refugium. This means that its current Areal still includes its refugium. But the current Areal of *Dicrostonyx hudsonius* is apochor to its refugium. Ungava Collared Lemming (*Dicrostonyx hudsonius*) distributes now only in Labrador and northern Quebec (Wilson, 1993). However it left its fossil only in the Appalachia Refugium during the glacial time. So its current Areal does no longer contain its refugium. It must be emphasized that refugia recongnized this way can be also well tested by the method of the analysis of dispersal centre, by overlapping some range maps of its monocentric species.

2. 3 RESULTS AND DISSCUSIONS

The results obtained through the methods above could be briefly presented in Fig. 2.

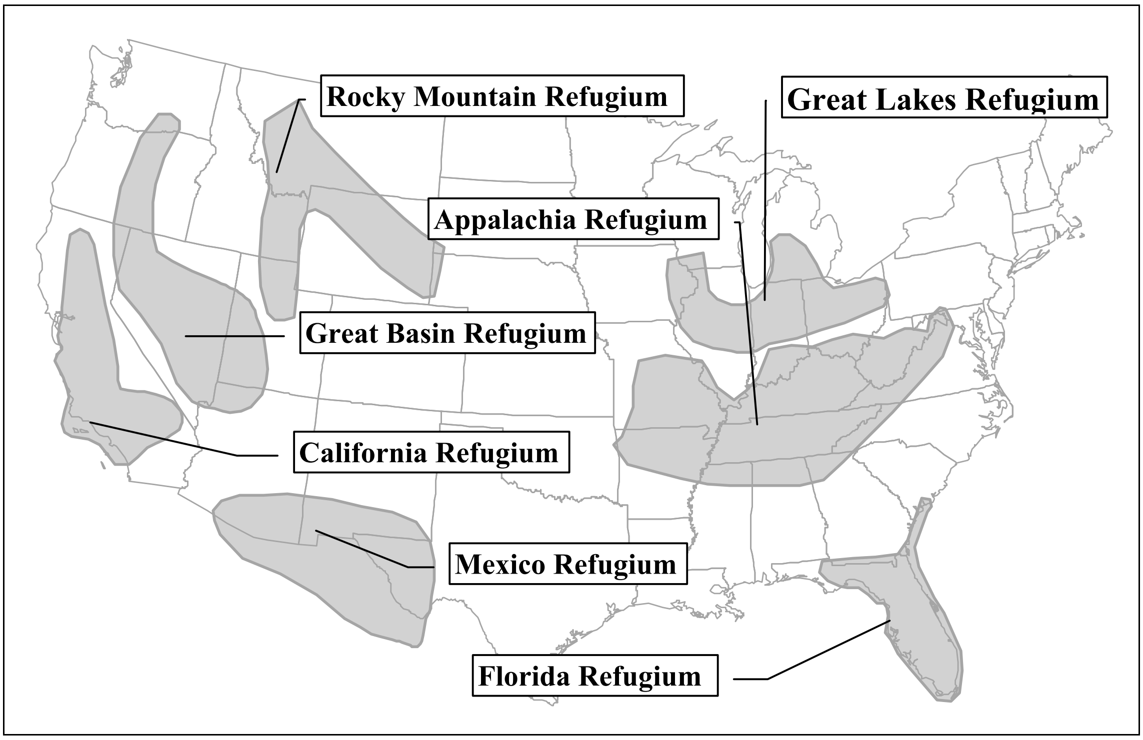


Fig. 11 The Refugia of the Last Glacial Time in North America

2. 3. 1 The California Refugium

The California Refugium can be delimitated by the past distribution (before 15 ka,)of *Sylvilagus bachmani*, *Neotoma fuscipes*, *Spermophilus beecheyi*, *Microtus californcus*, and *Scapanus latimanus* (Fig. 12). There are another 26 species (Tab. 3), which also only distributed in this area during this regressive period. It ranges from Shasta County south through the Great Valley to Los Angeles, including the Channel Islands, and east to the Mojave desert (Fig. 12).

California has the highest diversity in temperate North America and a high proportion of endemic species. For example, in the 411,000 km^2 it has 5046 species of native flora, 30% of which are endemic. It has primarily coniferous forests (27% of land area) in mountains and northern coast ranges, woodlands mainly Oaks (10% of land area) in drier inland areas in central California, Shrubland (Scrub and Chaparral, 12% of land) in cismontane southern California and Grassland (13%) in interior valleys and dry coastal foothills. 33% of the land is desert with from barren to open woodlands (Joel, 2002). The ecological requirements of these species also show that this area must have very diverse ecological conditions: from coniferous forests to woodland, from shrubland (chaparral and scrub) to grassland, from riparian sites to dry desert (Tab. 3). But paleovegetation data showed that it might be covered from 25 to 15 ka mainly by dry temperate woodland (Ray, 2001).

As the icesheet receded, these monocentric species seemed to have no response to the environmental changes. Many of them did not disperse northward to Oregon and Washinton till about 3 ka. Some of them might also migrated southward to Baja California and Sonora. Of the 31 species, 5 might have got extinct at the end of the Last Glacial time (16%). *Dipodomys heermani*, *Dipodomys ingens* and *Neotoma fuscipes* now become critically endangered, *Enhydra lutris*, *Ammospermophilus nelsoni* endangered (Data from Smithsonian National Musuem of Natural History).

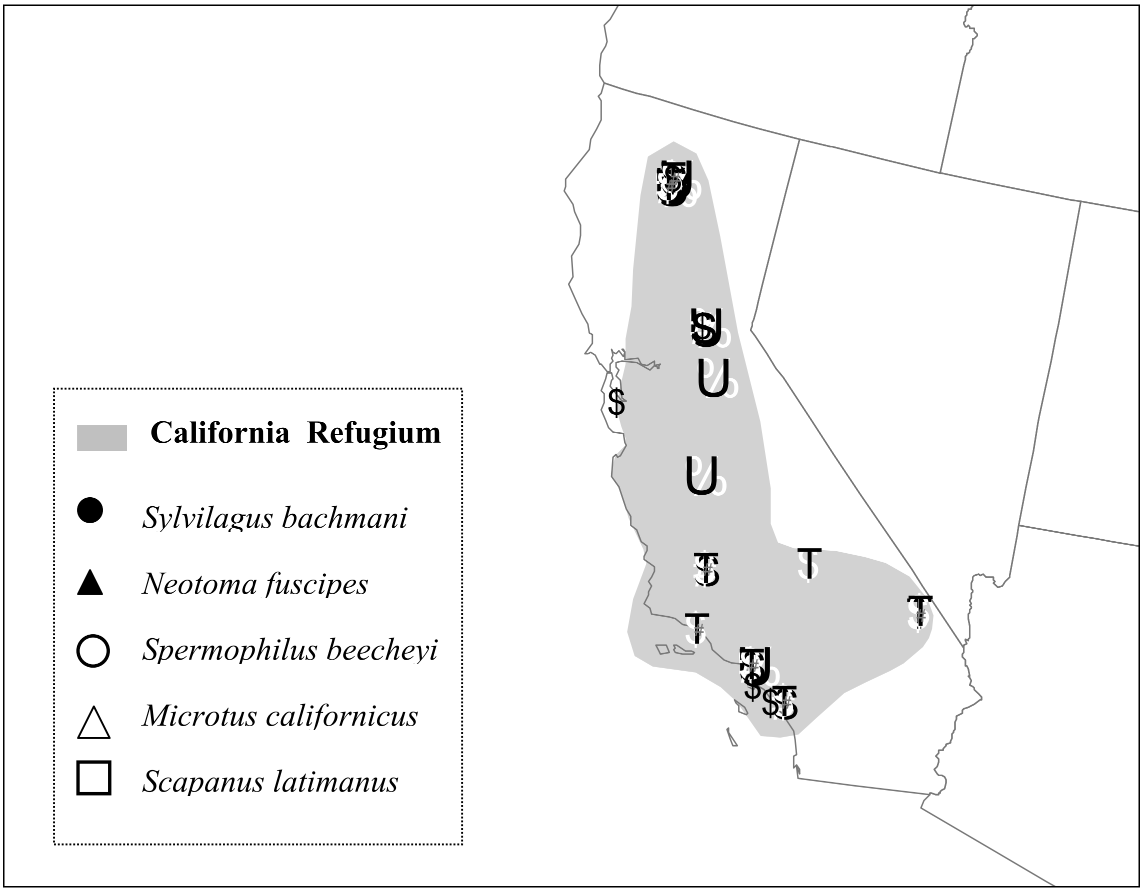


Fig. 12 The California Refugium and Some of Its Monocentric Species

De Lattin has recognized four dispersal centres in California (Lattin, 1967). First, the Californian Arboreal Centre, defined by *Neotoma fuscipes*, *Sylvilagus bachmani*, *Scapanus townsendii*, is located in the Great Valley of California. *Scapanus townsendii* now distributed from southwestern British Columbia (Canada) to California, but only in the northwestern corner. It might be that the distribution area cited by De Lattin was not yet exact, or the distribution of this mammal had contracted from central and southern California. No matter what it might maybe, the overlapping area of the 3 current Areals is now located in western Oregon, but not in the Great Valley of California. Second, the California Eremic Centre, defined by the overlapping area of *Spermophilus nelsoni* (=*Ammospermophilus nelsoni*), *Spermophilus beecheyi* and *Perognathus inornatus*, is located in the South of Great Valley.

It could be very difficulty to distinguish an eremic area from an arboreal one. Fossils of both dispersal centres were found from the same sites. For example, Fossils of *Perognathus inornatus*, *Ammospermophilus nelsoni*, *Spermophilus beecheyi* and *Sylvilagus bachmani* were

Species	Ecological Requirements
Aplodontia rufa	Dense, riparian-deciduous forests
Dipodomys heermanni	Chaparral, coastal scrub, woodland
Hemiauchenia blancoensis	Extinct
Microtous californicus	Dense annual grassland, wet meadow
Myotis yumanensis	Open forests and woodland with sources of water
Neotoma fuscipes	Chaparral, Conifer and hardwood forests
Peromyscus californicus	Chaparal, Coastal scrub, hardwood
Scapanus latimanus	Annual and perennial grassland, wet meadow, open forests
Sciurus griseus	Conifer, hardwood and mixed
Sorex bendirii	Marshes and streamsides, moist forests
Sorex tenellus	Riparian sites in sagebrush scrub, pinyon-juniper
Sorex trowbridgii	Mature coniferous forests of the Pacific Coast, hardwood
Spermophilus beecheyi	0pen rocky aera or sparsely woodeded field
Spermophilus mohavensis	Open desert scrub, alkali desert scrub and Joshua tree
Sylvilagus bachmani	Thick, brushy areas
Tamias panamintinus	Rocky areas in pinyon-juniper and Juniper
Tamiasciurus douglasii	Primarily coniferous forests, hardwood-conifer, and riparian
Thomomys microden	Extinct
Thomomys monticola	Alpine dwarf-shrub, perennial grassland and wet meadow
Ammospermophilus nelsoni	Dry alkali scrub, loam soils with annual grassses
Chaetodipus californicus	Coastal sage scrub, chaparral, grassland, hardwood
Dipodomys agilis	Coastal sage scrub, open chaparral, conifer woodlands
Dipodomys ingens	Fine sandy loam soils supporting sparse annual vegetation
Enhydra lutris	Sea Otter
Perognathus inornatus	Dry, open grasslands or scrub areas on fine-texured soils
Peromyscus imperfectus	Extinct
Peromyscus nesodytes	Extinct
Sorex ornatus	Woodland, chaparral, montane riparian
Tamias merriami	Chaparral, hardwood, coniferous habitats
Tapirus californicus	Extinct
Urocyon littoralis	Mixed chaparral, coastal scrub

Tab. 3 The Monocentric Species of California Centre

found in Mckittrick of Elk Hills at the southern end of the Great Valley, in which *Peromyscus californicus*, *Sorex bendirri* also occured. However, over 1/3 of its monocentric species left their fossils only in the Southern California Coast, the Transverse Ranges and the southern end of the Great Valley (Fig. 13). The ecological requirements of these species are mainly coastal sagebrush, chaparral and dry woodland. Furthermore, these species seemed to have lost their ablilities to migrate. Their current Areals had not expanded a lot from their past distribution of this period. In turn, some ranges had since then even contracted. Of the 12 elements, three got extinct (25%). The elements of this area contain *Ammospermophilus nelsoni* and *Perognathus inornatus*, so it may correspond to De Lattin's California Eremic Centre. But evidences are not at present strong enough to seperate it as another refugium. It may represent a subregion of the California Refugium especially for animals preferring xerophytic crub habitat.

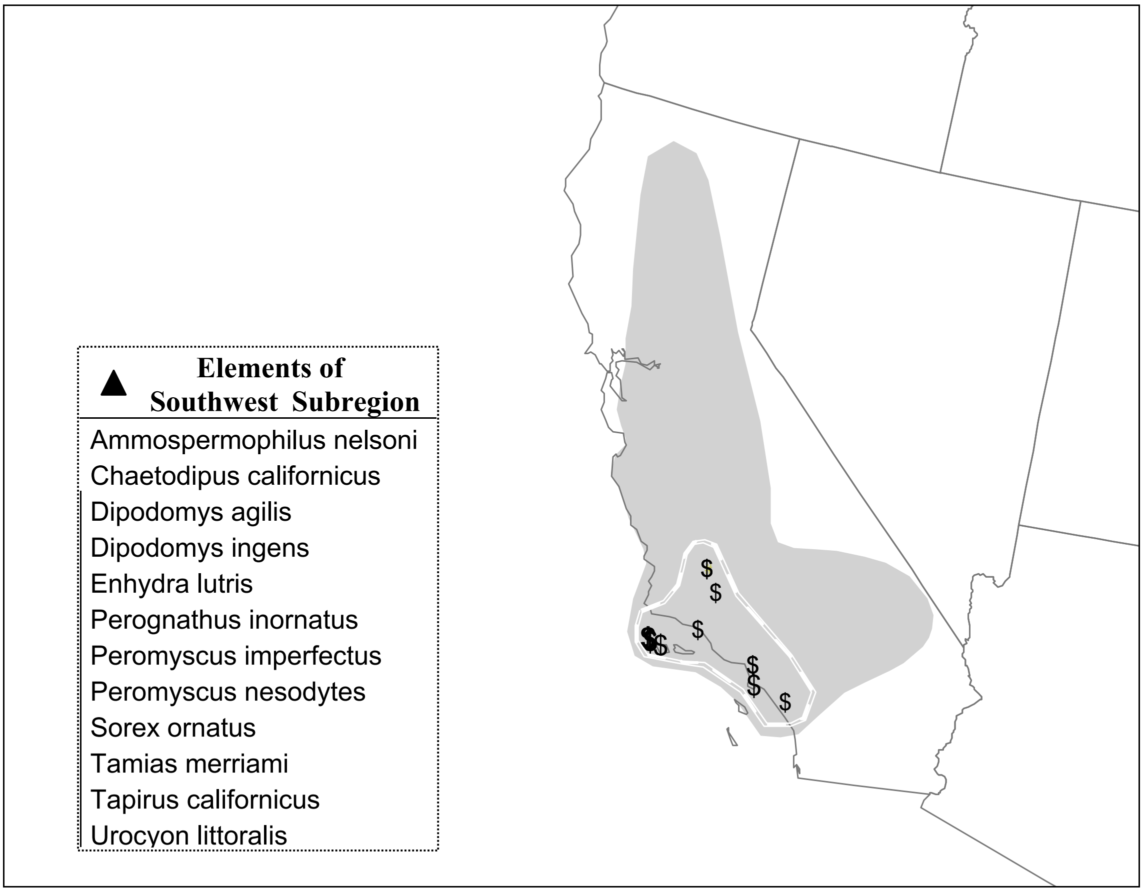


Fig. 13 The subregion of California Refugium and their elements

The third is the Mohave Eremic Centre, defined by *Spermophilus mohavensis*, *Spermophilus tereticaudus*, *Perognathus fallax* (= *Chaetodipus fallax*, reviewed by Huey, 1964) and *Perognathus spinatus* (=*Chaetodipus spinatus*, Lackey, 1991). The overlapping area of these species should be in the Mojave and Colorado Desert, according to De Lattin's data, but the nuclear area of the 4 current Areals now is a very small area and only in the Mojave Desert.

Unfortunately, only *Spermophilus mohavensis* had left its fossil remains, the other three had no fossil records. *Sorex tenelus*, *Hemiauchenia blancoensis* (extinct) and *Tamias panamintinus* also left their fossil records only in this small area before 15 ka. *Sorex tenelus* preferred Riparian sites in sagebrush scrub, pinyon-juniper, and deciduous and aspen habitats. *Tamias panamintinus* resides in rocky outcrops in pinyon-juniper and juniper habitats, which disappeared now from this dry dessert (Wilson, 1993). This indicates that woodlands had once dominated this area, and it was a little more humid than at present. *Sylvilagus bachmani* once occurred also in this area. At present it might be difficult to distinguish Mohave Eremic Centre from California Refugium.

The fourth is Gila Eremic Centre, defined by *Perognathus intermedius* (=*Chaetodipus intermedius*), *Perognathus penicillatus* (=*Chaetodipus penicillatus* Hoffmeister and Lee, 1967) and *Dipodomys deserti*. The congruent area of these 3 species is located in Sonoran (Gila) desert, according to the data cited by De Lattin. But the overlapping area of their current Areals is in the Southwest of Arizona. The first one left 2 records, which were found far from their overlapping area. The last 2 had no fossil records. In SW Arizona and the Sonoran desert no other speiceis had left their fossil records. So this centre might not be a refugium.

2. 3. 2 The Mexico Refugium

The Mexico Refugium can be delimitated by the fossil records of *Tamias cinereicollis*, *Dipodomys spectabilis*, *Spermophilus spilosoma*, and 24 other species, which left their fossils only in this small area during the last glacial time (Fig. 14). In North America it includes the SE Arizona, S New Mexico and SW Texas. In the 27 monocentric species contains the element of De Lattin's Mexico Dispersal Centre: *Peromyscus pectoralis*. The other two elements, *Sciurus apache* and *Myotis thysanodes* had left no fossil records in this period. But from the geographical position it could be concluded that the Mexico Refugium is equivalent to De Lattin's Mexico Dispersal Centre.

Comparing with the California Refugium, the Mexico Refugium had relatively monotonous ecological conditions, which can be reflected by the ecological requirements of the monocentric species: mainly sandy and rocky area with sagebrush and scrub (Tab. 4). The paleovegetation data of this area also showed that it was covered mainly by tropic thorn scrub and scrub woodland (Ray, 2001). Another characteristic of this refugium is the high extinct ratio. Of the 27-monocentric species, 9 had got extinct before 15 ka (33%). *Peromyscus* *pectoralis* now got extinct in wild (Data from Smithsonian National Musuem of Natural History).

Around 8 ka the monocentric species of this refugium started to disperse. About 60% of them migrated to Southern Mexico. About 35% migrated a little bit to their northern areas, reaching, for example, northern New Mexico and Colorado. About 21% dispersed northwest to Arizona and the Neveda deserts and about 20% dispersed a little bit to eastern Texas. Of course, many species dispersed more than one of these directions.

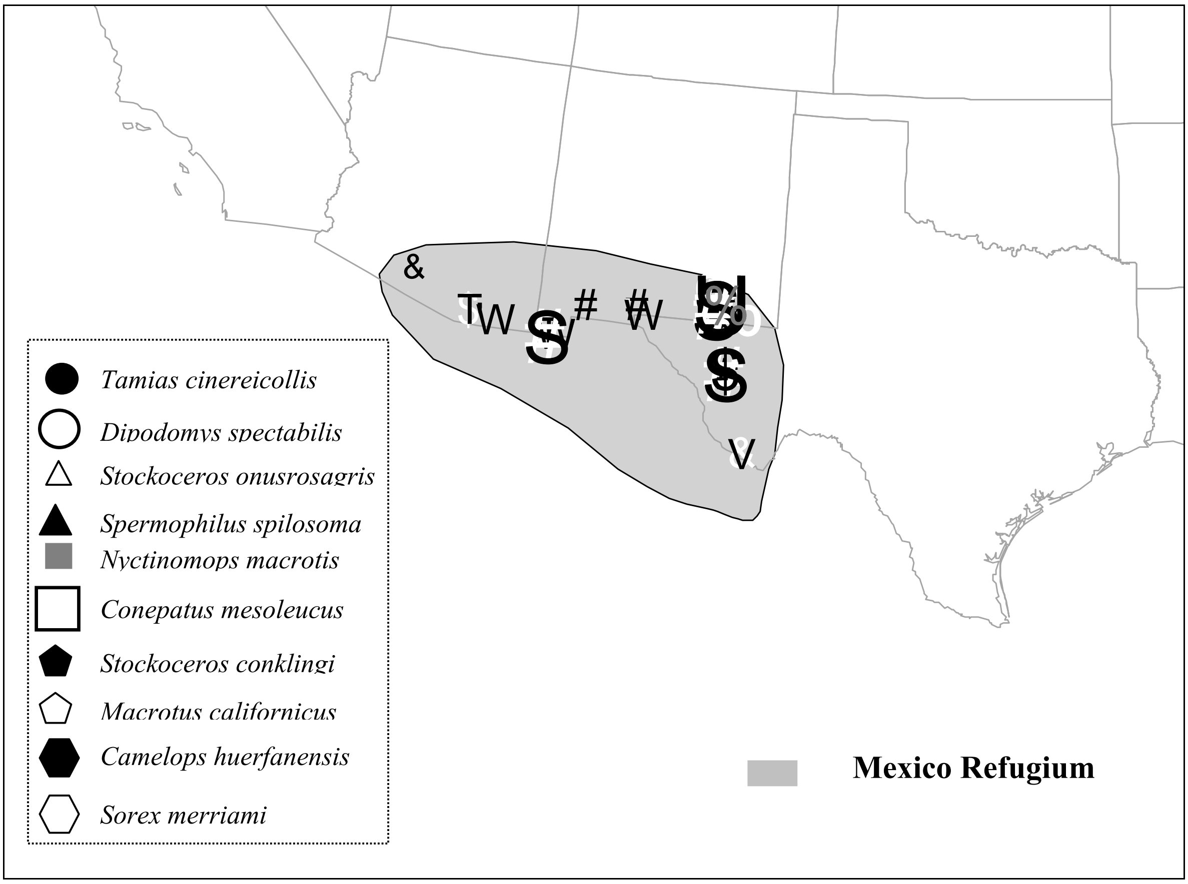


Fig. 14 The Mexico Refugium and some of its monocentric species

De Lattin defined the Arizona Dispersal Centre with *Sciurus arizonensis*, *Myotis occultus* (= *Myotis lucifugus occultus* Wilson, 1993) and *Eutamias cinereicollis* (= *Tamias cinereicollis* Wilson, 1993). But *Tamias cinereicollis* left its fossil records in Mexico Center, and the other species had no fossil records. The Colorado Dispersal Centre was defined with *Tamiasciurus hudsonicus fremonti*, *Sciurus kaibaensis* (=*Sciurus aberti kaibaensis* Wilson, 1993) and *Peromyscus nasutus*, which overlap now but in western New Mexico. *Sciurus kaibaensis* left its fossil record in the Great Basin Refugium, *Tamiasciurus hudsonicus* left its fossil records manily in the Appalachia Refugium before 15 ka, and *Peromyscus nasutus* had no fossil records during this period. More important, no other species left their fossils only in the overlapping area of the above 2 dipersal centres. So these two centres might not be refugium.

The Texas Arid Dispersal Centre should be in Liano Estacado area delimitated with *Perognathus hispidus* (= *Chaetodipus hispidus* Wilson, 1993), *Spermophilus spilosoma* and *Antilocapra americana* (De Lattin, 1967). *Spermophilus spilosoma* left its fossil records in the Mexico Refugium. *Antilocapra americana* was a polycentric species with its fossil records before 15 ka mainly in the California and Great Basin Refugium. Only Hispid Pocket Mouse (*Chaetodipus hispidus*) left a lot of its fossils in the overlapping area, but its foosils were also found in the Mexico Refugium. A few other species could be found to leave their fossils only in this overlapping area (*Dipodomys elator*, *Tetrameryx shuleri*). But as a separate refugium it still needs other strong evidences.

Species	Ecological Conditions
Aztlanolagus agilis	Extinct
Bassariscus sonoitensis	Extinct
Camelops huerfanensis	Extinct
Conepatus mesoleucus	Foothills and brushy areas
Dipodomys spectabilis	Dessert grasslands with scattered shrubs
Equus tau	Extinct
Macrotus californicus	Grassy meadows from sea level to mountains
Microtus mexicanus	Grassy openings of the yellow pine forest
Myotis rectidentis	Extinct
Neotoma goldmani	Desert
Neotoma mexicana	Rocky outcrops, slopes, most common in ponderosa forests
Neotoma pygmaea	Extinct
Nyctinomops macrotis	Rocky areas
Papogeomys castanops	Sandy soil or open plains
Perognathus merriami	Sandy or stony soils with sparse vegetation
Peromyscus difficilis	Rocky areas
Peomyscus pectoralis	Rocky areas
Plecotus rafinesquii	Forested regions
Sorex merriami	Arid area, sagebrush or bunchgrass
Sorex vagrans	Mixed forests
Spermophilus spilosoma	Dry sandy areas, grass areas and pinewood
Spilagale gracilis	Rocky bluffs, cliffs
Stockoceros conklingi	Extinct
Stockoceros onusrosagris	Extinct
Tadarida constantinei	Extinct
Tamias cinereicollis	Coniferous foests
Tayassu tajacu	Dessert with cacti

Tab. 4 The Monocentric Species of Mexico Refugium

2. 3. 3 The Florida Refugium

The Florida Refugium can be easily delimitated by its special geographical position and some of its monocentric species. The refugium includes Florida, and the coastal area of Georgia and South Carolina (Fig. 15). About 26 species had left their fossil records only in this area during the last glacial time, in which contain *Neofiber alleni*, *Dasypterus intermedius* (= *Lasiurus intermedius* Wilson, 1993), *Myotis austroriparius*, elements of De Lattin's Florida Dispersal Center. Another element *Lasiurus seminolus*(=? *Lasiurus borealis seminolus*, Baker, 1988) had no fossil records. But it is sure that theFlorida Dispersal Center was a refugium.

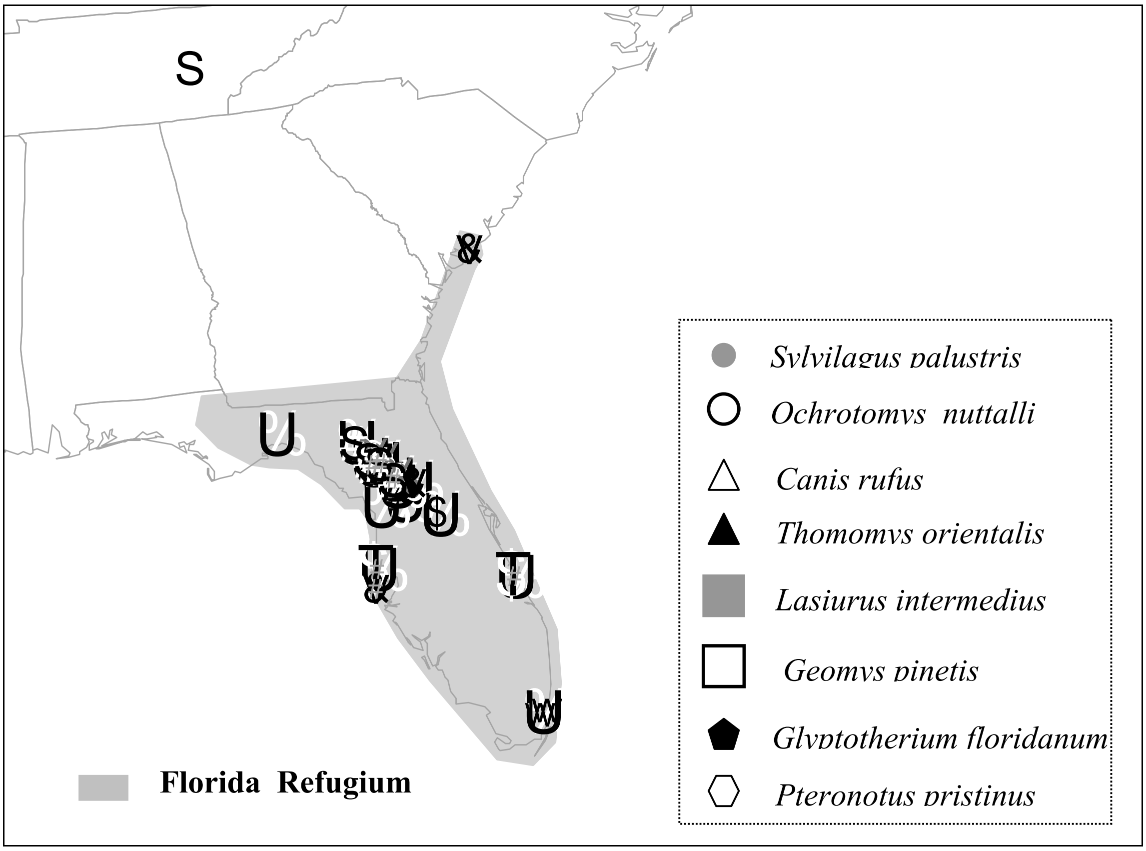


Fig. 15 The Florida Refugium and some of its monocentric species

The paleovegetation data of the last glacial time showed that Florida was covered by semi-arid temperate woodland, very similar to that of California of the same period. But the ecological requirements of the monocentric species show that its ecological conditions were a little more diverse: mainly sandy, dune with scrub and chaparral, but also existing swamps, marshes and other humid areas (Tab. 5). This refugium had a very high extinct ratio: of the 26 monocentric species, 11 had got extinct at the end of the last glacial time (about 42%). *Canis rufus* and *Peromyscus polionotus* now become critically endangered, *Felis pardalis* and *Sylvilagus* *palustris* endangered, and *Geomys pinetis*, *Peromyscus gossypinus* has got extinct in wild (Data from Smithsonian National Musuem of Natural History)

Many species did not migrate after the glacial time, while others dispersed northward to the around states such as Georgia, Alabama, Missippi and Texas, some through Texas south to Mexico. The dispersal time stiil cannot exactly be asserted. It may be around 5 ka. But it is sure that their dispersal time was much later than 15 ka.

De Lattin had defined the Virginia Dispersal Centre with two species frogs (*Rana capito*, *Rana heckscheri*) and *Corynorhinus rafinesquii(=Plecotus rafinesquii) Pitymys pinetorum* (*=Microtus pinetorum*). The fossils of *Plecotus rafinesquii* were found in Mexico Refugium, and the fossils of *Microtus pinetorum* were found both in the Florida and Appalachia Refugium. Therefore this dipersal centre might not be a refugium.

Species	Ecological Requirements
Canis rufus	Mountains, lowland forests, and wetland
Eremotherium rusconii	Extinct
Eumops glaucinus	Subtropical forests
Eumops underwoodi	Plains and desert grassland
Felis amnicola	Extinct
Felis pardalis	Dense, almost impenetrable chaparral thickets
Geomys pinetis	The sandhill or xeric hammock ecosystem
Glyptotherium floridanum	Extinct
Halichoerus grypus	Gray seal, Temperate and subarctic waters
Hydrochoerus holmesi	Extinct
Lasiurus intermedius	Hardwood and pine forests in permanent water
Mormoops megalophylla	Desert shrub where temperate and humidity are high
Mylohyus fossilis	Extinct
Myotis austroriparius	Cave
Neochoerus pinckneyi	Extinct
Neofiber alleni	Wet moist areas, swamps, bogs, marshes
Ochrotomys nuttalli	Thick woodlands, swampy areas, among vines
Palaeolama mirifica	Extinct
Peromyscus gossypinus	Woodland
Peromyscus polionotus	Beach dunes and scrub habitats
Podomys floridanus	High, dry sandy ridges where black-jack, turkey-oak are abundant
Pteronotus pristinus	Extinct
Sylvilagus leonensis	Extinct
Sylvilagus palustris	Swamps, lake borders, coastal waterways
Thomomys orientalis	Extinct
Tremarctos floridanus	Extinct

Tab. 5 The Monocentric Species of the Florida Refugium

2. 3. 4 The Appalachia Refugium

The Appalachia Refugium has been introduced in the Methods Section. This refugium could be easily delimitated by the fossil records of many monocentric species, which mainly located in the Appalachian area, including Kentucky, Tennessee, West Virginia, s Illinois, Indiana and Ohio, n Mississippi, Alabama and Georgia, w Virginia and North Carolina, ne Arkansas and se Missouri (Fig. 7). About 21 species had left their fossil records only in this area, which contain *Myotis grisescens*, *Myotis sodalis*, *Myotis keenii*. With these three mammals and two frog species (*Rana palustris* and *Rana sylvatica*) De Lattin had defined the Algonk (Alabama, Georgia, S. Carolina) Dispersal Centre. Keen's Myotis (*Myotis keenii*) now distributed only in some caves on the Hotsprings Island, Canada. But its fossil records were only found in the Appalachia Refugium during the glacial time. There is no problem that the Appalachia Refugium is equivalent to De Lattin's Algonk Dispersal Centre.

The paleovegation data of this area in the glacial time was Main Taiga (Ray, 2001), which was also reflected by the ecological requirements of its monocentric species: coniferous and deciduous forests, prairies, woodl and swamp (Tab. 6). Of the 21 species, only 1 got extinct

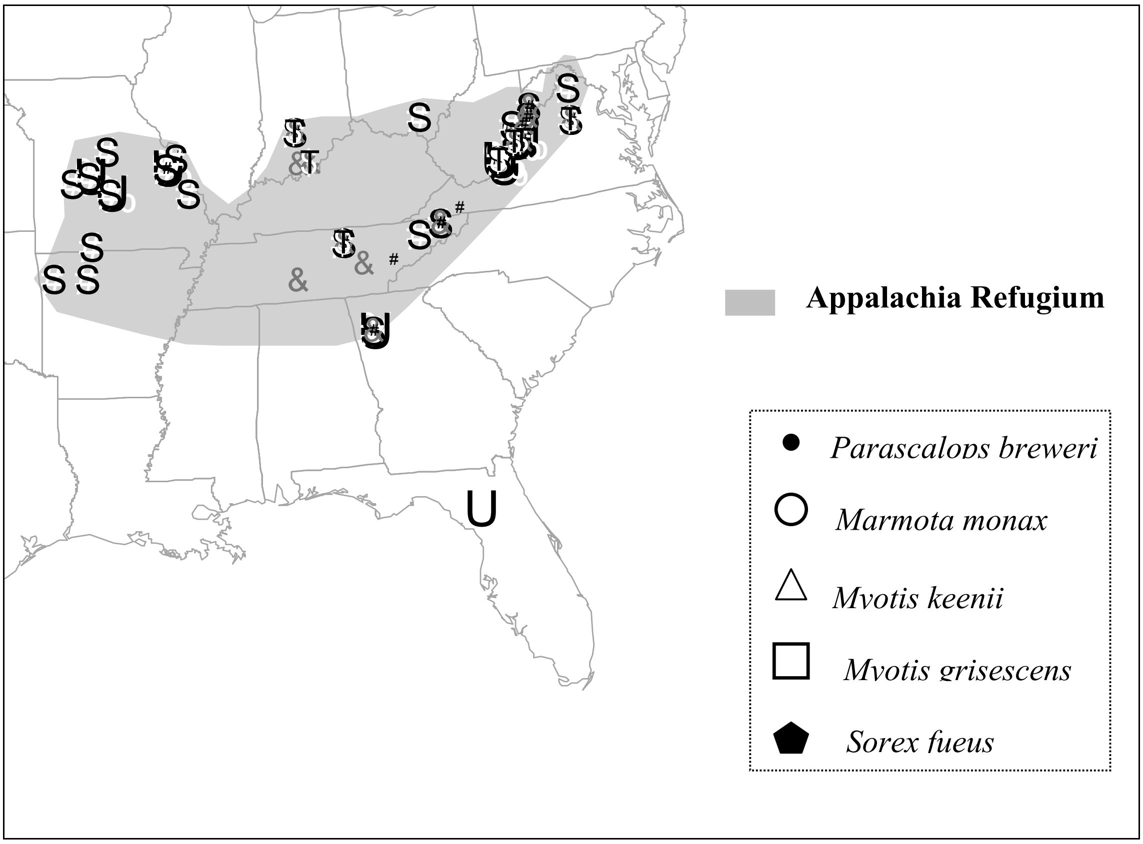


Fig. 16 The Appalachia Refugium and some of its monocentric species

Myotis grisecens, *Myotis sodalis* and *Zapus hudsonius* now become endangered (Data from Smithsonian National Musuem of Natural History)

In the 21 species also contain *Sorex dispar*, *Sylvilagus transitionalis*, *Sorex fumeus*, *Napaeozapus insignis*, which are elements of De Lattin's Laurent Dispersal Centre. It is clear that this centre is the same thing as the Appalachia Refugium.

De Lattin had also defined the Kanso Eremic Dispersal Centrer, which should be in Nebraska and Kansas with *Perognathus flavescens*, *Spermophilus franklinii*, and *Spermophilus tridecemlineatus*. Only *Spermophilus franklinii* (Franklin's Ground Squirrel) had left its fossil records in the overlapping area. *Perognathus flavescens* (Plains Pocket Mouse) left its fossil records in the Mexico Refugium, and *Spermophilus tridecemlineatus* had left its fossil records in the Appalachia Refugium and the Middle Rocky Mountain Refugium, the Mexico Refugium and Northern Texas. Few species left their fossils only in the overlapping area here during the glacial time. Thus it might need more evidence for a refugium.

Of the monocentric species, only a few migrated southward (*Myotis grisescens*, *Sylvilagus aquaticus*). The others dispersed northeastward, northward, and northwesternward. Many species now still distributed in their refugium, but many others contracted from the refugium.

Species	Ecological Conditions
Capra hircus	
Condylura cristata	Damp or muddy soil
Dicrostonyx hudsonius	
Equus calobatus	Extinct
Glaucomys sabrinus	Coniferous or mixed coniferous/deciduous forests
Marmota monax	A variety of forest types
Martes pennanti	Conifer and hardwood forests
Microtus chrotorrhinus	Cool, moist, northern hardwoods and mixed forests
Mustela nivalis	Open forests, meadows, prairies
Myotis grisescens	
Myotis keenii	Cavities
Myotis sodalis	Cool caves in winter, within the loose bark of trees in summer
Napaeozapus insignis	Cool, moist area with dense fir andhardwood forests
Parascalops breweri	In secondary growth hardwood forests and meadows
Peromyscus cumberlandensis	
Rattus norvegicus	Widespread
Sorex dispar	The moist forested areas of high altitude regions
Sorex fumeus	Deciduous and coniferous forests
Sylvilagus aquaticus	Swamp and lowland areas close to water
Sylvilagus transitionalis	Dense forests at higher level elevation
Zapus hudsonius	Moist grassland

Tab. 6 The Monocentric Species of Appalachia Refugium

A few even disappeared in this region (*Dicrostonyx hudsonius*). The dispersal time started about 15 ka, although from 15 – 8 ka they migrated only a little bit in distance.

2. 3. 5 The Great Basin Refugium

The Great Basin Refugium looks like a pan including most of Nevada, SW Utah, NW Arizona and with the panhandle extending through Oregon to central Washington (Fig. 17), in which about 14 species left their fossils. The monocentric species contain Chisel-toothed Kangaroo Rat (*Dipodomys microps*) and Dark Kangaroo Mouse (*Microdipodops megacephalus*), which were the elements of De Lattin's Salso Arid Dispersal Centre. It's another element Townsend's Ground Squirrel (*Spermophilus townsendii*) now only distributes in SE Washington (USA), S of Yakima River and W and N of Columbia River, but its fossils were not only found in this refugium, but also in another refugium. So it was a polycentric species. However, there is no problem that both might be similar

The ecological requirements of the monocentric species indicated that the ecological conditions were diverse, dominated by desert scrub and coniferous forests (Tab. 7). The paleovegetation of this area was mainly subalpine parkland during this time (Ray, 2001). The dispersal directions of this refugium were maily southward to the deserts of California and Arizona, and a little bit northward to the Rocky Mountain area. Others did not expanded a lot. The dispersal time started about 15 ka. Of the 14 species, two had got extincted (14%). *Perognathus longimembris* and *Tamias umbrinus* now become critically endangered (Data from Smithsonian National Musuem of Natural History)

De Lattin had found the Oregon Dispersal Centre by *Eutamias ruficaudus* (=*Tamias ruficaudus* Wilson, 1993), *Eutamias amoenus* (=*Tamias amoenus* Wilson, 1993), and *Neotoma cinerea*. But *Tamias amoenus* left its fossil records in southern Nevada, and *Neotoma cinerea* were a polyecentric species, leaving fossils in Californa, Mexico and Great Basin Refugium. So it might not be true that it was a refugium.

2. 3. 6 The Rocky Mountain Refugium

The shape of the Rocky Mountain Refugium is a reverse "Y", which sits on the Rockies, with one arm extending south through e Idaho to n Utah, another southeast through Montana to n Nebraska, and its body north perhaps to Canada (Fig. 18). This refugium is near the Oregon Dispersal Centre of De Lattin, but it has different elements. About 7 species left their fossils only here, but *Gulo gulo* and *Dicrostonyx torquatus* left their fossils mainly here.

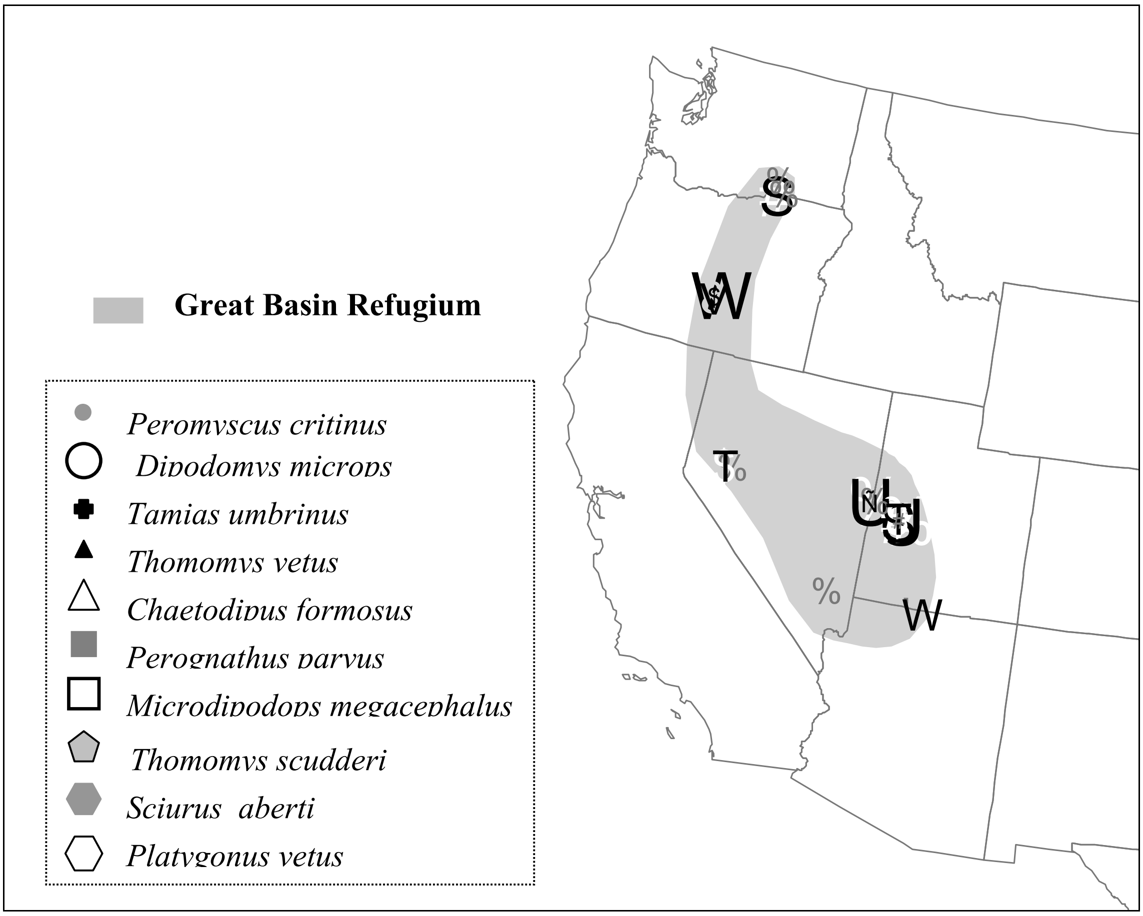


Fig. 17 The Great Basin Refugium and Some of Its Monocentric Species

Species	Ecological Conditions
Chaetodipus formosus	Rocky soil
Dipodomys microps	Dense desert scrub with sandy or gravelly substrate
Equus caballus	Extinct
Microdipodops megacephalus	Bushes on sand dunes
Ovis aries	Desert or forests
Perognathus longimembris	Desert scrub, desert wash, coastal scrub and sagebrush
Peromyscus crinitus	Rocky areas, desert, chaparral and conifer
Platygonus vetus	Extinct
Sciurus aberti	Coniferous forests, including yellow or panderosa pine
Tamias amoenus	Coniferous forests, Montane hardwood, pinyon-juniper
Tamias umbrinus	Coniferous forests, in open area or nea the forest edge
Thomomys scudderi	
Thomomys vetus	

Tab. 7 The Monocentric Species of the Great Basin

This refugium was almost reaching the icesheet, but it could still provide ecological conditions for tundra and boreal forest fauna. Some species did not lived in this area any more such as

Dicrostonyx torquatus. Others still live here, but most of their distribution areas are far north from this area. So it is difficult to find this refugium by overlapping the Areals. No monocentric species got extinct. *Ovis canadensis* (Data from Smithsonian National Musuem of Natural History)

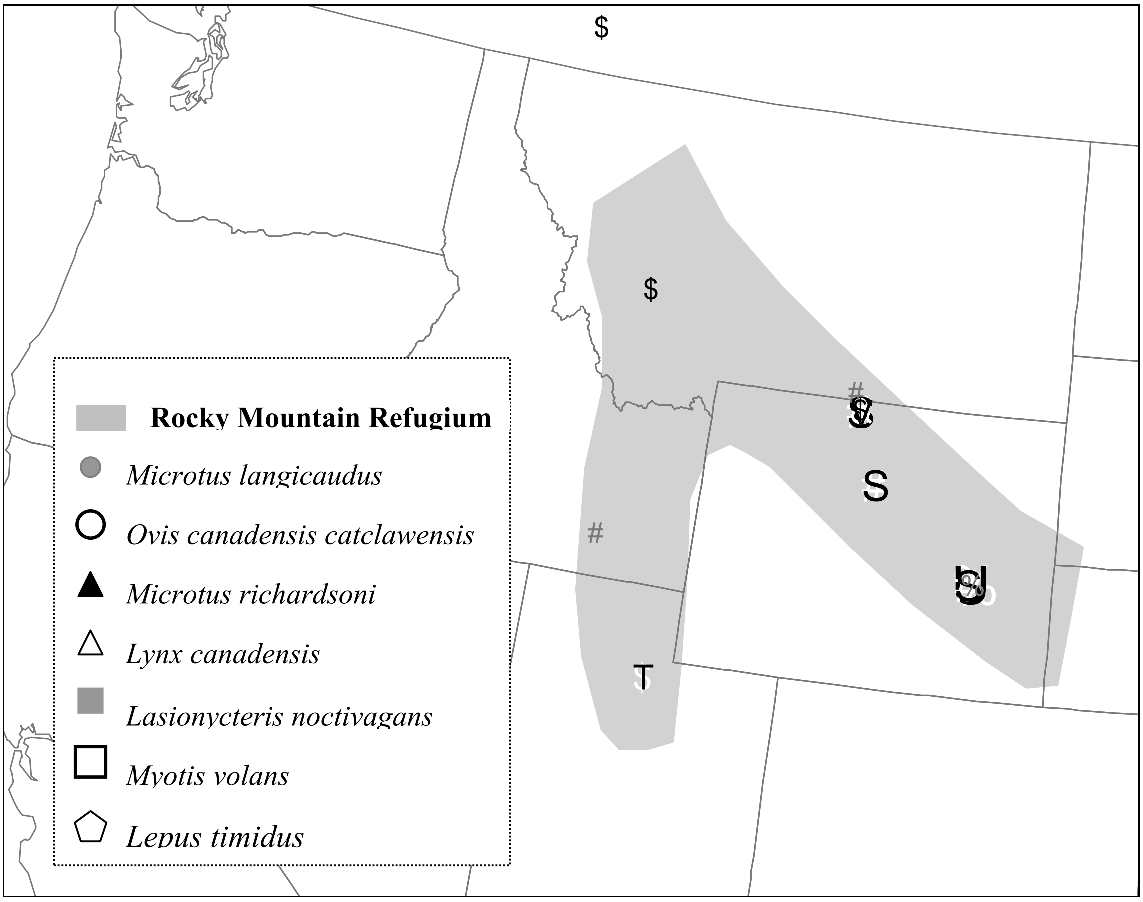


Fig. 18 The Rocky Mountain Refugium and some of its monocentric species

2. 3. 7 The Great Lake Refugium

The Great Lake Refugium was located in the area around the Great Lake such as s Minnesota, Wisconsin, Michigan, Illinois, Indiana, and Ohio. But it was driven to contract in the Last Glacial Maximum and located mainly in the last three states (Fig. 19). About 8 species left their fossils only in or maily in this area. Some are arctic tundra species such as *Lemmus sibiricus, Microtus miurus*, *Ovibos moschatus*. The last two are elements of De Lattin's Alasko Tundra Centre and Neotundra Centre. Of the 8 species, 4 got extinct (50%).

Tab. 8 The Elements of the Great Lake and Rocky Mountain Refugium

Species	Great Lake Refugium	Rocky Mountain Refugium	Ecological Reqirements
Bootherium bombifrons	*		extinct
Cervalces scotti	*		extinct
Lemmus sibiricus	*		tundra
Mammathus jeffersoni	*		extinct
Mammathus primigenius	*		extinct
Microtus miurus	*		
Ovibos moschatus	*		tundra
Spermophilus parryii	*		tundra, mountains
Brachylagus idahoensis		*	dense sage brush
Dicrostonyx torquatus		*	arctic tundra
Gulo gulo		*	boreal forests, mountains or open plains arctic
Lasionycteris noctivagans		*	temperate northern hardwoods
Lepus timidus		*	tundra and forest regions of the far northarctic
Lynx canadensis		*	forests, rocky areas and tundra
Microtus longicaudus		*	
Microtus richardsoni		*	semiaquatic habitats of subalpine meadows
Myotis volans		*	pinon-juniper to coniferous forests
Ovis canadensis catclawensis		*	

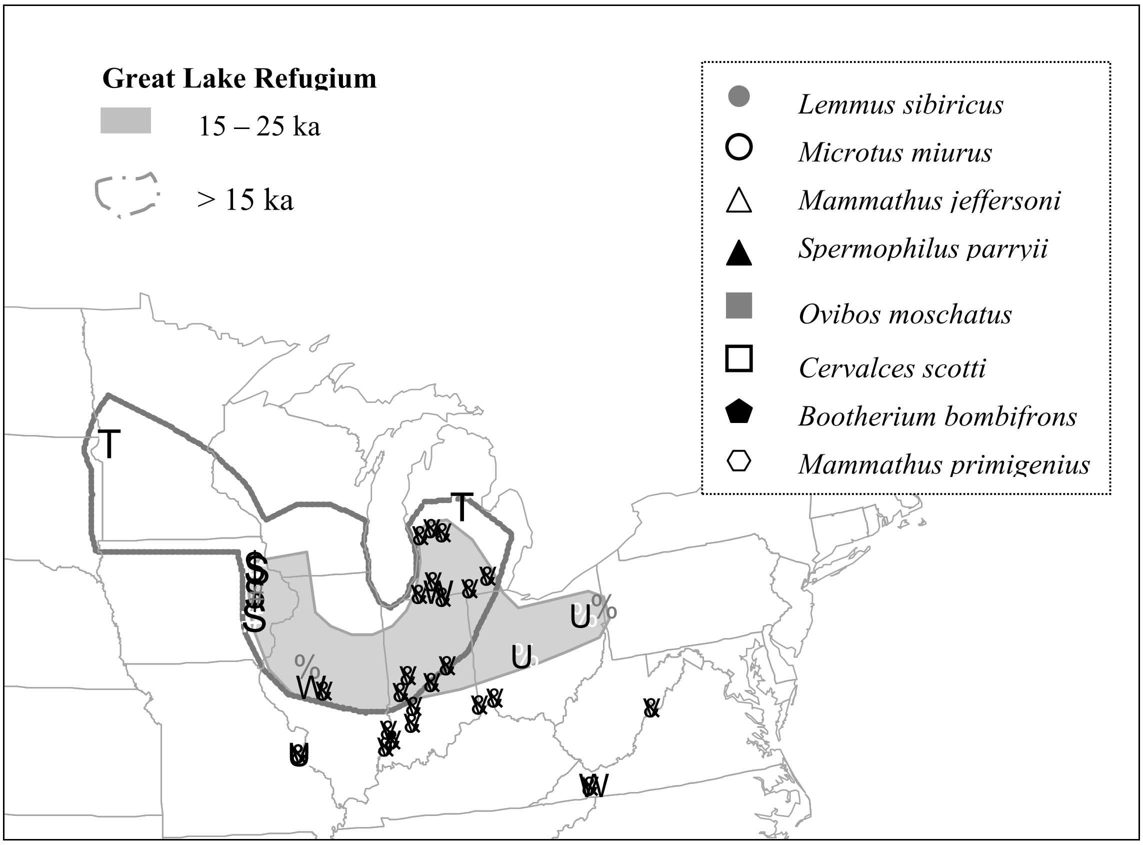


Fig. 19 The Great Lake Refugium and some of its monocentric species

CHAPTER 3 THE “HOT SPOTS” WITHIN A SPECIES RANGE INFERRED FROM MNIS

Why does a famous ecologist who has studied the dynamics of beaver population for most of his life does not have his idea of where the highest population area of beaver is locateded within the range in North America? For most a century, when ecologists have studied abundance, they have almost always studied population dynamics: fluctuations in the number of a single local population over several years; When ecologists have studied distribution, they focused primarily on territoriality, foraging movements, habitat selection, and other processes that influence the spatial dispersion of individual organisms within populations or among habitats; When biogeographers have studied distributions, they have been concerned primarily with the influence of contemporary processes and historical events on the size, location, and limits of the Areals of species as they appear on maps. But much less attention has been paid to the patterns and processes of spatial variation in abundance within a species. Ecologists have rarely made comparative geographic studies of abundance, and biogeographers have equally rarely studied the abundance and distribution of individuals or populations within the Areal. The studies of the spatial variation in local population density within the range, which have important implications for basic ecology and biogeography, especially for the dynamics and regulation of abundance in both time and space, the limits and internal structure of the Areal, and the interspecific variation in abundance observed within local communities, are just in their infancy (Brown, 1995b). It is almost impossible for a scientist or a group, using limited research funds within limited research time, to study the fluctuations of different local populations over the whole range of a species. Therefore it is not strange that population ecologists can not answer a question such as the one above. To answer the question above, we need a monitoring program, which should extend for at least 20 or 30 years. Is this not an arduous task? Here it will be argued that fossil data can provide valuable quantitative information not only about a local site, but also about the whole range, not only about 10 or 20 years, but also about hundreds and even thousands of years. By using a method of analyzing fossil data, we can easily predict that the high population area of beaver may be located in the upper Mississippi River in Minnesota, in the Wisconsin River in Wisconsin and in the upper Missouri River in South Dakota. Through this method we can also know that the high population areas might once have been located in the Tennessee River in Tennessee and in the Middle Mississippi River in Illinois before 1000 years ago (see 4.2). Our methods will assist ecologists and biogeographers to find the high population areas (hot spots) within a range. Our results can be tested with their own modern data. If the results can be proved true, a breakthrough could then be made in the study of the temporal and spatial variation in abundance within a range. Before we introduce our methods, we would first try to answer the following questions: which quantitative information can fossil data provide? How accurately can the information provided by a fossil assemblage reflect the composition of their living communities?

3.1 The Ecological Meaning of MNIs

The higher the population density, the higher the probability that it will be discovered (Hengeveld, 1990). This principle is commonly used in the study of population ecology. For example, 14 mammalian species were evident in a population study area during a 22 month investigation (Drabek, 1977): Virginia opossum (*Didelphis virginiana*), short-tailed shrew (*Blarina carolinensis*), least shrew (*Cryptotis parva*), eastern cottontail (*Sylvilagus floridanus*), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), plains pocket gopher (*Geomys bursarius*), hispid pocket mouse (*Perognathus hispidus*), plains harvest mouse (*Reithrodontomys montanus*), deer mouse (*Peromyscus maniculatus*), white-footed mouse (*P. leucopus*), hispid cotton rat (*Sigmodon hispidus*), prairie vole (*Microtus ochrogaster*), woodland vole (*M. pinetorum*), and house mouse (*Mus muscuslus*). The five species in Tab. 9 accounted for 98% of the captures and 99% of the recaptures, with *S. hipidus* alone representing 61% and 70% respectively. The higher the population density, the higher the proportion of rodents marked. From Table 9 it is clearly seen that the densest rodent populations were represented by *S. hispidus*, *P. maniculatus*, and *P. leucopus*.

Tab. 9 The five densest rodent species in the investigation (Drabek, 1977)

Species	Males	Females	% Of rodents marked	Recaptures	% Of all recaptured
Sigmodon hispidus	176	88	60.5	1136	69.7
Peromyscus maniculatus	63	34	22.2	305	18.7
Peromyscus leucopus	23	12	8.0	134	8.0
Reithrodontomys montanus	13	9	5.0	37	2.0
Microtus ochrogaster	7	3	2.0	17	1.0

Hengeveld’s principle could be aslo implied to the study of the fossil or subfossil assemblage. A fossil or subfossil assemblage can be considered as captures of cave, lacustrine or fluvial sediments, which might have trapped for hundreds or even thousands of years. The sediments may not be as efficient as modern trapping instruments, but their captures could provide reasonably accurate information population dynamics of long periods, if this process has not been severely disturbed by other factors.

MNIs, the Minimum Number of Individuals already mentioned in 1.4.1, is the key term to the understanding of the quantitative information provided by fossil data. After the fossils have been excavated from the sediments, they must be sorted and identified; otherwise they are only a pile of broken bones and teeth. Most bones and teeth can be identified to species while others can only be identified to genus (sp.). However, in most cases there are often more or less bones, which can not be identified. Sometimes it is even for experts difficulty to know their position in the skeleton, because they are too fragmentary. Careful palaeontologists will take note in the description how many of identified specimens a species may have (NISP, the Number of Identified Specimens). They can also estimate how many individuals these specimens may represent (MNI, the Minimum Number of Individuals). For example, there are 1000 specimens of bones and teeth excavated from a cave. About 50 specimens could be assigned to Red deer (*Cervus elaphus*). And there are 10 right lower M1, 8 left upper P3, 15 right antlers and so on. Then the NISP of Red Deer is 50, and its MNIs are 10 (not 15, because the antlers shed every year and may come from the same individual). The relative abundance of each species in the assemblage can be estimated by the formula: RA = MNIs of the species/ Total MNIs of the assemblage *100. It is already clear that not only the population density but also other factors such as the formational history and collection history (archaeological recovery) influence the relative abundance of a species in an assemblage (Klein, 1984). It is supposed here that this cave have been excavated in a right way, no sample errors have been made in archaeological recovery, no mistakes have been made in the identification. How accurately the relative abundance of a species in the assemblage then reflect its current population densities?

Tab. 10 shows the relative abundances of species in the Lammar assemblage, which is a palaeontological site located in Wyoming. This site was devided from surface to bottom into 10 levels. Level 1 to 5 were formed about 480 years ago, Level 6 to 10 were formed about 1300 years ago. The relative abundance of each species in each level was calculated (=MNIs of a species/Total MNIs of a level), and the relative abundance of each species in the assemblage were then calculated by adding their relative abundances in each level. The following population densities of species were found from literature (Rapopport, 1982, P. 235-237): *Spermophilus richardsoni* (71.041 per ha), *Microtus pennsylvanicus* (81,543 per ha), *Thomomys talpoides* (12,355 per ha), *Peromyscus maniculatus* (22,239 per ha), *Ondatra* *zibethicus* (26,872 per ha), *Lepus townsendii* (,173 per ha), *Sorex vagrans* (,959 per ha), *Mustela frenata* (,519 per ha), *Tamiasciurus hudsonius* (6,968 per ha).

Tab. 10 The Relative Abundance of Species in the Lammar Assemblage

Analyse Unit	Revised Name	MNI	Relative Abundance
Level I	Canis latrans	1	5,88
Level I	Canis sp.	1	5,88
Level I	Cervus elaphus	2	11,76
Level I	Lepus americanus	1	5,88
Level I	Marmota flaviventris	2	11,76
Level I	Microtus longicaudus/montanus	1	5,88
Level I	Microtus pennsylvanicus	1	5,88
Level I	Microtus sp.	2	11,76
Level I	Neotoma cinerea	1	5,88
Level I	Ovis canadensis	1	5,88
Level I	Spermophilus richardsonii	3	17,65
Level I	Thomomys talpoides	1	5,88
Level II and III	Castor canadensis	1	5,88
Level II and III	Cervus elaphus	2	11,76
Level II and III	Clethrionomys gapperi	1	5,88
Level II and III	Lepus townsendii	1	5,88
Level II and III	Marmota flaviventris	2	11,76
Level II and III	Mephitis mephitis	1	5,88
Level II and III	Microtus longicaudus/montanus	9	52,94
Level II and III	Microtus pennsylvanicus	2	11,76
Level II and III	Microtus sp.	7	41,18
Level II and III	Myotis sp.	1	5,88
Level II and III	Neotoma cinerea	8	47,06
Level II and III	Ondatra zibethicus	1	5,88
Level II and III	Peromyscus maniculatus	3	17,65
Level II and III	Phenacomys intermedius	2	11,76
Level II and III	Spermophilus richardsonii	12	70,59
Level II and III	Sylvilagus nuttallii	1	5,88
Level II and III	Tamias sp.	1	5,88
Level II and III	Tamiasciurus hudsonicus	1	5,88
Level II and III	Thomomys talpoides	8	47,06
Level IV and V	Antilocapra americana	1	5,88
Level IV and V	Bison bison	1	5,88
Level IV and V	Cervus elaphus	1	5,88
Level IV and V	Marmota flaviventris	2	11,76
Level IV and V	Microtus longicaudus/montanus	2	11,76
Level IV and V	Microtus pennsylvanicus	1	5,88
Level IV and V	Microtus sp.	2	11,76
Level IV and V	Mustela frenata	1	5,88
Level IV and V	Neotoma cinerea	4	23,53
Level IV and V	Ondatra zibethicus	1	5,88
Level IV and V	Ovis canadensis	1	5,88
Level IV and V	Peromyscus maniculatus	2	11,76

Level IV and V	Phenacomys intermedius	1	5,88
Level IV and V	Spermophilus richardsonii	8	47,06
Level IV and V	Spermophilus sp.	1	5,88
Level IV and V	Taxidea taxus	1	5,88
Level IV and V	Thomomys talpoides	3	17,65
Level IV and V	Vulpes vulpes	1	5,88
Level VI	Canis lupus	1	5,88
Level VI	Cervus elaphus	1	5,88
Level VI	Microtus longicaudus/montanus	2	11,76
Level VI	Microtus pennsylvanicus	1	5,88
Level VI	Neotoma cinerea	2	11,76
Level VI	Ondatra zibethicus	1	5,88
Level VI	Peromyscus maniculatus	1	5,88
Level VI	Phenacomys intermedius	1	5,88
Level VI	Sorex sp.	1	5,88
Level VI	Sorex vagrans	1	5,88
Level VI	Spermophilus richardsonii	3	17,65
Level VI	Thomomys talpoides	1	5,88
Level VII	Bison bison	1	5,88
Level VII	Clethrionomys gapperi	2	11,76
Level VII	Marmota flaviventris	3	17,65
Level VII	Microtus longicaudus/montanus	8	47,06
Level VII	Microtus pennsylvanicus	3	17,65
Level VII	Microtus sp.	4	23,53
Level VII	Mustela frenata	1	5,88
Level VII	Neotoma cinerea	4	23,53
Level VII	Ondatra zibethicus	2	11,76
Level VII	Ovis canadensis	1	5,88
Level VII	Peromyscus maniculatus	8	47,06
Level VII	Phenacomys intermedius	2	11,76
Level VII	Sorex hoyi	1	5,88
Level VII	Sorex vagrans	2	11,76
Level VII	Spermophilus richardsonii	8	47,06
Level VII	Tamias sp.	1	5,88
Level VII	Thomomys talpoides	5	29,41
Level VII	Vulpes vulpes	1	5,88
Level VII	Zapus princeps	1	5,88
Level VIII	Antilocapra americana	1	5,88
Level VIII	Clethrionomys gapperi	1	5,88
Level VIII	Marmota flaviventris	2	11,76
Level VIII	Microtus longicaudus/montanus	5	29,41
Level VIII	Microtus pennsylvanicus	2	11,76
Level VIII	Microtus sp.	4	23,53
Level VIII	Neotoma cinerea	4	23,53
Level VIII	Peromyscus maniculatus	4	23,53
Level VIII	Phenacomys intermedius	1	5,88
Level VIII	Sorex hoyi	1	5,88
Level VIII	Sorex vagrans	1	5,88
Level VIII	Spermophilus richardsonii	2	11,76
Level VIII	Tamias sp.	1	5,88
Level VIII	Tamiasciurus hudsonicus	1	5,88

Level VIII	Thomomys talpoides	2	11,76
Level VIII	Zapus princeps	1	5,88
Level VIIIa	Antilocapra americana	1	5,88
Level VIIIa	Cervus elaphus	1	5,88
Level VIIIa	Clethrionomys gapperi	1	5,88
Level VIIIa	Marmota flaviventris	1	5,88
Level VIIIa	Microtus longicaudus/montanus	11	64,71
Level VIIIa	Microtus ochrogaster	1	5,88
Level VIIIa	Microtus pennsylvanicus	4	23,53
Level VIIIa	Microtus sp.	13	76,47
Level VIIIa	Neotoma cinerea	6	35,29
Level VIIIa	Peromyscus maniculatus	6	35,29
Level VIIIa	Phenacomys intermedius	1	5,88
Level VIIIa	Sorex hoyi	1	5,88
Level VIIIa	Sorex vagrans	1	5,88
Level VIIIa	Spermophilus richardsonii	7	41,18
Level VIIIa	Sylvilagus audubonii	1	5,88
Level VIIIa	Tamias sp.	1	5,88
Level VIIIa	Tamiasciurus hudsonicus	2	11,76
Level VIIIa	Thomomys talpoides	5	29,41
Level VIIIa	Zapus princeps	1	5,88
Level IX	Antilocapra americana	1	5,88
Level IX	Clethrionomys gapperi	1	5,88
Level IX	Lepus americanus	1	5,88
Level IX	Lepus sp.	1	5,88
Level IX	Marmota flaviventris	2	11,76
Level IX	Microtus longicaudus/montanus	16	94,12
Level IX	Microtus ochrogaster	2	11,76
Level IX	Microtus pennsylvanicus	6	35,29
Level IX	Microtus sp.	18	105,88
Level IX	Mustela frenata	1	5,88
Level IX	Myotis sp.	1	5,88
Level IX	Neotoma cinerea	7	41,18
Level IX	Ondatra zibethicus	1	5,88
Level IX	Ovis canadensis	1	5,88
Level IX	Peromyscus maniculatus	19	111,76
Level IX	Phenacomys intermedius	2	11,76
Level IX	Sorex cinereus	1	5,88
Level IX	Sorex merriami	1	5,88
Level IX	Sorex palustris	2	11,76
Level IX	Sorex sp.	2	11,76
Level IX	Sorex vagrans	3	17,65
Level IX	Spermophilus richardsonii	9	52,94
Level IX	Spermophilus sp.	1	5,88
Level IX	Sylvilagus sp.\Brachylagus sp.	1	5,88
Level IX	Tamias sp.	1	5,88
Level IX	Tamiasciurus hudsonicus	1	5,88
Level IX	Thomomys talpoides	6	35,29
Level IX	Ursus arctos	1	5,88
Level IX	Zapus princeps	2	11,76

The relationship between the relative abundance of a species in the Lammar assemblage (WY, palaeontological site) and its current population density has been tested, and it has been shown that the correlation between the relative abundance and the population density was extremely high significant, r (9) = .905, p < .01. Species with high population density at present also tended to have high relative abundances in the subfossil assemblage. Species with low population density at present tended to have low relative abundances in the assemblage. And the population density of a species account for 81% of its relative abundance in the assemblage (Fig. 20).

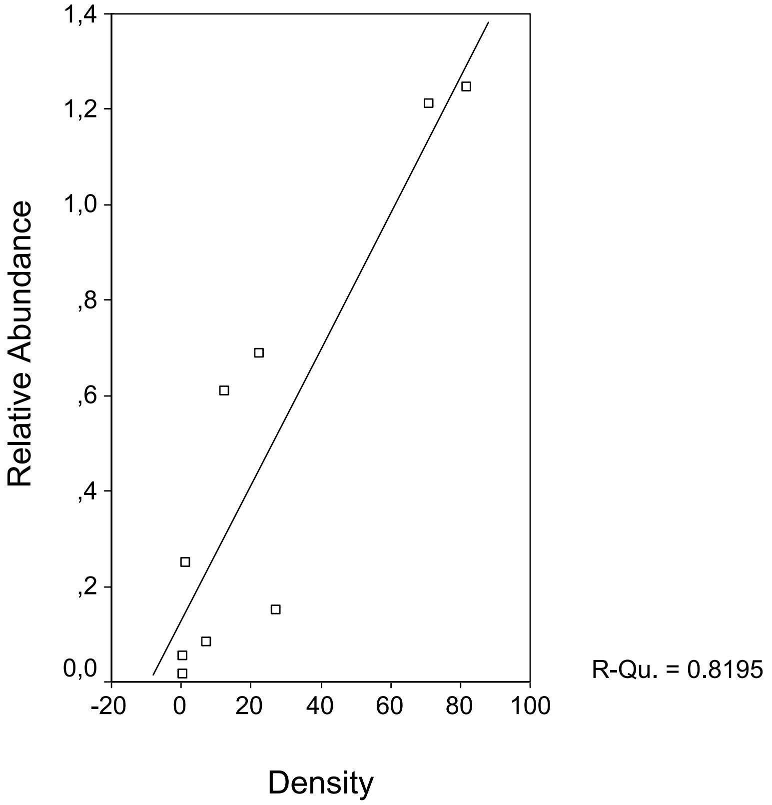


Fig. 20 Correlation between the relative abundances and their current population densities

Similar conclusions have also been reached by comparing the relative abundances of all mollusc species in a current storm sample with a Pleistocene sample. The significant positive correlation indicates that the storm deposit fairly accurately reflected the abundances of living mollusc (Enquist, 1995, Marquet, 1993). The opinion that the relative abundance of species in assemblages could fairly accurately reflected the density of their living species can be further tested, but the following requirements should be satisfied: (1). Correct citation of population density. For example, *Sigmodon hispidus* has 3 population densities (per ha): 19; 65.1 and 98.84, which one should be used in the test? Ideally the data from the same area of the assemblage should be used. If there is no data from the same area of the assemblage, the data from a site, which is nearest to the assemblage locality, should be used. (2). The information an assemblage provided should reflect its original state. Bias caused in the excavation and identification should be avoided.

3. 2 SPATIAL VARIANCE IN ABUNDANCE: BROWN’S MODEL

Species ranges are often not as uniform and static as the solid blots on maps suggest. Most maps of Areals and most quantitative studies based on range maps ignored the spatial variation in abundance within the range. Recent researches show that there appears to be wide variation in abundance within the range (Brown, 1995). First, many areas within the boundaries of published range maps are uninhabited, i.e. local abundance is zero. These are “holes”. But where has the highest population density among those localities where the species occurs within the range? Hutchinson (1957) considers that both abundance and distribution are limited by abiotic and biotic environmental factors that comprise the dimensions of the multidimensional ecological niche. To answer this question, Brown (1984) extended Hutchinson’s concept of niche to develop a model of how abundance varies over the range. The model is based on two assumptions: (1). Local abundance is determined primarily by the extent to which different resources and conditions of local environment meet the requirements of a given species. These requirements can be defined so as to be independent of each other, thereby constituting orthogonal axes of the species-specific niche. Thus the niche is a characterization of environmental requirements of a species. (2). Local environments vary in their capacities to meet these niche requirements. Spatial variation in the relevant environmental parameters exhibits substantial autocorrelation, so that nearby sites are likely to provide more similar combinations of variables than those that are more separated.

From these assumptions it follows that the abundance of a species should be highest where the combination of environmental variables fits its niche requirements best and should decline with increasing distance from this site. If the pattern of variation is both spatially autocorrelated and relatively heterogeneous, then abundance should be highest near the centre of the Areal and should decline relatively gradually and symmetrically towards the edges of the range. This predicts a pattern of abundance along a transect through the Areal that resembles a normal curve (Fig. 21a)

But this is still a great oversimplification. Recent studies show that there is typically enormous variation in abundance at those localities where the species occurs: Zero or a very few individuals occur at most locations, but tens or hundreds are found at a few sites. For example, for most common passerine birds censused in the North American Breeding Bird Survey

(BBS), the modal number of individuals counted at a site is typically one (and almost always less than five), although the maximum number can be in the hundreds or even thousands (Brown, 1995b). Locations that have only a few individuals are called “cool spots”, and sites that have tens or hundreds of individuals called “hot spots”. In a word, there exist holes, cool spots as well as hot spots within the ranges of species. This is Brown’s modified model: the hot spots model (Fig. 21b)

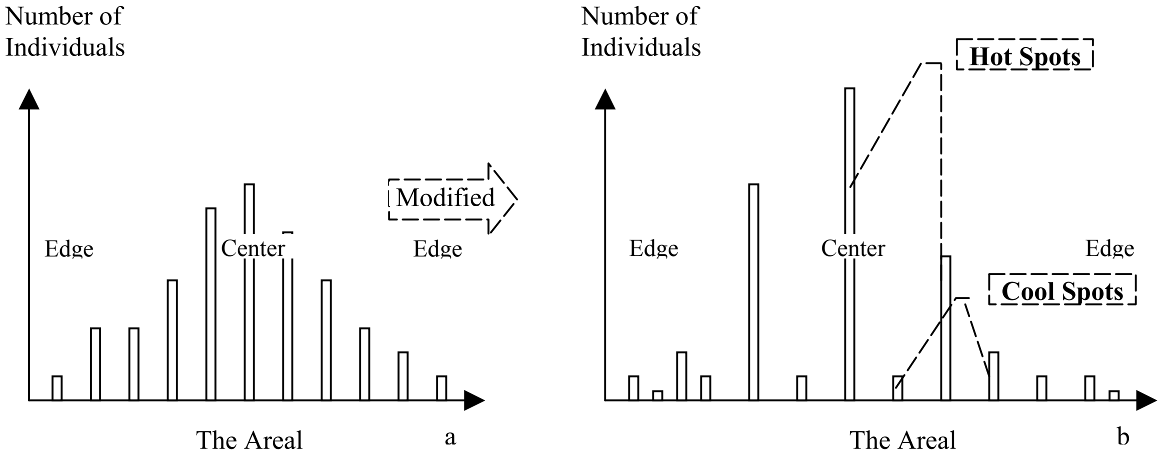


Fig. 21 Brown’s Model: spatial variation in abundance across a transect of the Areal of a single hypothetical species

At least 5 patterns in the spatial distribution of abundance within the range have been revealed through the studies of avian distributions based on the BBS and the distributions of other organisms (Brown, 1995b): (1). There is spatial autocorrelation: Abundances tend to be more similar among nearby localities than distant ones. (2). While there are some changes in abundance at local sites over time, at many sites abundances of particular have remained quite similar over the last 20 years. (3). Spatial variation in abundance tends to be greatest near the centre of the range, where the sites of highest abundance but also sites with zero and low abundance occur. Abundance tends to be uniformly low near the boundaries of the range. (4). An exception to the previous pattern is that when the range boundary coincides with coastline, abundance often tends to be relatively high right up to the coast rather than decreasing as the boundary is approached as it does toward the other edges of the range. (5). Comparisons among species, even closely related, ecologically similar ones, show that both the spatial patterns of abundance and the temporal changes in abundance at sites are highly species specific.

3. 3 THE IMPLICATIONS OF BROWN'S MODEL FOR ANALYZING MNIS

Brown's hot spots model has direct implications for analyzing fossil and subfossil data from palaeontological and archaeological sites: Hot spots have a much higher local population density than cool spots. As argued above, species with high population density at present also tend to have high relative abundances in the fossil or subfossil assemblage (high MNIs), while species with low population density tend to have low relative abundances (low MNIs) in the assemblage. “The lower the abundance, the greater the effort required to discover it” (Lyman, 1995, Nance, 1983). Therefore there will be much more chances for individuals to be “trapped” in the sediments located in the “hot spots” area than in the “cool spots” area, and thus much higher MNIs should be found in the hotspots than in the cool spots area. Because there are only a few hot spots but many cool spots within a range of a single hypothetical species, therefore only a few sites will be found with much higher MNIs, while most sites have only several MNIs. If this prediction is true, the temporal and spatial variation in abundance could be reconstructed from the spatial distribution of MNIs of a species over the range. Areas with no fossil records of the last thousands of years may be holes, and sites with much higher MNIs may be its hot spots, while locations with only a few MNIs may be the cool spots.

To test the predictions made above, species with over 100 fossil records (70 species in total) are analyzed with ArcView 3.2. Here we also take *Geomys bursarius* as an example to show the methods. Firstly, dividing the fossil or subfossil records into several time slices. There are 376 records of *Geomys bursarius* in the Faunmap, mainly found in the last 25,000 years (Fig. 23). Its distribution frequency fits the normal temporal distribution pattern: the more the recent, the higher the number of fossil records found (see 1.5). This shows that the records cannot be divided into equal length of time. The evolution of a range has been divided into 6 stages: the human disturbing stage, the last 500 years (< 0.5 ka), the primitive stage, from 5,00 to 1,000 years ago (0.5 – 1 ka), the transitional stage, from 1,000 to 3,000 years ago (1 – 3 ka), the developing stage, from 3,000 to 8,000 years ago (3.0 – 8.0 ka), the dispersal stage, from 8,000 to 15,000 year ago (8.0 – 15 ka) and the refuge stage, before 15,000 years ago (> 15 ka). The transitional stage is further divided into two segments: from 1,000 years ago to 1,500 years ago (1.0 – 1.5 ka) and from 1,500 years ago to 3,000 years ago. This dividing will cause a relatively equal distribution frequency of records in each time slice (Fig. 24) and is also suitable for most species analyzed.

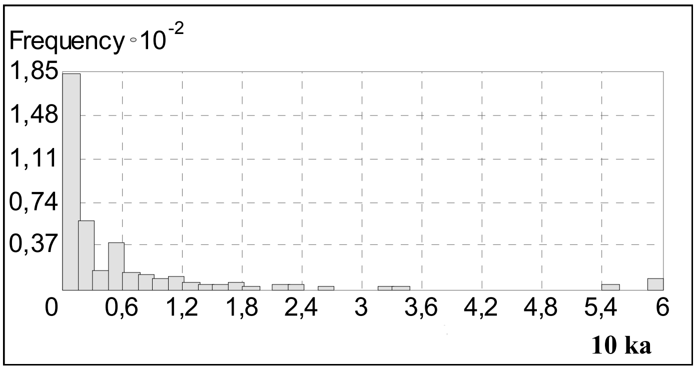


Fig. 23 The distribution frequency of records of *Geomys bursarius* in the last 60,000 years

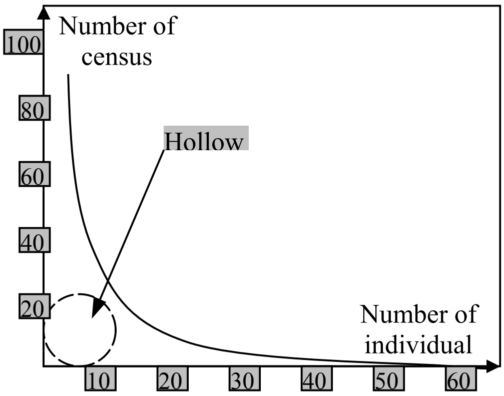


Fig. 22 A hollow curve of frequency as a function of abundance

Secondly, making the graph of frequency (number of fossil or subfossil records) as a function of MNIs. In Brown's study, this graph was made by plots of frequency (number of census sites) as a function of abundance (number of individuals counted at a census) (Fig. 22). All species examined in his study exhibit similar distributions: a hollow curve. Just like the plots of

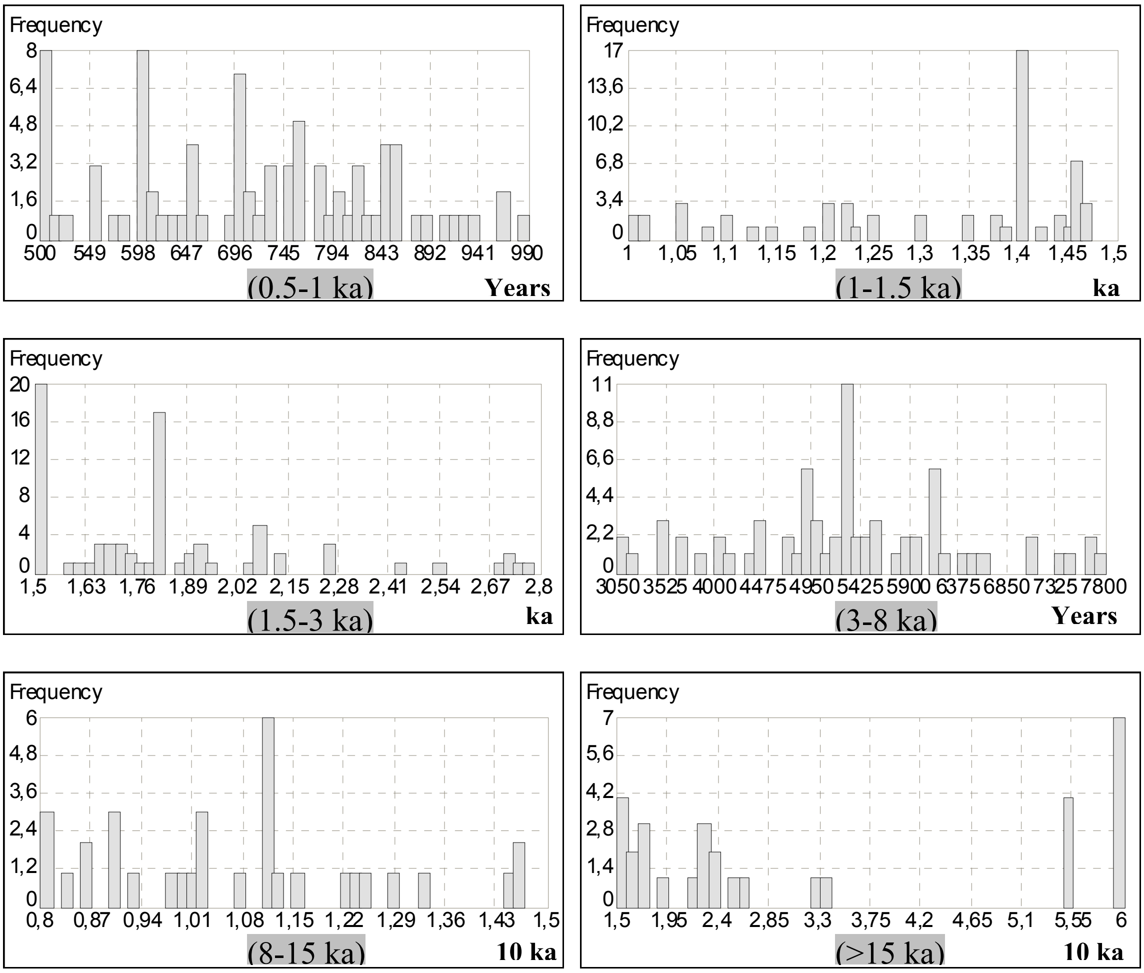


Fig. 24 The dividing and distribution frequency of the records of *Geomys bursarius*

frequency as a function of abundance, the graphs of frequency as a function of MNIs show a similar hollow curve (25a, 25b, 26a, 26b, 27a, 27b). This indicates that typically enormous variations in MNIs at those fossil localities: one or a very few individuals occur at most locations, but tens or hundreds are found at few sites. These enormous variations in the MNIs among sites can not be caused by differences of sedimentary environment and sample errors, but follow exactly the prediction of Brown's "hot spots" model. Sites with much higher MNIs might be located in the hot spots area, while locations with only a few MNIs might be located in the cool spots area. "The more sediment we examine, the more animal remains we find and the more taxa we find represented by those remains" (Lyman, 1995, Grayson, 1984). But intensities of excavation may influence the number of records, but not possibly the MNIs. If the site is in the cool spots of a species, no matter in which sedimentary environment the site is located, no matter how intensively this site has been excavated, the MNIs could not be raised much more.

Thirdly, calculating the Index of Spatial Variation in Abundance (ISVA). ISVA is another parameter for describing the spatial variation in quantity. In the studies of avian distributions based on the BBS, ISVA means the percentage of BBS routes in which more than 50% of the total individuals were recorded. If ISVA<25%, the spatial variation in abundance of the species can be characterized as varying from many "cool spots" where it is very rare, to a few "hot spots" where it is orders of magnitude more abundant (Brown, 1995b). Here ISVA means the percentage of fossil records in which more than 50% of the total MNIs of a species were contained. For example, from 1 to 0.5 ka there are 140 fossil records of *Antilocapra americana* found, which contained 391 fossil individuals in total. >50% of the total MNIs were comprised in only about 13 fossil records, so ISVA can be calculated: 13/140*100% =9%. The criteria of ISVA<25% is also adopted to judge the spatial variation in MNIs. Tab. 2 shows the 70 species' ISVA of different time slices.

The evolution of the range of *Geomys bursarius* has been briefly described in 1.3. Here we focus on the hot spots inferred from MNIs and their movements as the shift of its range. Before 15 ka, about 10% of the records contained more than 50% of the total MNIs (ISVA=10%), and from 15 to 8 ka the ISVA=3%. Fig. 25a shows the frequency distribution of the MNIs: most records contained from one to 5 MNIs, only a few records contained over 20 MNIs. It could also be noticed that the hollow bellow the curve might be much smaller than Brown's curve. In the Faunmap, many records have no information about MNIs. Researchers can easily neglect several MNIs while large number of MNIs can be usually noted in the publication. We enter

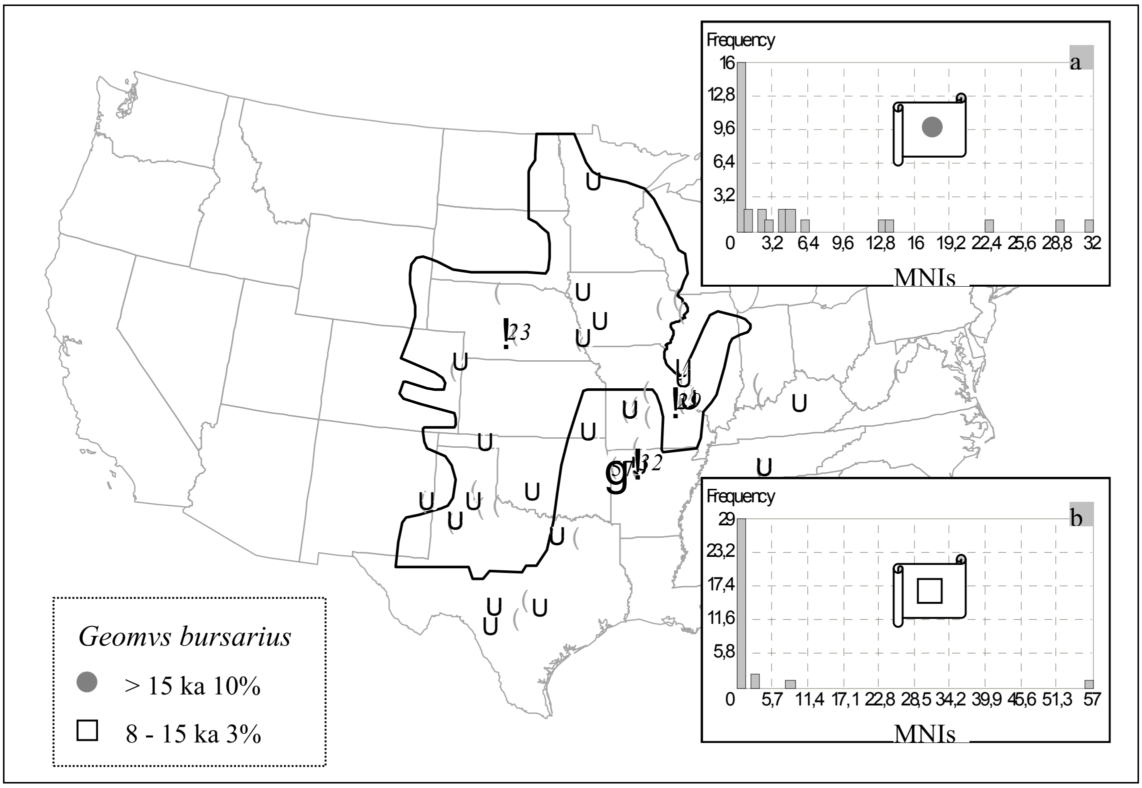


Fig. 25 The evolution of the Arealsystem of *Geomys bursarius* (before 8 ka)

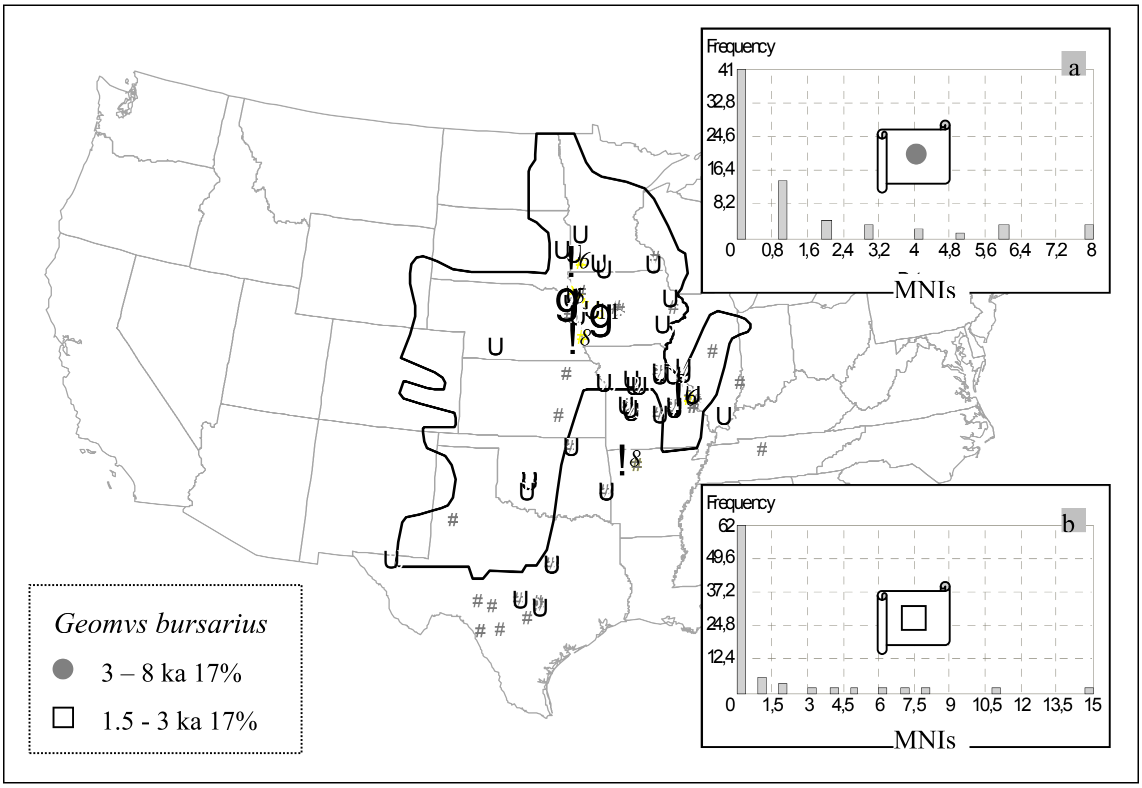


Fig. 26 The evolution of the Arealsystem of *Geomys bursarius* (8-1.5 ka)

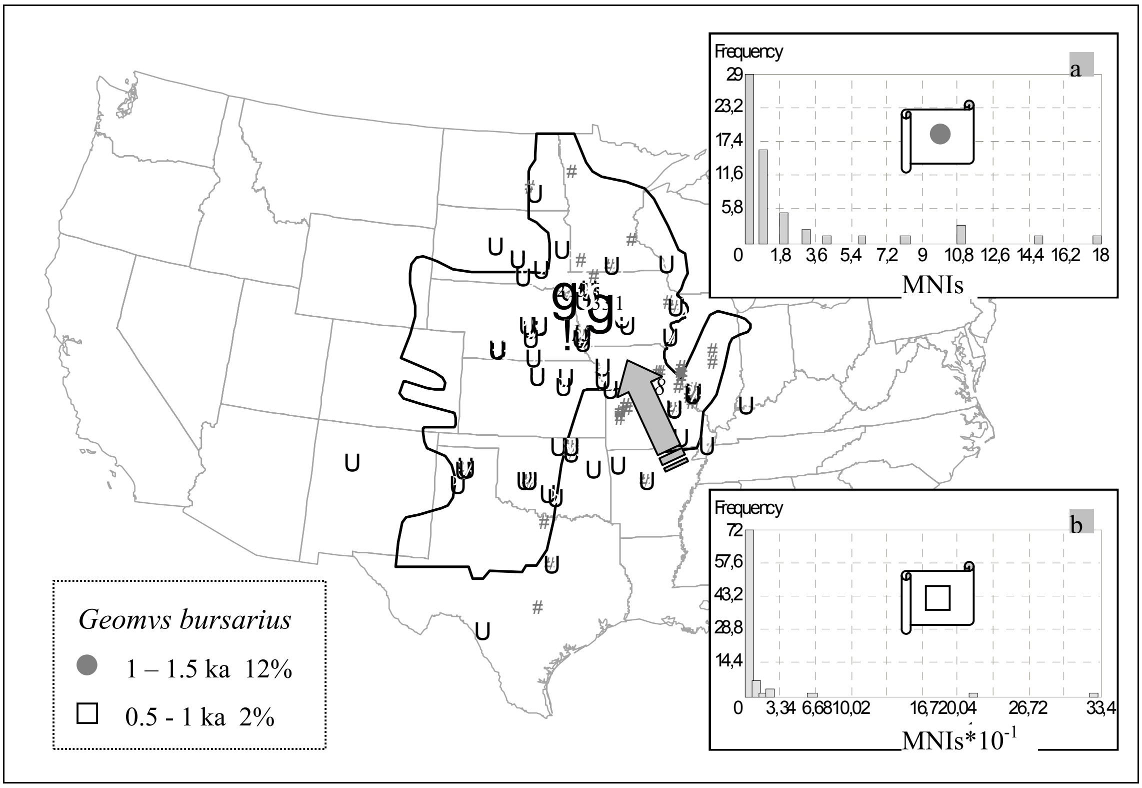


Fig. 27 The evolution of the Arealsystem of *Geomys bursarius* (from 1.5 to 0.5 ka)

“1” into all blank fields of MNIs. This may cause a smaller hollow. The hot spots might be located in northwestern Arkansas, eastern Missouri before 15 ka. And from 15 to 8 ka the hot spots were still in northwestern Arkansas, but might also be in eastern Missouri.

Tab. 11 Index of Spatial Variation in Abundance of different time slices (100%)

Species / Time slices (Ka)	< 0.5	0.5 - 1.0	1.0 - 1.5	1.5 - 3.0	3.0 - 8.0	8.0 - 15	>15
Antilocapra americana	0,10	0,09	0,26	0,15	0,31	0,29	0,50
Bison bison	0,04	0,04	0,03	0,10	0,02	0,03	0,28
Bos taurus	0,13	0,38	0,44	0,50	0,50		
Brachylagus idahoensis	0,25	0,42	0,25	0,04	0,08	0,14	0,05
Canis familiaris	0,06	0,10	0,08	0,35	0,22	0,38	0,50
Canis latrans	0,20	0,18	0,36	0,20	0,44	0,03	0,35
Canis lupus	0,24	0,25	0,38	0,43	0,50	0,29	0,50
Castor canadensis	0,12	0,14	0,18	0,35	0,28	0,48	0,15
Cervus canadensis	0,14	0,17	0,27	0,38	0,26	0,33	0,50
Chaetodipus hispidus	0,11	0,18	0,45	0,50	0,27	0,06	0,17
Clethrionomys gapperi	0,33	0,13	0,40	0,17	0,27	0,07	0,02
Cryptotis parva	0,50	0,50	0,07	0,42	0,02	0,05	0,22
Cynomys ludovicianus	0,14	0,02	0,50	0,29	0,18	0,48	0,48
Didelphis virginiana	0,30	0,27	0,13	0,04	0,01	0,50	0,46
Dipodomys ordii	0,50	0,03	0,21	0,14	0,14	0,17	0,50
Eptesicus fuscus	0,50	0,50	0,33	0,11	0,02	0,02	0,03
Erethizon dorsatum	0,48	0,39	0,43	0,40	0,15	0,46	0,38
Felis concolor	0,39	0,46	0,47	0,50	0,50	0,50	0,50
Geomys bursarius	0,05	0,02	0,12	0,17	0,17	0,03	0,10

Glaucomys volans	0,25	0,17	0,08	0,08	0,03	0,48	0,16
Lemmiscus curtatus	0,14	0,07	0,26	0,24	0,37	0,33	0,08
Lepus americanus	0,20	0,13	0,43	0,15	0,23	0,06	0,14
Lepus californicus	0,06	0,02	0,06	0,04	0,03	0,02	0,47
Lepus townsendii	0,24	0,24	0,36	0,10	0,46	0,08	0,09
Lutra canadensis	0,30	0,31	0,35	0,30	0,29	0,5	0,5
Lynx rufus	0,45	0,29	0,39	0,43	0,26	0,28	0,48
Marmota flaviventris	0,36	0,19	0,38	0,24	0,08	0,07	0,05
Marmota monax	0,30	0,13	0,14	0,26	0,01	0,31	0,27
Martes pennanti	0,45	0,41	0,50	0,50	0,47	0,50	0,40
Mephitis mephetis	0,25	0,17	0,30	0,35	0,01	0,48	0,45
Microtus ochrogaster	0,12	0,06	0,15	0,18	0,15	0,03	0,03
Microtus pennsylvanicus	0,13	0,08	0,29	0,11	0,08	0,03	0,03
Microtus pinetorum	0,29	0,42	0,17	0,17	0,13	0,03	0,06
Mustela frenata	0,43	0,38	0,50	0,04	0,35	0,03	0,38
Mustela vision	0,22	0,37	0,35	0,29	0,10	0,38	0,39
Neotoma cinerea	0,22	0,16	0,19	0,04	0,13	0,08	0,03
Neotoma floridana	0,10	0,40	0,04	0,38	0,01	0,08	0,06
Neotoma lepida	0,50	0,30	0,31	0,07	0,07	0,10	0,50
Ochotona princeps					0,45	0,37	0,38
Odocoileus hemionus	0,30	0,01	0,05	0,17	0,13	0,28	0,26
Odocoileus virginianus	0,03	0,04	0,02	0,03	0,02	0,05	0,41
Ondatra zibethicus	0,17	0,10	0,13	0,19	0,12	0,44	0,36
Onychomys leucogaster	0,11	0,14	0,33	0,50	0,09	0,08	0,20
Oryzomys palustris	0,27	0,12	0,31	0,50	0,11	0,50	0,50
Ovis canadensis	0,23	0,09	0,15	0,05	0,11	0,34	0,50
Perognathus parvus	0,50		0,20		0,10	0,17	0,20
Peromyscus maniculatus	0,11	0,04	0,16	0,14	0,18	0,03	0,03
Scalopus aquaticus	0,06	0,39	0,20	0,33	0,15	0,39	0,20
Sciurus carolinensis	0,15	0,16	0,11	0,11	0,02	0,42	0,31
Sciurus niger	0,39	0,09	0,09	0,19	0,15	0,44	0,44
Sigmodon hispidus	0,20	0,19	0,46	0,13	0,06	0,07	0,41
Sorex cinereus		0,36		0,50	0,45	0,11	0,06
Spermophilus townsendii	0,25	0,33	0,21	0,12	0,11	0,20	0,04
Spermophilus tridecemlineatus	0,03	0,14	0,31	0,29	0,43	0,08	0,18
Spermophilus variegutus	0,43	0,04	0,41	0,33	0,13	0,43	0,50
Spilogale putorius			0,40	0,50	0,07	0,50	0,30
Sus scrofa	0,13	0,50	0,50	0,50	0,50		
Sylvilagus auduboni	0,06	0,05	0,08	0,06	0,12	0,14	0,50
Sylvilagus floridanus	0,30	0,09	0,05	0,18	0,01	0,42	0,04
Sylvilagus nuttallii	0,12	0,09	0,13	0,05	0,03	0,05	0,05
Synaptomys cooperi		0,33	0,15	0,36	0,05	0,04	0,05
Tamias hudsonicus	0,50	0,08	0,22		0,19	0,08	0,14
Tamias striatus	0,19	0,13	0,11	0,09	0,02	0,13	0,07
Taxidae taxus	0,38	0,20	0,43	0,32	0,31	0,04	0,50
Thomomys bottae	0,30	0,03	0,20	0,19	0,18	0,10	0,04
Thomomys talpoides	0,20	0,12	0,23	0,32	0,02	0,06	0,08
Urocyon cinereoargenteus	0,23	0,06	0,46	0,38	0,14	0,50	0,44
Ursus americanus	0,15	0,08	0,44	0,39	0,28	0,50	0,30
Vulpes velox	0,10	0,36	0,50	0,11	0,44	0,47	0,44
Vulpes vulpes	0,50	0,30	0,50	0,02	0,45	0,03	0,41

Both ISVAs from 8 to 3 ka and from 3 to 1.5 ka are 17%, and <25%. From 8 to 3 ka the hot spots started to appear in the northern part of its range such as in Iowa. From 3 to 1.5 ka, the hot spots might have disappeared from northwestern Arkansas. From 1.5 to 1 ka the ISVA = 12%, and from 1 to 0.5 ka the ISVA= 2%. Both are less than 25%. After 1.5 ka its distribution was much more northerly oriented than before, and the hot spots was also in the northern part of its range. The gray arrow shows the movement of hot spots.

3. 4 THE SPATIAL MOVEMENT OF HOT SPOTS WITHIN THE RANGES

Our study has revealed similar patterns in the spatial distribution of abundance within a range as revealed in the Brown’s studies of avian distributions based on the BBS. But several new patterns have been found in our analysis of fossil data:

(1). The center of range may not always present the place where highest abundance occurs. In the dispersal stage and the developmental stage the highest abundance often occurred on the expanding edge of the range. This can be seen in the distributions of many species such as *Odocoileus virginianus*, *Odocoileus hemionus*, *Clethrionomys gapperi*, *Brachylagus idahoensis*

(2). From Tab. 11 it can be seen that for 68 of the 70 mammal species analyzed, their ISVA < 25% in more than one time slice. but there exist temporal differences (Fig. 28). In the last 500 years, of the 50 mammals analyzed, 32 species have an ISVA < 25%, the percentage is 64%, while from 500 to 1000 years ago the percentage is 73%. This can also be seen from Tab. 12. But this could be well explained with Brown’s Model. Different periods have different environmental conditions. In the glacial time, the environmental conditions were much worse than in other periods. Such conditions of local environment could not meet the requirements of much more species. These species had thus no chance to develop their hot spots, so the percentage is relatively low (61%). In contrast to that, the period between 3000 and 8000 years ago is often referred to as the Holocene Climatic Optimum, which was much warmer than the present. Much more species could develop their hot spots in such conditions. That is why the percentage is relatively high (79%). Comparing with artiodactyls and rodents, the ISVA of carnivores is often more than 25%, especially during periods of unstable environment (Tab. 11, 12). This indicates that the development of hot spots of carnivores can more easily be affected by environmental conditions.

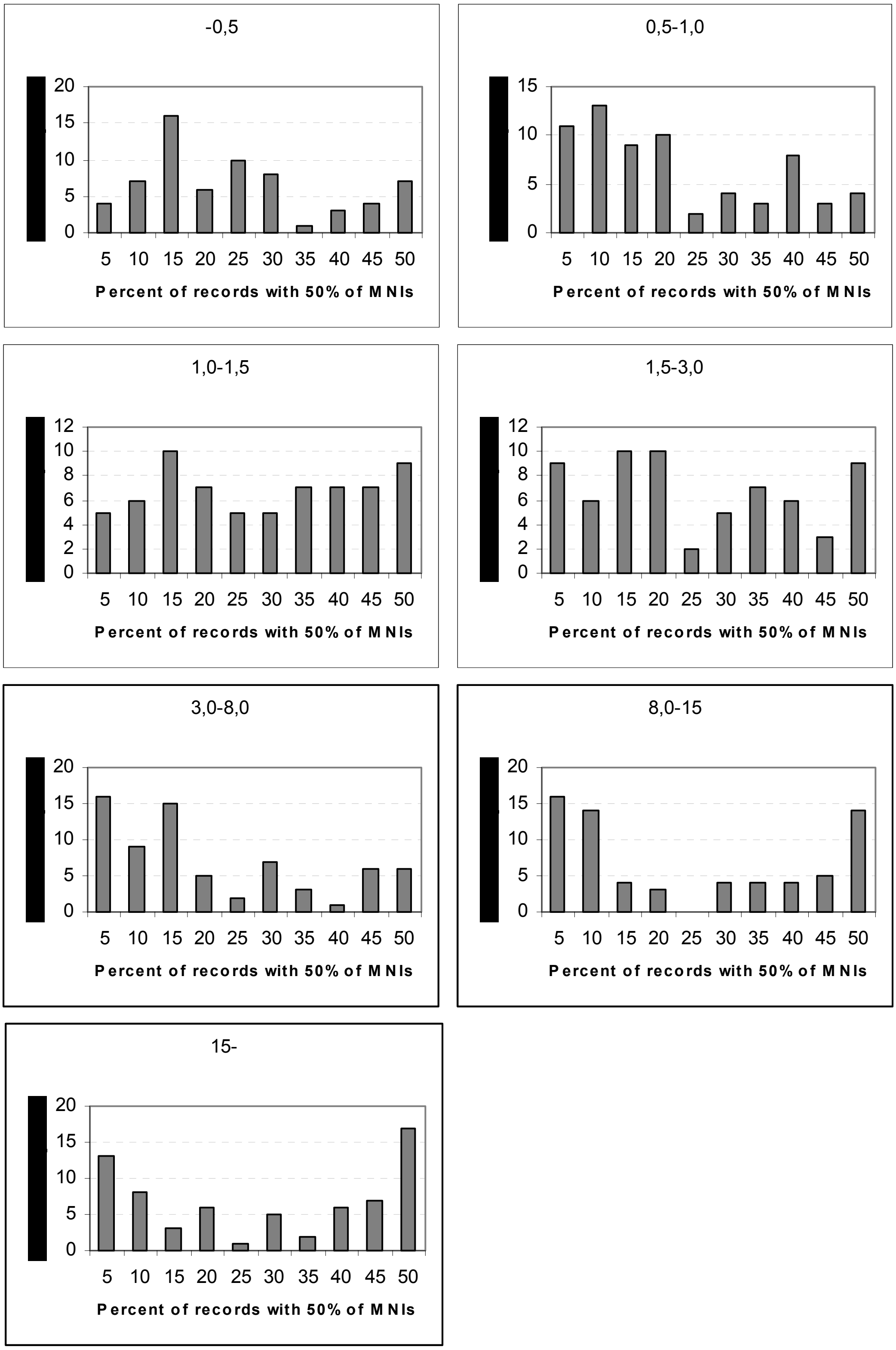


Fig. 28 The temporal differences in number of species

(3). Brown’s study shows that at many sites abundances of particular have remained quite similar over the last 20 years, while there are some changes in abundance at local sites over time. But we can not still know from Brown’s study if the hot spots of many species tend to concentrate relatively in one area. Owing to the separate of record in time, we did not check the spatial autocorrelation between abundances and the distances among localities. Our study shows that the hot spots of many species can remain relatively in a place over thousands of years. Of the 70 mammals analysed, 27 species show that their hot spots have not moved a lot within their ranges over the last 15 ka. Many species could keep their hot spots in the Rocky Mountain Refugium till 1.5 ka. However, our study also shows that a large movement of hot spots happened mainly around 1.5-1 ka (Fig 29). This is coincident with the temporal differences in the percentage of species with an ISVA < 25% (Tab. 12), which shows that during 1.5-1 ka the percentage is lowest. This will be discussed in detail in chapter 4 and chapter 5.

Tab. 12 The percentage of species with an ISVA < 25% of different periods

Time slices (ka)	< 0.5	0.5 – 1.0	1.0 – 1.5	1.5 – 3.0	3.0 – 8.0	8.0 – 15	>15
with carnivore	0,65	0,67	0,49	0,55	0,67	0,54	0,46
with out carnivore	0,64	0,73	0,62	0,65	0,79	0,62	0,61

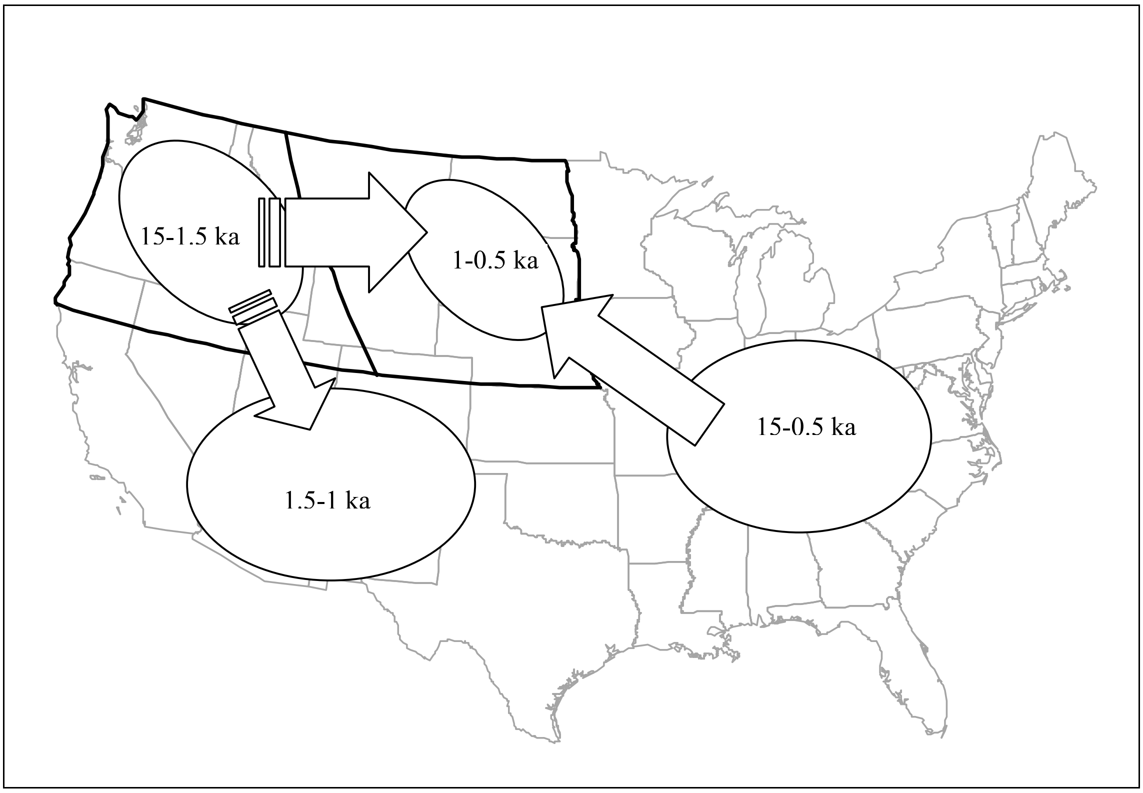


Fig. 29 The movement of hot spots around 1.5-1 ka

CHAPTER 4 TEMPORAL VARIATION IN ABUNDANCE IN NW USA: THE LEWIS AND CLARK'S PATTERN

In chapter 3 it is shown that large movements of hot spots happened mainly around 1.5-1 ka. There are three directions: (1) from the west side to the east side of the Rockies; (2), from the East of the USA to the east side of the Rockies; (3) from the west side of the Rockies to the Southwest of the USA. In this chapter, the first two directions of movement will be considered. The third one will be discussed in the next chapter. The evolution of Arealsystems of relevant mammals will be described here in detail. Two aspects have been emphasized in the description: the dispersal of mammals revealed by the spatial dynamic distribution of fossil records and the hot spots inferred from MNIs (ISVA and the frequency distribution). From the evolutionary process we know the time and directions of shift of the hot spots.

One may doubt the hot spots inferred from MNIs and their movements, but we will show that these findings can be verified by the historical observation of Lewis and Clark. In 1804, President Thomas Jefferson sanctioned and funded one of the most important expeditions in North America's history. Meriwether Lewis and William Clark set off from St Louis, Missouri, with a commission to survey the upper Missouri River basin and seek a means of crossing the Rocky Mountains to reach the west coast of the continent. The journals of the expedition written by Lewis and Clark supply data on the contemporaneous distribution and abundance of large game such as bison, Wapiti, pronghorn. These include qualitative observations, such as "immense quantities of buffalo, antelopes, bears, deer…" on the east side of the Rockies, while they met only few even no such game on the west side of the Rockies, and also quantitative data in the form of records of game killed to supply food for the expedition (Moore, 2002). These historical data are markers that will be used to test our finding. The western side of the Rockies includes ID, OR, WA and northern UT and NV, the southwest corner of WY, while the eastern side consists of MT, ND, SD, NE and WY (Fig 30). This would make sure that both sides are roughly equal in size and large enough for avoiding the errors of the random samples.

4. 1 THE MOVEMENT FROM THE WEST SIDE TO EAST SIDE OF THE ROCKIES

Artiodactyla

Antilocapridae

4. 1. 1 *Antilocapra americana* **Pronghorn**

The pronghorn lives in grassland, bunchgrass-sagebrush areas and desert. Its Arealsystem covers southeastern Oregon, southern Idaho, southern Alberta, southern Saskatchewan, Montana, and western North Dakota south to Arizona and western Texas (Dig. Ref., Fig. 30a).

Before 15 ka, it distributed mainly in the California, Great Basin, Mexico and Rocky Mountain Refugium. As it became warm, the pronghorn dispersed quickly from its refugia northward and eastward, and might have already reached its current shape and size at about 3000 year ago (Fig. 30). From 15 ka to 3 ka, records with the highest MNIs were found in Idaho and northern Nevada and Utah. The ISVA from 15 to 8 ka equals 29% and the ISVA from 8 to 3 ka equals 31%. Both are a little more than 25%. During 3 and 1,5 ka, about 15% of the records contained

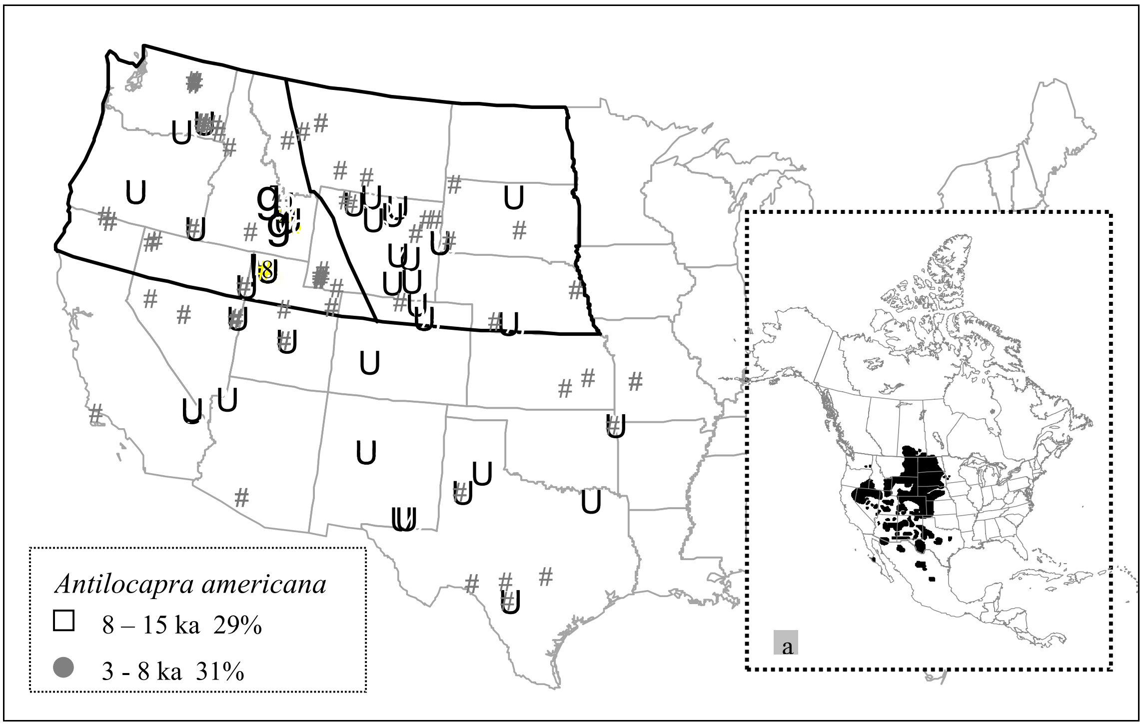


Fig. 30 The evolution of Arealsystem of *Antilocapra americana* (15 – 3 ka)

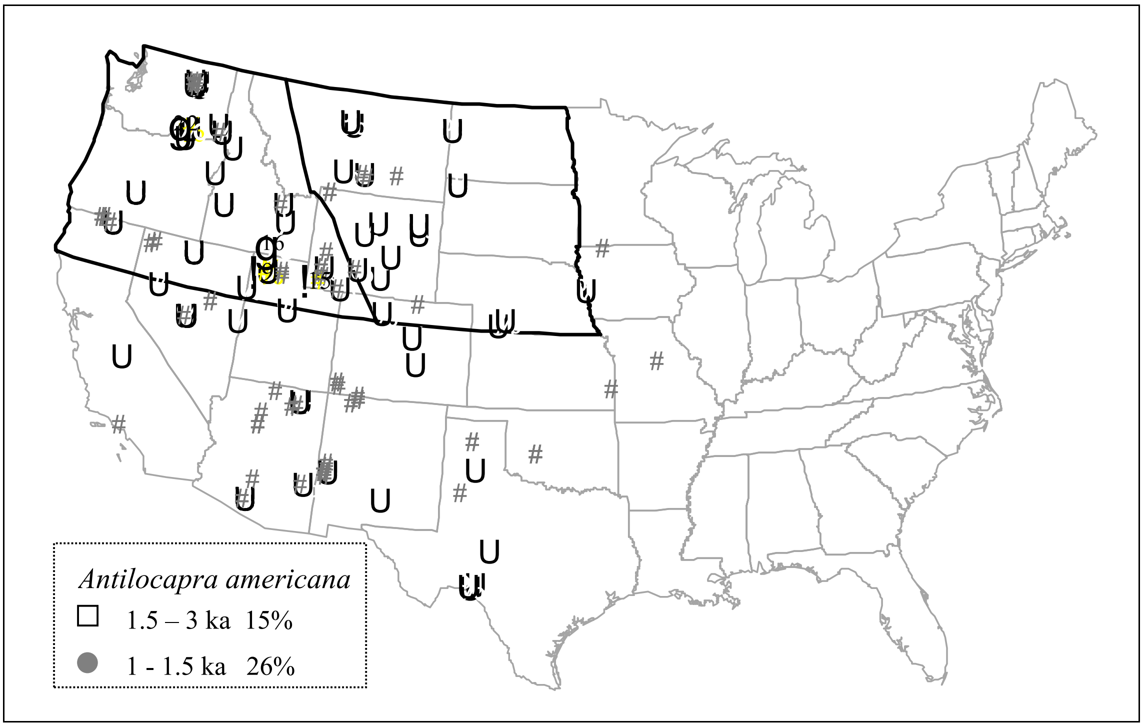


Fig. 31 The evolution of Arealsystem of *Antilocapra americana* (3 - 1 ka)

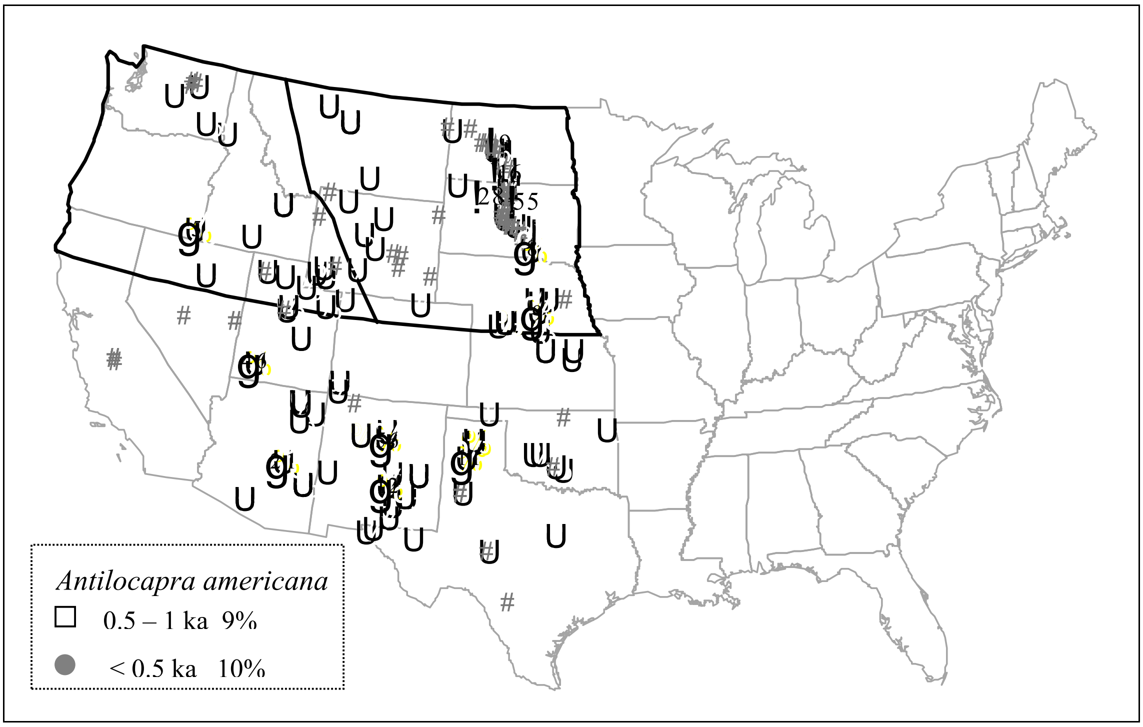


Fig. 32 The evolution of Arealsystem of *Antilocapra americana* (the last 1 ka)

more than 50% of the total MNIs (the ISVA = 15%). The hot spots might be located in southern Idaho and southeastern Washington. From 1,5 to 1 ka about 26% of records contained more than 50% of the total MNIs (the ISVA equals 26%). Records of the highest MNIs appeared still in northern Utah (Fig. 31). After 1 ka the hot spots might have disappeared from the west side of the Rockies. From 1 to 0.5 ka only about 9% records contained more than 50% of the total MNIs, and the hot spots first appeared in southern Utah, Arizona, New Mexico, and then also in Nebraska and South Dakota (Fig. 32). In the last 500 years, the ISVA equals 10%, and the hot spots might be located only in the upper Missouri River area such as North and South Dakota (Fig. 32).

Artiodactyla

Bovidae

4. 1. 2 Bison *bison* American **Bison**

The American bison lives primarily on plains, prairies, and in river valleys, sometimes also in forests. Historically it ranged from southern Northwest Territories to northwestern Mexico, Texas, and Mississippi, and east to southwestern New York, South Carolina, and Georgia (Fig. 34a). Now large, free-ranging herds can only be found at Wood Buffalo National Park, Mackenzie Bison Sanctuary, and Slave River Lowlands in Northwest Territories, Canada, and

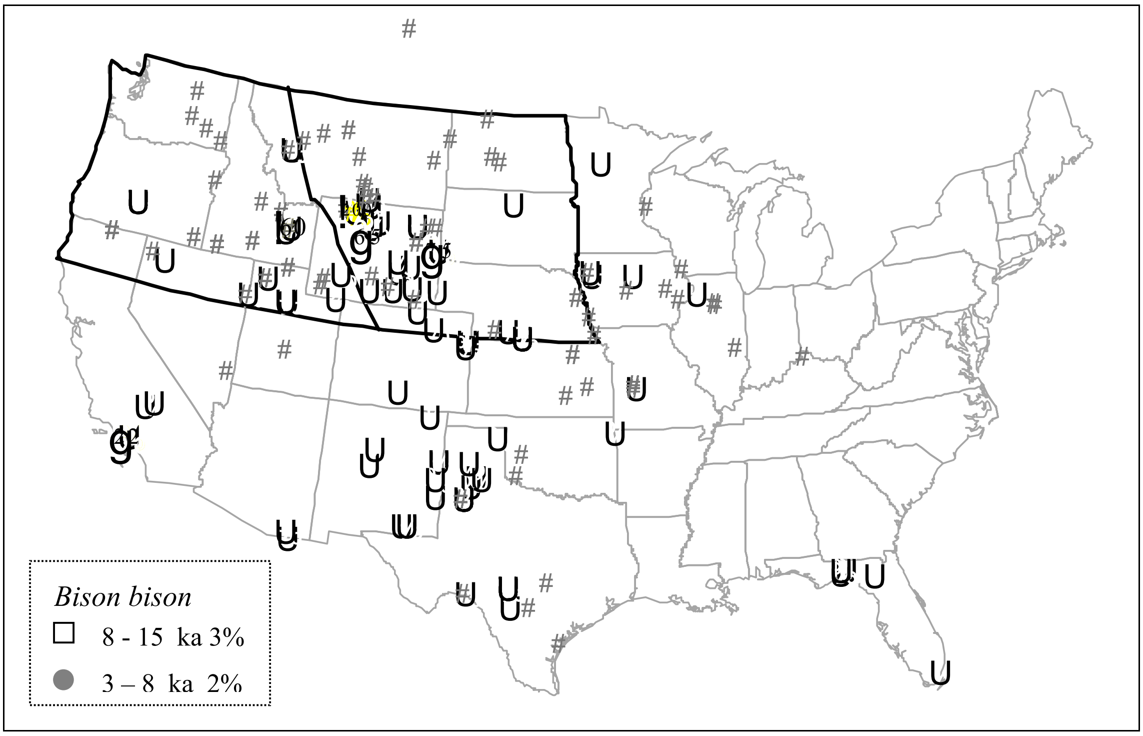


Fig. 33 The evolution of Arealsystem of *Bison bison* (15-3 ka)

in Yellowstone National Park, Wyoming. Small free-ranging herds can be found in Alaska, northeastern British Columbia, northwestern Saskatchewan, and Northwest Territories. Many smaller herds exist in fenced areas (Dig. Ref.) .

During the Last Ice Age, the bison distributed mainly in the California, Rocky Mountain and Florida Refugium, with its hot spots in California. As the ice sheet receded northward, its range expanded rapidly to the area around their refugia. From 15-8 ka its fossil records had already appeared in Illinois. About 3% of the records contain more than 50% of the total MNIs (the ISVA =3%), and the hot spots first appeared in eastern Wyoming. From 8-3 ka it migrated further to the East, reaching Ohio, but might have disappeared in Florida. About 2% of the records contain more than 50% of the total MNIs. And its hot spots started to appear in southern Idaho (Fig. 33).

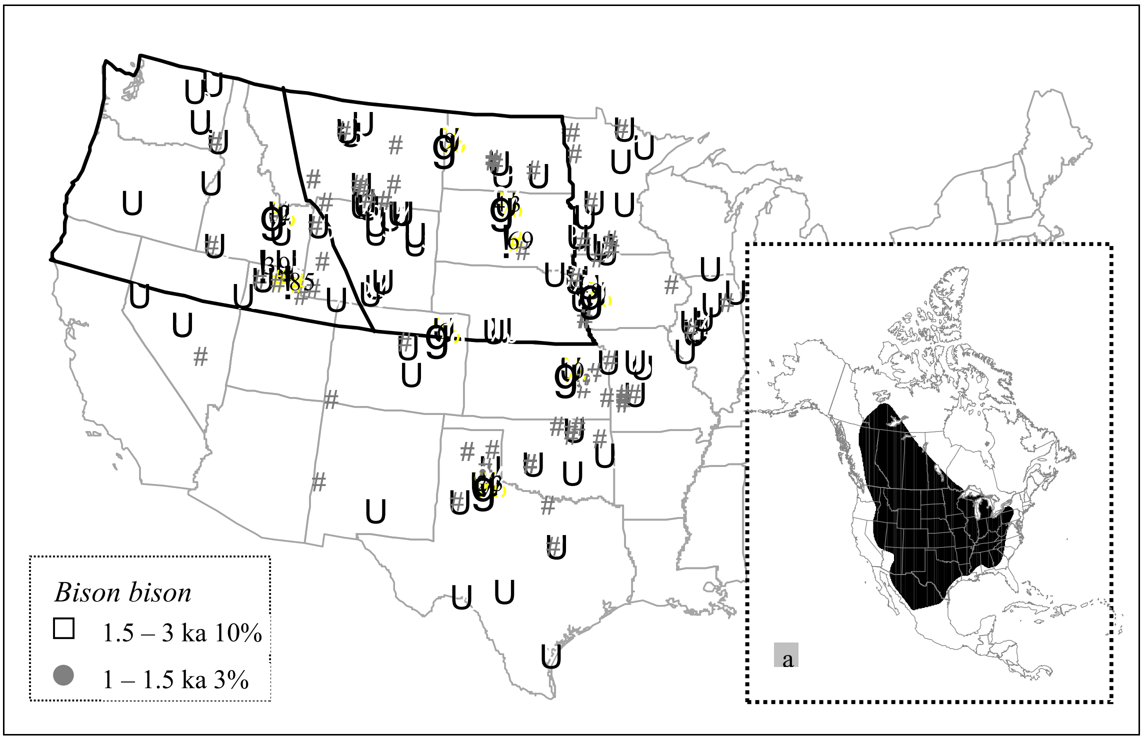


Fig. 34 The evolution of Arealsystem of *Bison bison* (3-1 ka)

Since about 3 ka, it might have disappeared from the California Refugium. From 3-1.5 ka about 10% of the records contained more than 50% of the total MNIs, and the hot spots on the west side of the Rockies were in Idaho, but the hot spots on the east side started to move eastwards to South Dakota, and also first appeared in Texas. From 1.5-1 ka about 3% of the records contained more than 50% of the total MNIs. And the hot spots were almost the same as before. From 1-0.5 ka there were no fossil records found in Minnesota. About 4% of the records contained more than 50% of the total MNIs (Fig. 35). The position of hot spots remained unchanged. In the last 500 years about 4% of the records contained more than 50% of the total MNIs. And the hot spots might have disappeared from the west side of the Rockies, from Texas, and were located only on the east side of the Rockies.

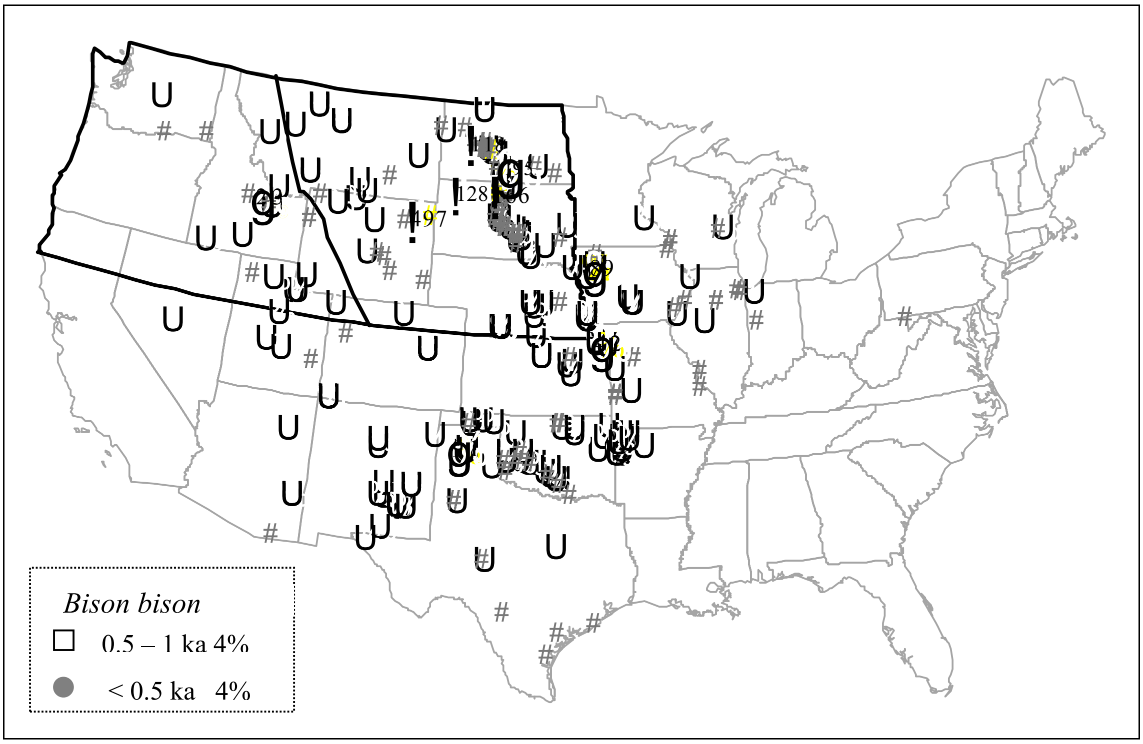


Fig. 35 The evolution of Arealsystem of *Bison bison* (the last 1 ka)

Artiodactyla

Cervidae

4. 1. 3 *Cervus elaphus* **Wapiti**

The Wapiti ranges from eastern British Columbia, central Alberta, central Saskatchewan, and southern Manitoba south to central New Mexico and Arizona, with great numbers in Washington, Montana, Wyoming, and Colorado. Also along the coast from Vancouver Island to northern California, isolated populations elsewhere in California, Nevada, Utah, Arizona, New Mexico, Oklahoma, South Dakota, Minnesota, and Michigan. Small numbers in several eastern states, notably Pennsylvania (Bryanty, 1982) (Fig. 36a).

Before 15 ka the Wapiti mainly distributed in the Appalachia and Rocky Mountain Refugium. From 15-8 ka, it dispersed from the Appalachia Refugium northward, and from the Rocky

Mountain Refugium westward to Oregon and Washington, where records with the highest MNIs

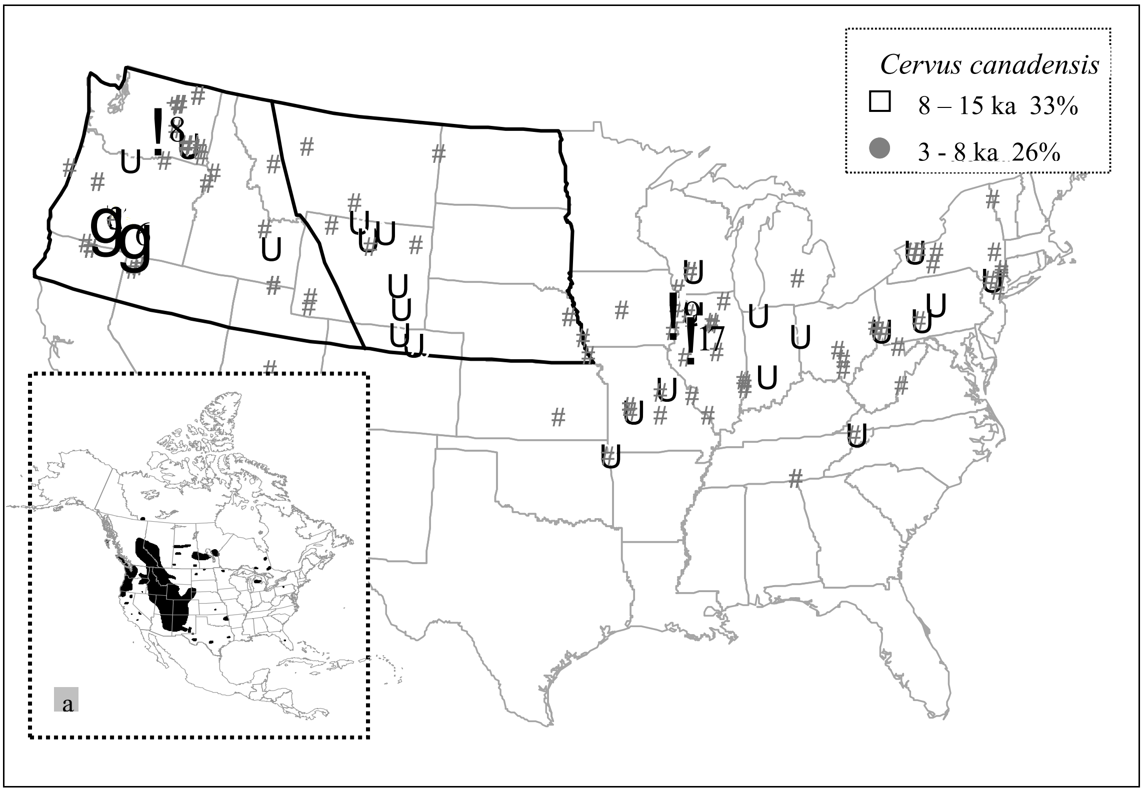


Fig. 36 The evolution of the Arealsystem of *Cervus canadensis* (15-3 ka)

During 3 and 1 ka its distribution remained almost the same as before. Records of the highest MNIs were found again in Illinois, but also in Indiana and coastal Oregon. There were large changes in the internal structure within Wapiti's range during 1-0,5 ka. About 17% of the records contained more than 50% of the total MNIs. The hot spots might have disappeared from northern Illinois and Indiana, and moved eastward to West Virginia, and also northwestwards to Iowa and Nebraska. Since 500 years ago, the hot spots have appeared in South Dakota and coastal Oregon.

However, the Wapiti in the East have been exterminated through overkill and alteration of habitat. The approximate dates of extinction are as follows: Pennsylvania 1867; Arkansas 1834; Indiana, 1812 to 1840; Illinois, 1850s; Maryland, mid-1850s; Kentucky, 1850; Louisiana, 1850; Michigan, 1870s; Missouri, 1898; New Jersey, early 1800s; New York, 1847; North Carolina, late 1700s; Ohio, 1840; South Carolina, late 1700s or early 1800s; Tennessee, 1865; Vermont, 1800; Virginia, 1855; West Virginia, 1875; and Wisconsin, 1875 (Dolan, 1988, Groves, 1987).

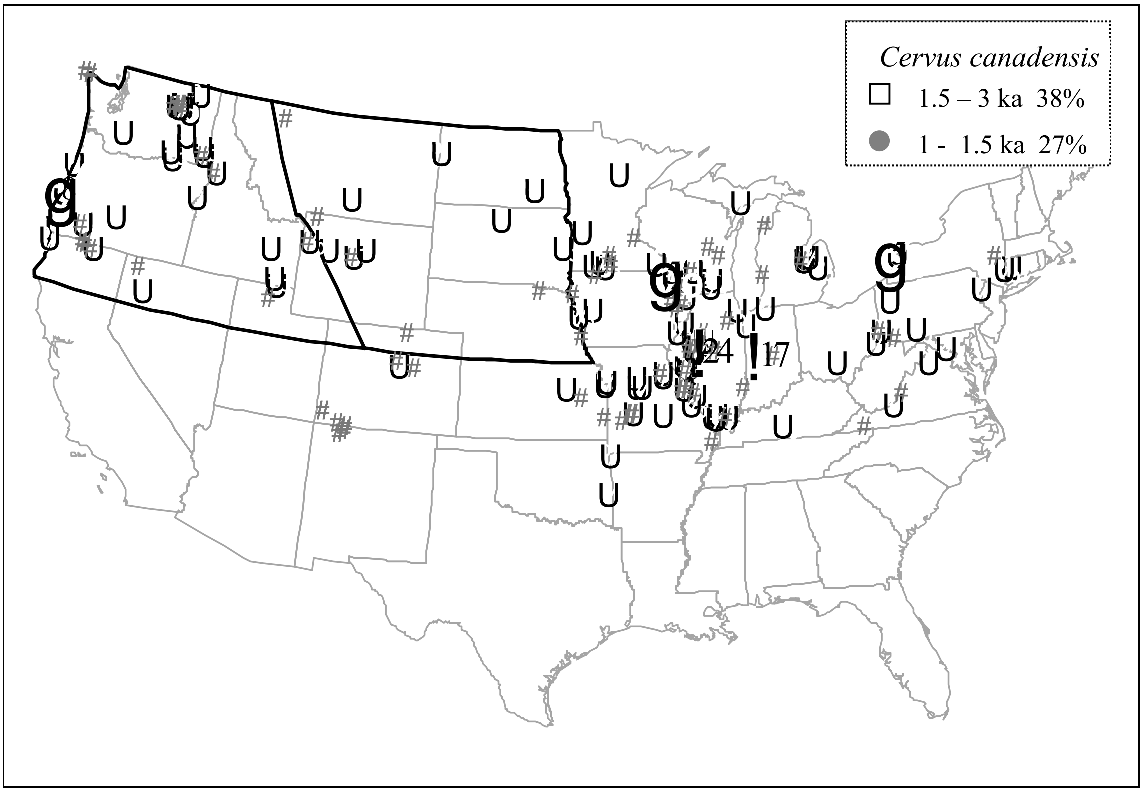


Fig. 37 The evolution of Arealsystem of *Cervus canadensis* (3-1 ka)

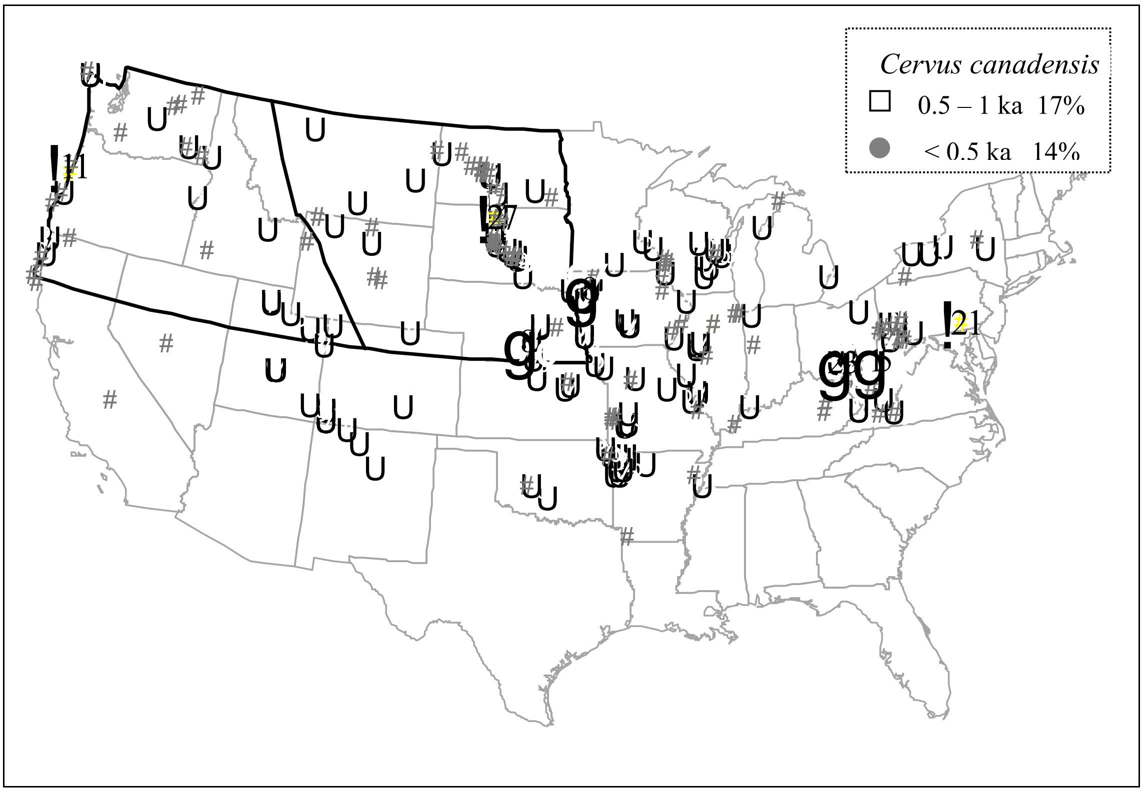


Fig. 38 The evolution of Arealsystem of *Cervus canadensis* (the last 1000 years)

Carnivora

Canidae

4. 1. 4 *Canis latrans* **Coyote**

The coyote lives on open plains in the West, and in brushy areas in the East. Generally it is common throughout eastern and southern Alaska, southern and western Canada. Fossils were found mainly in the West, but it has now extended its range into the entire United States (Dig. Ref., Fig. 40 a).

The coyote distributed almost in all refugia before 15 ka. From 15 to 8 ka, 3% of the records contained more than 50% of the total MNIs. The hot spots were mainly located in California and Idaho. But during the 8 – 3 period, about 44% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were found in Oregon, southern Texas (Fig. 39).

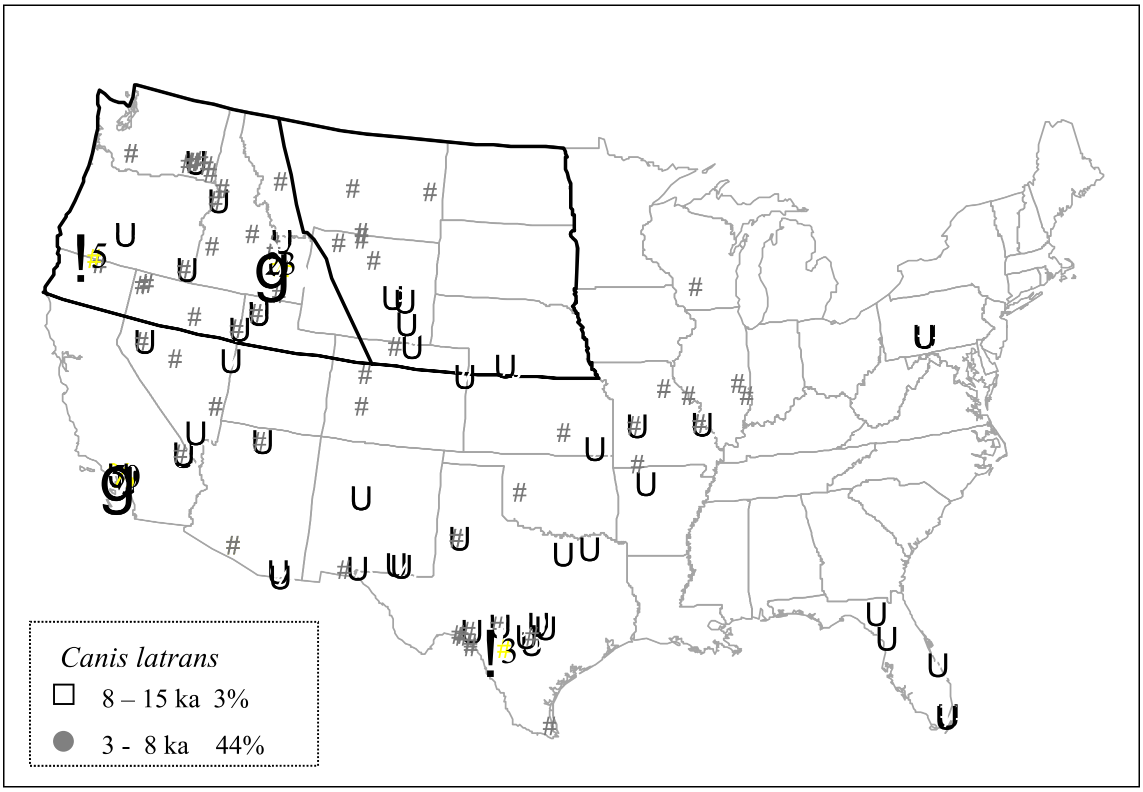


Fig. 39 The evolution of Arealsystem of *Canis latrans* (15 – 3 ka)

During 3 and 1.5 ka, about 20% of the records contained more than 50% of the total MNIs. The hotspots were still in Idaho, but also appeared in southern Arizona. From 1.5 – 1 ka it started to enter the east side of the Rockies. At the same time the hot spots seemed to have left the west

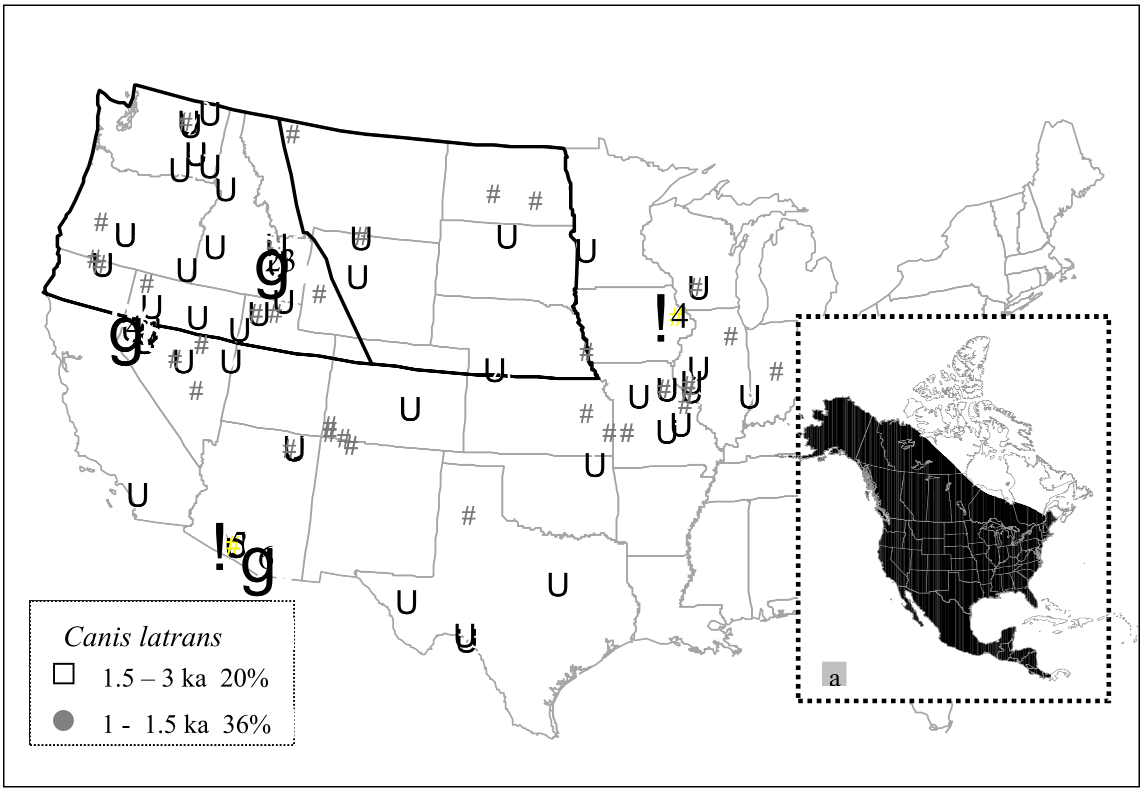


Fig. 40 The evolution of Arealsystem of *Canis latrans* (3 – 1 ka)

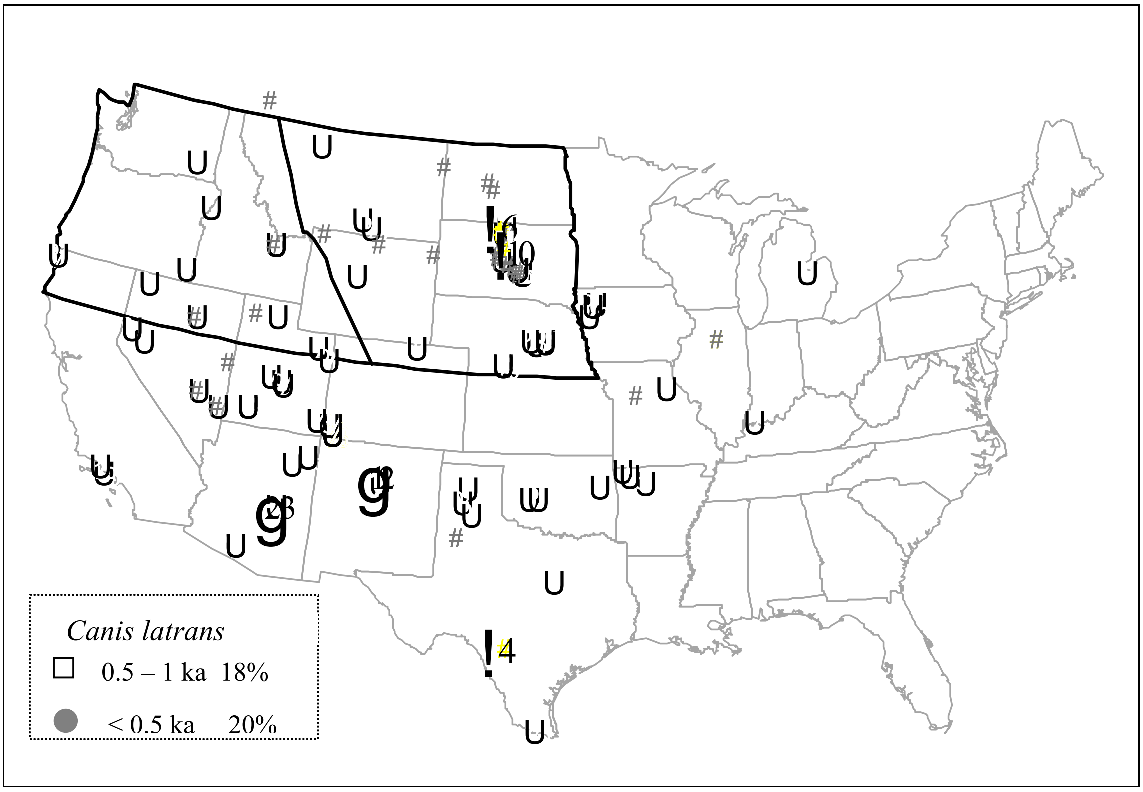


Fig. 41 The evolution of Arealsystem of *Canis latrans* (the last 1 ka)

side of the Rockies. About 36% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were still found in southern Arizona, but also in Iowa (Fig. 40). From 1 to 0,5 ka, 18% of the records contained more than 50% of the total MNIs. The hot spots might be located in Arizona and northern Mexico. In the last 500 years, about 20% of the records contained more than 50% of the total MNIs, and the hot spots first appeared in South Dakota. Since about 8 ka there were no fossil records found in southeastern parts of the USA. This means that the coyote extended its distribution in this area very recently.

Carnivora

Canidae

4. 1. 5 *Canis lupus* **Gray wolf**

Gray wolves' habitat preferences appear to be more prey dependent than cover dependent. It once ranged south to 20° N in Mexico, but has been extirpated from most of the continental USA (Ginsberg, 1990).

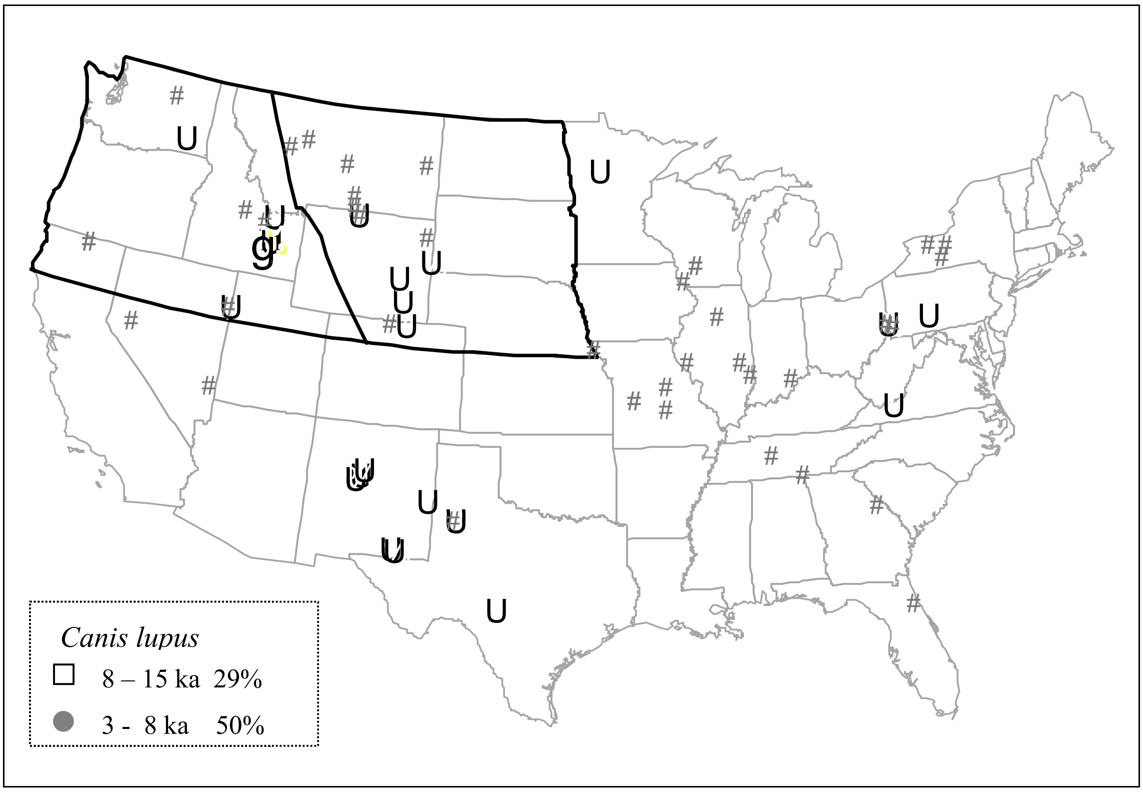


Fig. 42 The evolution of Arealsystem of *Canis lupus* (15 – 3 ka)

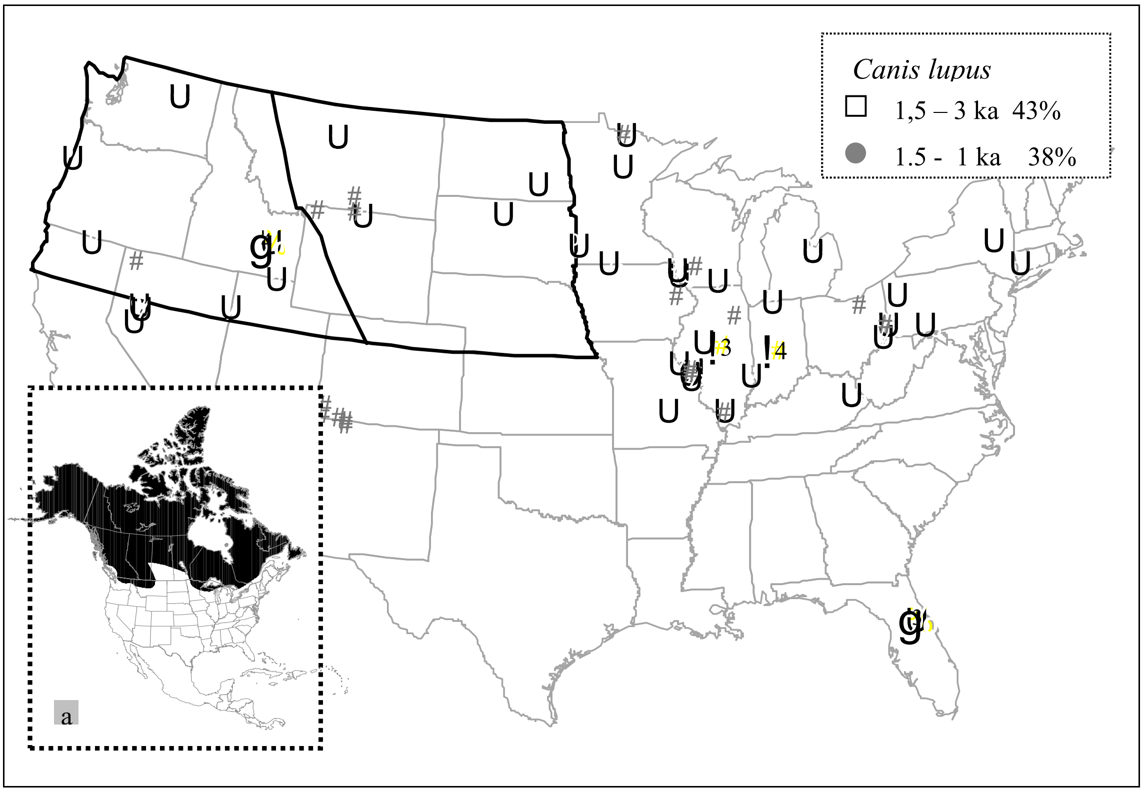


Fig. 43 The evolution of Arealsystem of *Canis lupus* (3 – 1 ka)

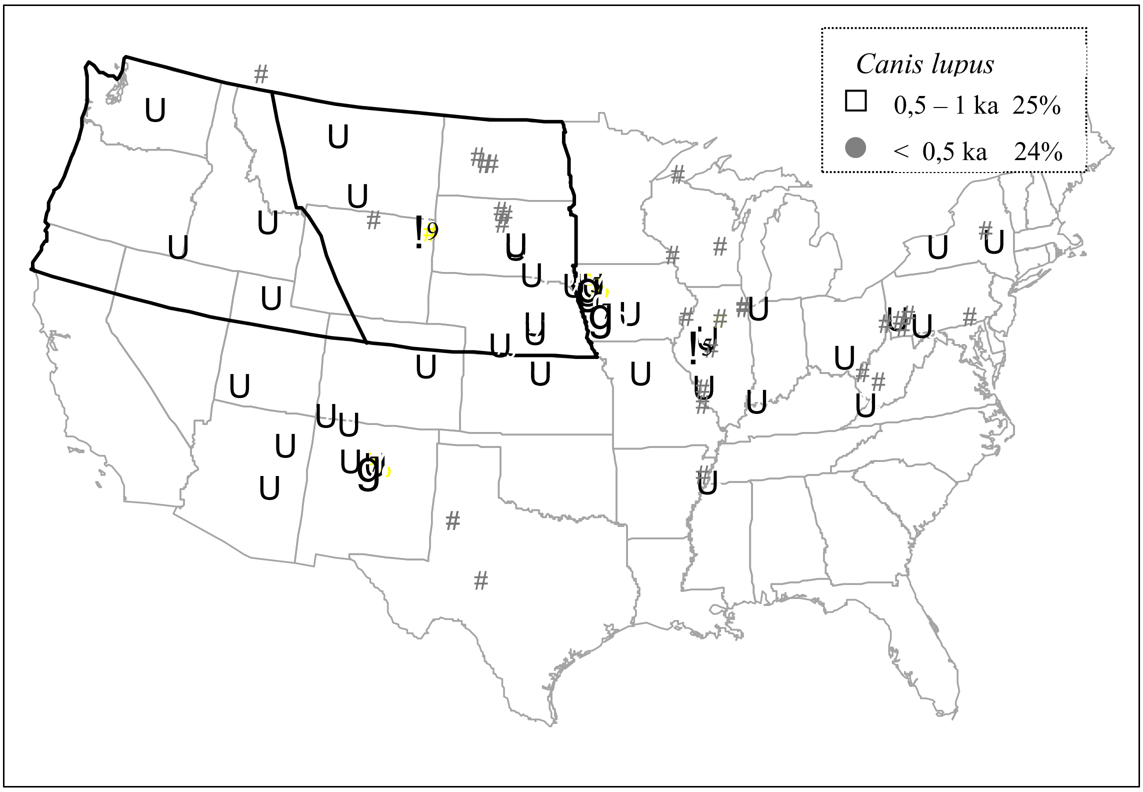


Fig. 44 The evolution of Arealsystem of *Canis lupus* (the last 1 ka)

Just like the coyote, the gray wolf was a polycentric mammal. But since 15 ka, it had disappeared from its California Refugium. During 15 and 8 ka about 29% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were found in Idaho (Fig. 42). From 8 to 1 ka, it seemed that the hotspots were not obvious. During 3 and 1.5 ka it started to enter the east side of the Rookies. About 43% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were still found in Idaho. During 1.5 and 1 ka about 38% of the records contained more than 50% of the total MNIs. Records of the highest MNIs first appeared in Illinois and Ohio (Fig. 43). From 1 to 0.5 ka, about 25% of the records contained more than 50% of the total MNIs, and the hotspots were located in northern Mexico and western Iowa. After 500 ka, about 24% of the records contained more than 50% of the total MNIs. The hot spots first appeared in Montana (Fig. 44).

Carnivora

Canidae

4. 1. 6 *Vulpes vulpes* **Red Fox**

The red fox lives in open areas, woodlands and forests. It reaches as far south as Texas and New Mexico, but absent in part of the Central Plains, Nevada and the Arctic (Fig. 45a).

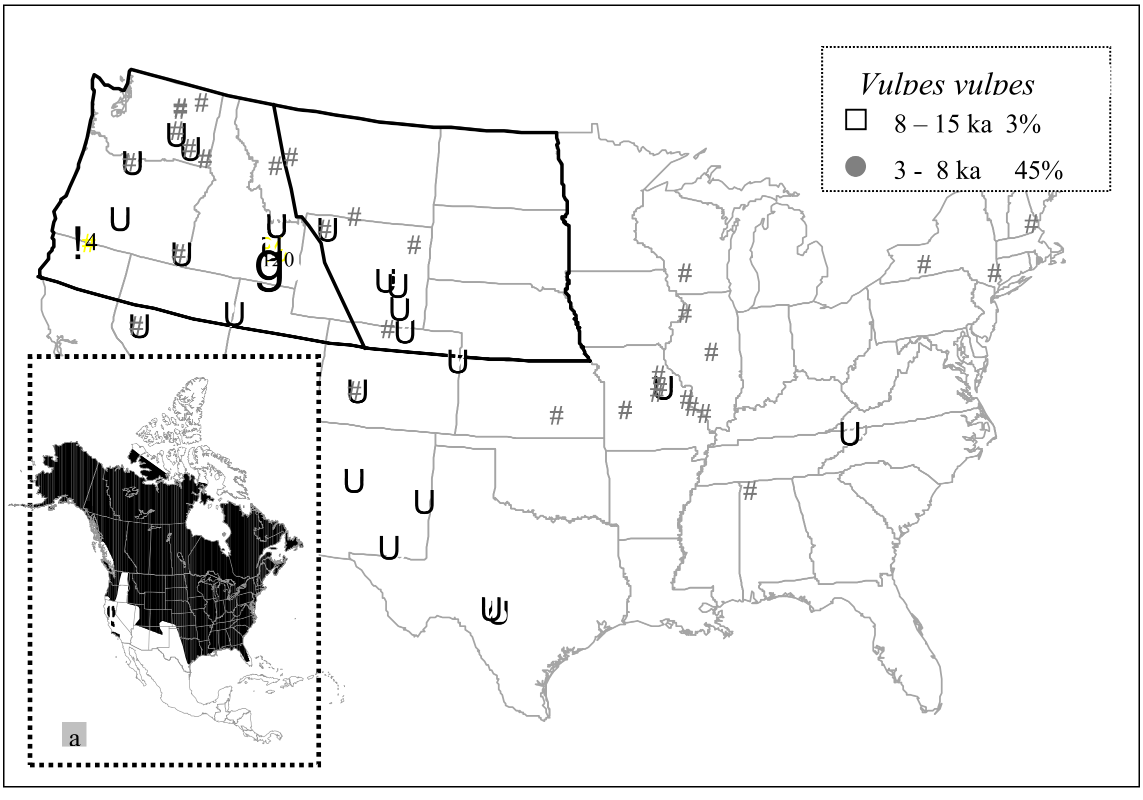


Fig. 45 The evolution of Arealsystem of *Vulpes vulpes* (15 – 3 ka)

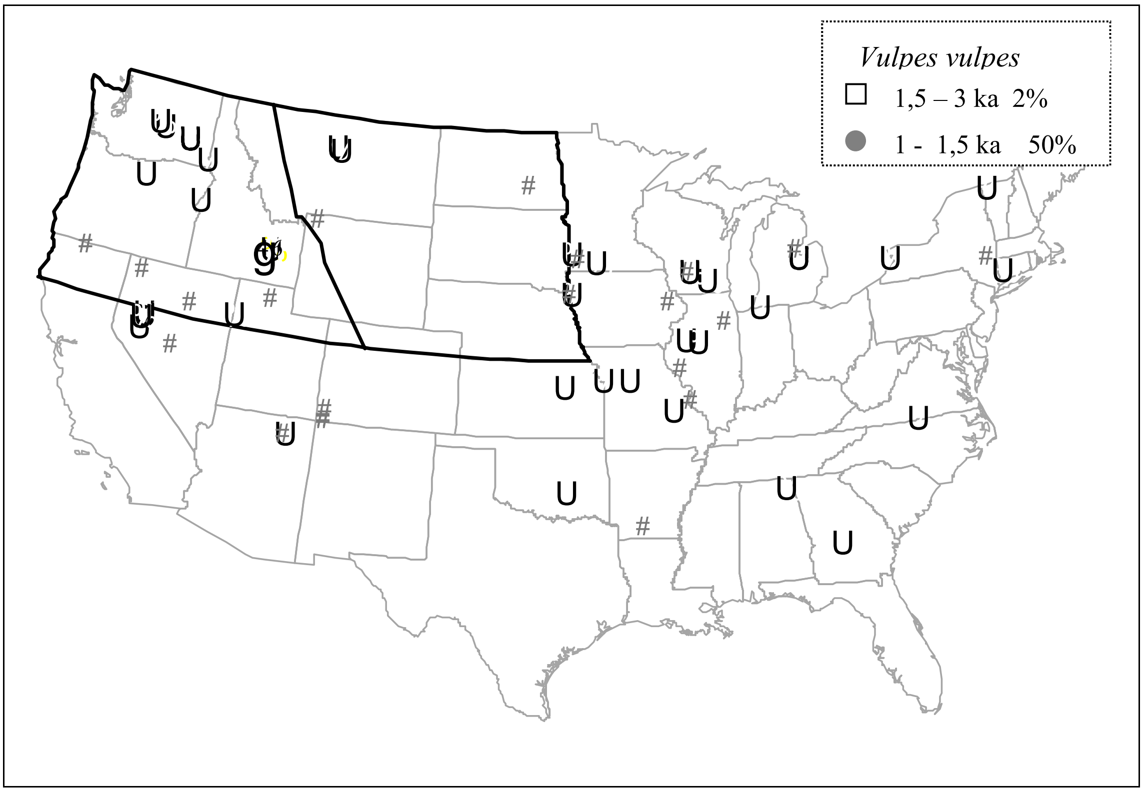


Fig. 46 The evolution of Arealsystem of *Vulpes vulpes* (3 - 1 ka)

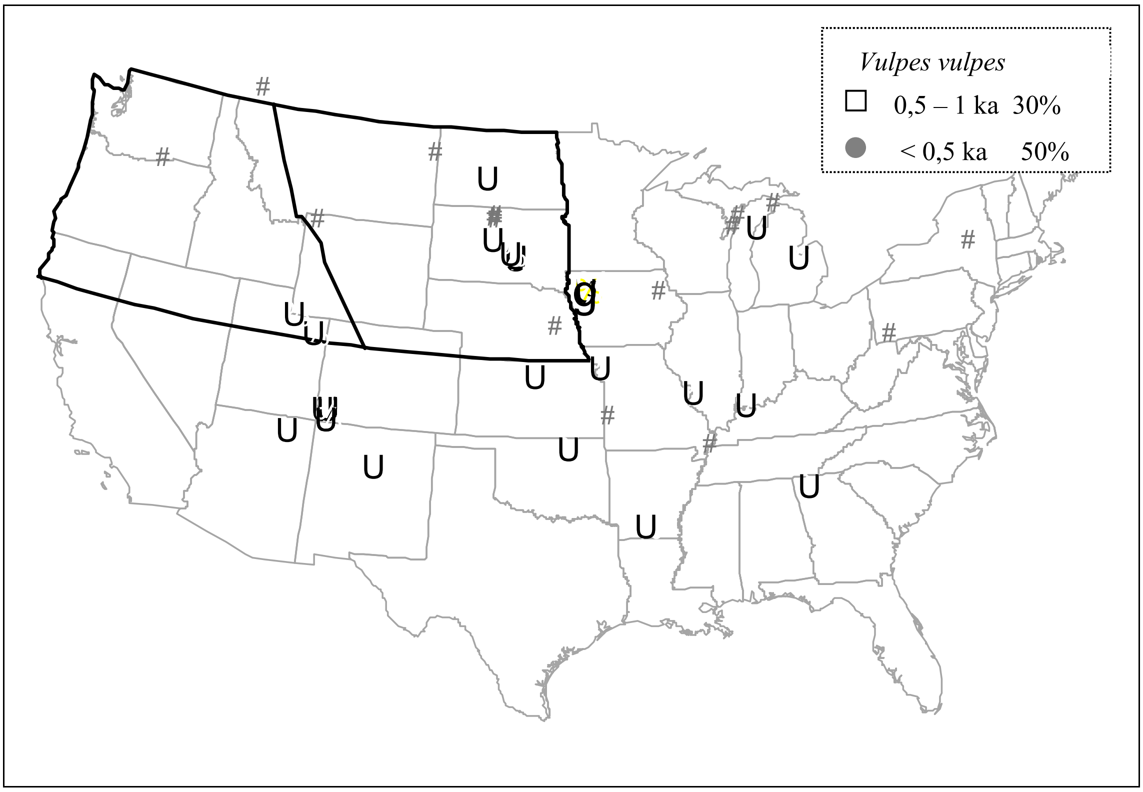


Fig. 47 The evolution of Arealsystem of *Vulpes vulpes* (the last 1 ka)

The red fox distributed mainly in the Appalachia and Rocky Mountain Refugium, and also in northern California and Nevada in the glacial time. From 15 to 8 ka only 3% of the records contained more than 50 % of the total MNIs. Its hot spots were located in southern Idaho (Fig. 45). From 3 to 1.5 ka only about 2% of the records contained more than 50% of the total MNIs. The hot spot were still in southern Idaho. But during 1.5 and 1 ka, the hot spots might have disappeared in the west of the Rockies (Fig. 46). Since 15 ka it had disappeared in California, but it did not disappear in Nevada till 1 ka. After 1 ka, it started to enter the upper Missouri River area. From 1 to 0.5 ka, and about 30% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were found in Iowa (Fig. 47).

Carnivora

Mustelidae

4. 1. 7 *Mustela frenata* **Long-tailed Weasel**

The long-tailed weasel has adapted well to the changes in environment caused by humans. It is found in temperate and tropical habitats in North and Central America (Dig. Ref., Fig. 49a).

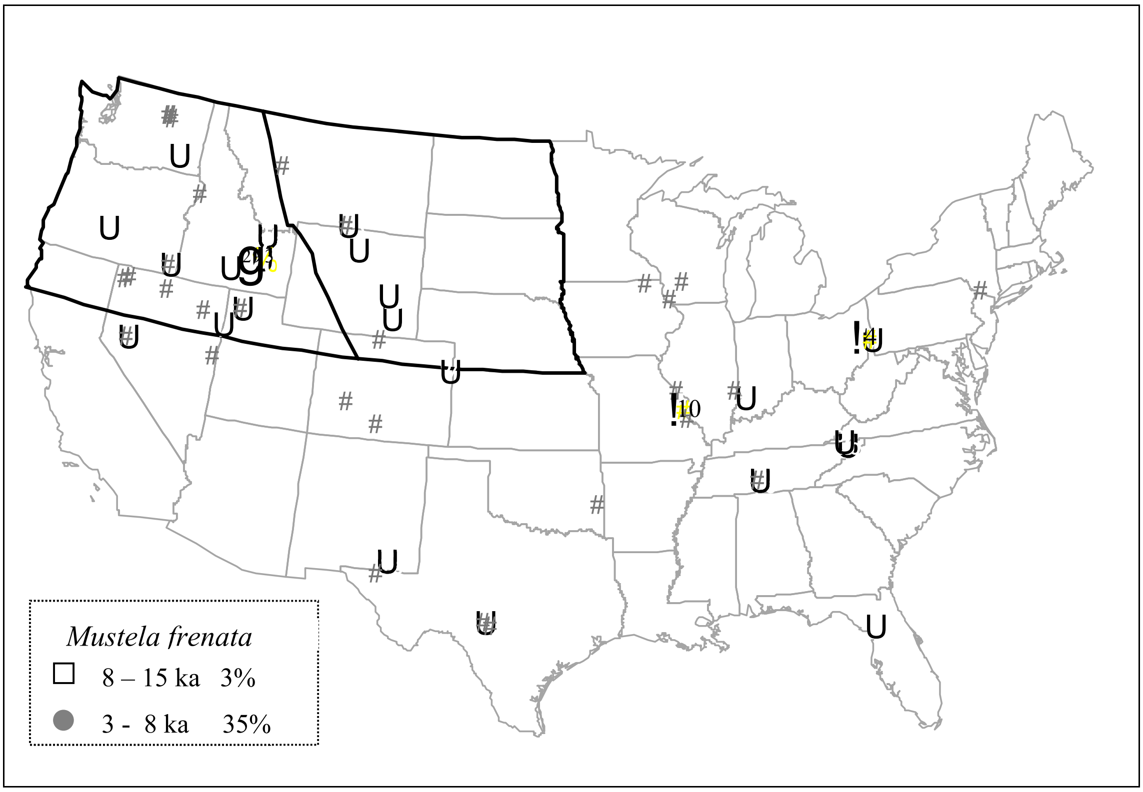


Fig. 48 The evolution of Arealsystem of *Mustella frenata* (15 – 3 ka)

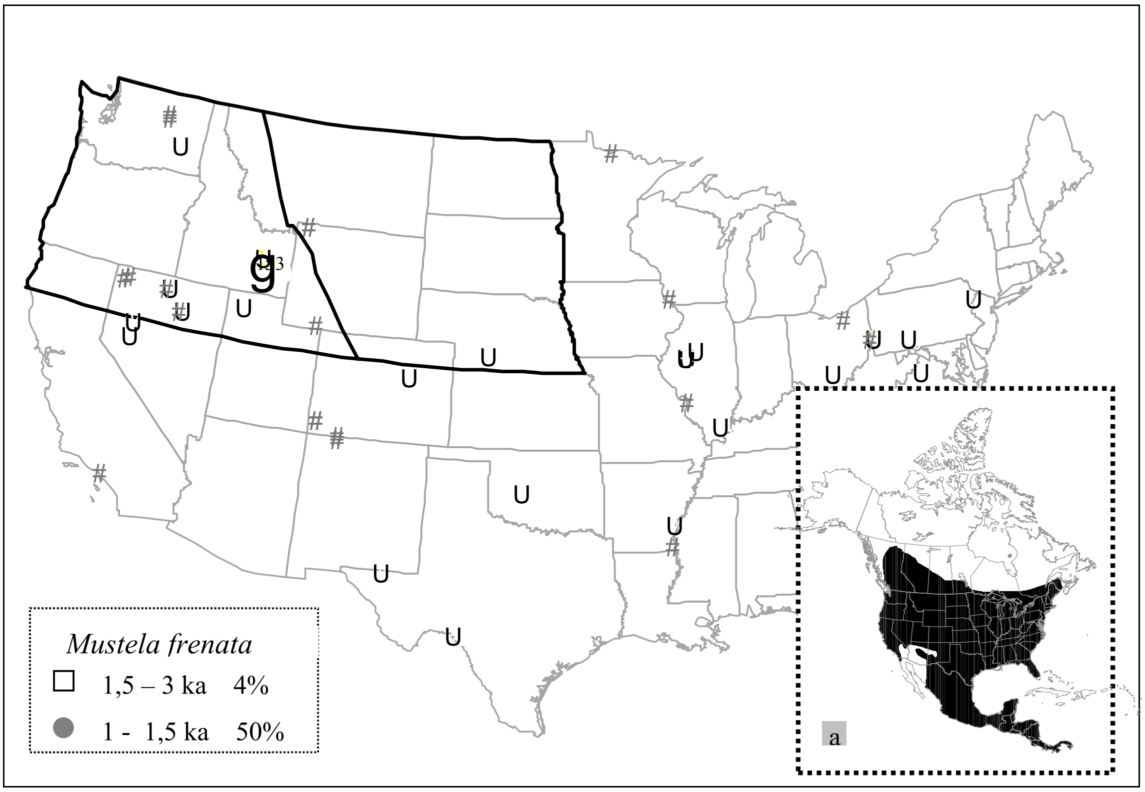


Fig. 49 The evolution of Arealsystem of *Mustella frenata* (3 - 1 ka)

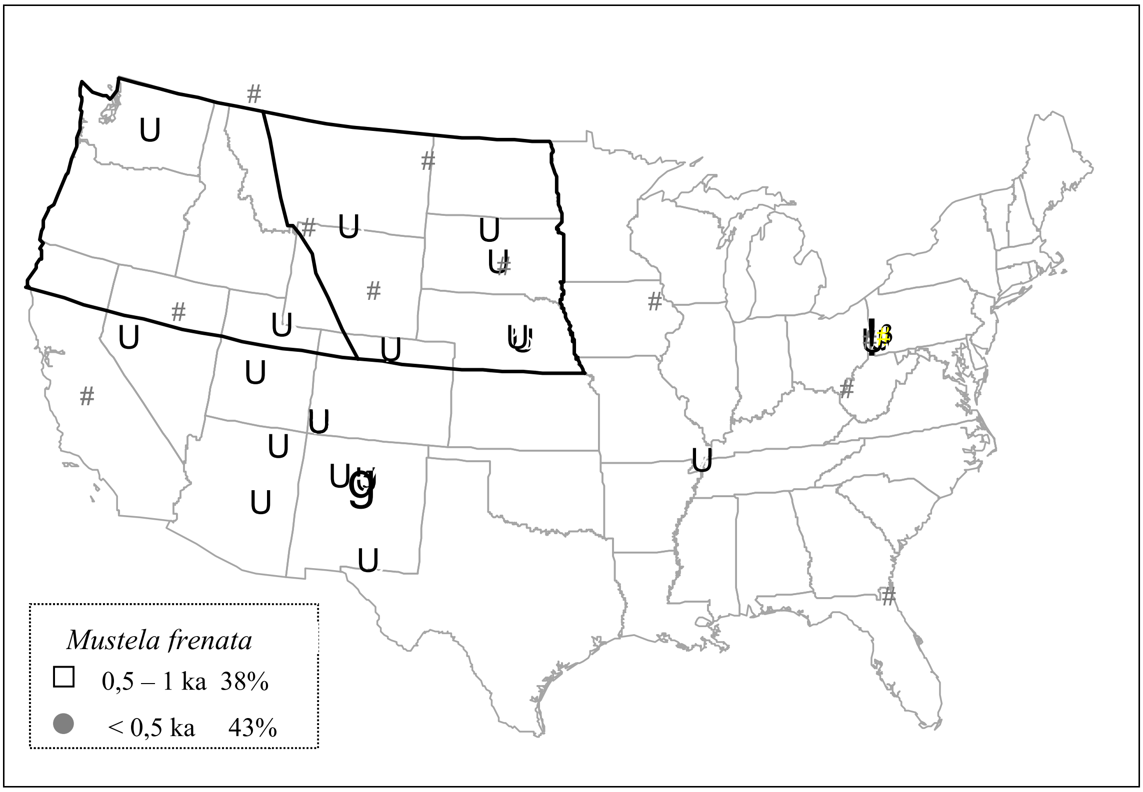


Fig. 50 The evolution of Arealsystem of *Mustella frenata*(the last 1 ka)

The long-tailed weasel distributed almost in all glacial refugia before 15 ka. From 15 to 8 ka, about 3% of the records contained more than 50% of the total MNIs, and the hot spots were located in southern Idaho. But during 8 and 3 ka, about 35% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were found in southern Illinois (Fig. 48). From 3 to 1.5 ka, about 4% of the records contained more than 50% of the total MNIs. The hot spots were still located in southern Idaho (Fig. 49). However, since 1.5 ka, the hot spots did not seem to be obvious any more. During 1 and 0.5 ka, it started to enter the east side of the Rockies. About 38% of the records contained more than 50% of the total MNIs. Records of the highest records were found in New Mexico. And in the last 500 years, about 43% of the records contained more than 50% of the total MNIs (Fig. 50).

Carnivora

Mustelidae

4. 1. 9 *Taxidae taxus* **American Badger**

American Badgers are found principally in dry, open country such as grassland and sagebrush, but some also in forests (Dig. Ref., Fig. 52a) . Badgers distributed mainly in the southwest area such as the California, Mexico, Great basin and Rocky Mountain Refugium before 15 ka. From 15 to 8 ka, about 4% of the records contained more than 50% of the total MNIs, and the hot spots were located in southern Idaho. During 8 and 3 ka, about 31% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were found in Washington (Fig. 51). From 3 to 1.5 ka about 32% of the records comprised more than 50% of the total MNIs. Records of the highest MNIs can still be found in southern Idaho, but also appeared in southern Arizona. During 1.5 and 1 ka the hot spots disappeared from the west side of the Rockies and started to enter the east side of the Rockies. During 1 and 0.5 ka about 32% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were found in northern Mexico and western Iowa.

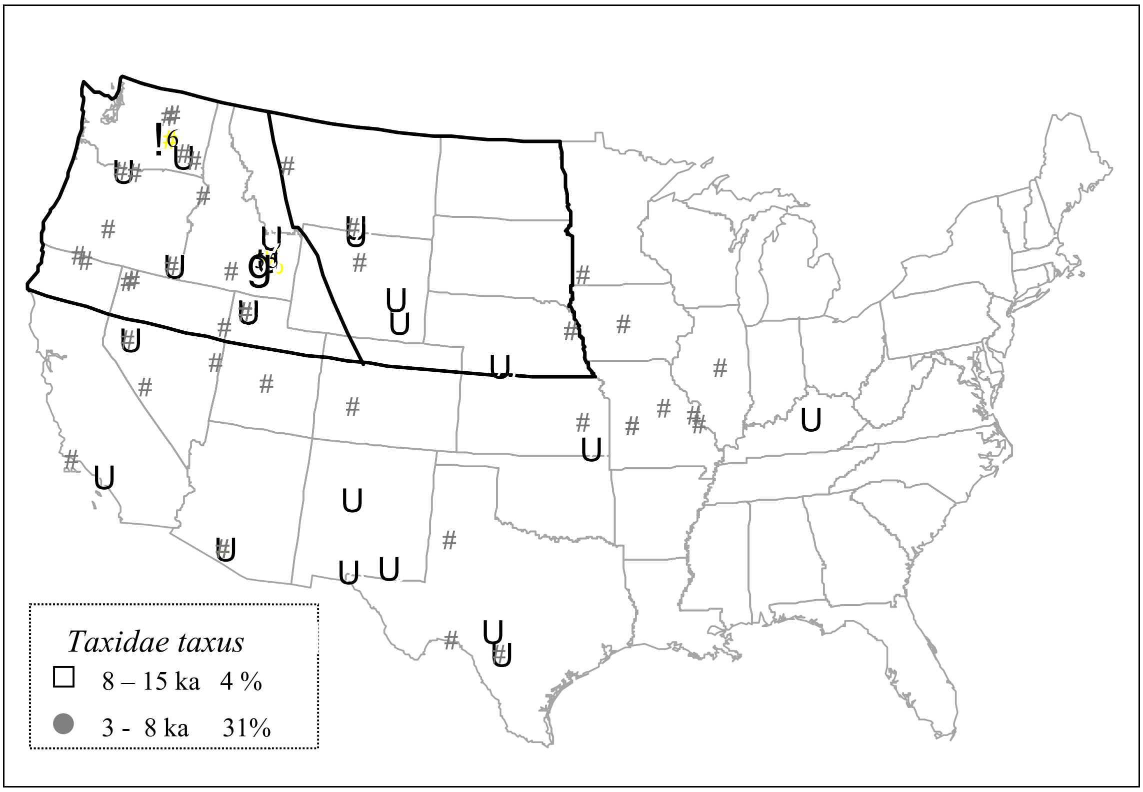


Fig. 51 The evolution of Arealsystem of *Taxidae taxus* (15 – 3 ka)

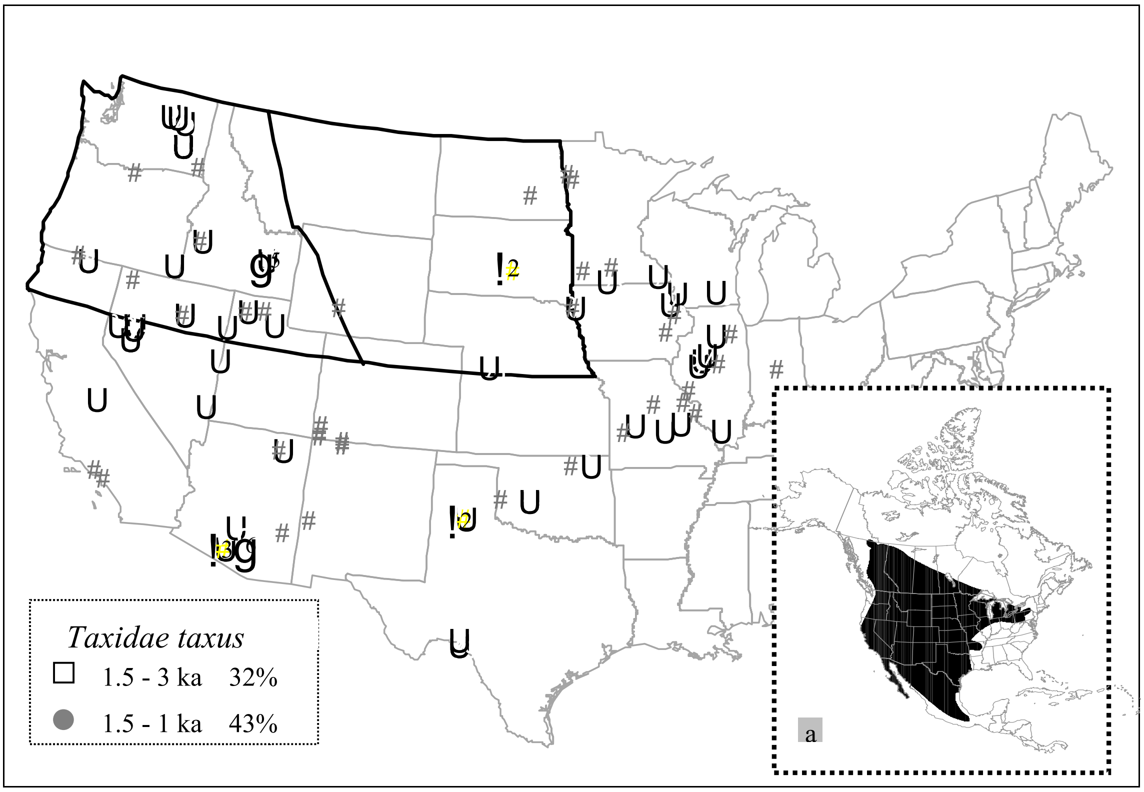


Fig. 52 The evolution of Arealsystem of *Taxidae taxus*(3 - 1 ka)

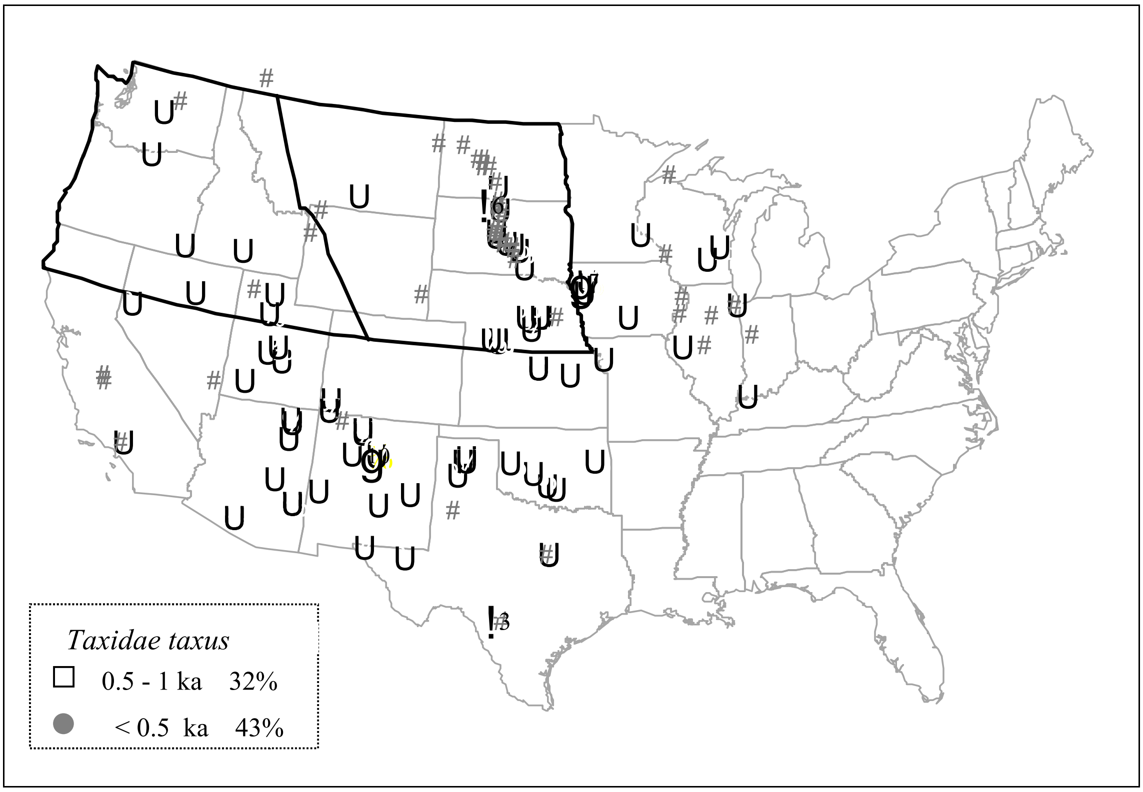


Fig. 53 The evolution of Arealsystem of *Taxidae taxus* (the last 1 ka)

Carnivora

Felidae

4. 1. 10 *Lynx rufus* **Bobcat**

The bobcat can be found in a variety of habitats, including forests, semi-deserts, mountains, and brushland. It ranges throughout North America from southern Canada to southern Mexico. In the United States population densities are much higher in the southeastern region than in the western states (Dig. Ref., Fig. 54a). The bobcat distributed in all refugia except the Great Lake Refugium before 15 ka. From 15 to 8 ka about 28% of the records contained more than 50% of the total MNIs, and records of the highest MNIs were located in southern Idaho. During 8 and 3 ka about 26% of the records comprised more than 50% of the total MNIs, and the records of the highest MNIs were found in northern Utah and Missouri (Fig. 54). From 3 to 1 ka the hot spots might not be obvious (Fig. 55). During 1 and 0.5 ka about 29% of the records contained more than 50% of the total MNIs, and the records of the highest MNIs were found in Arizona and northern Mexico (Fig. 56).

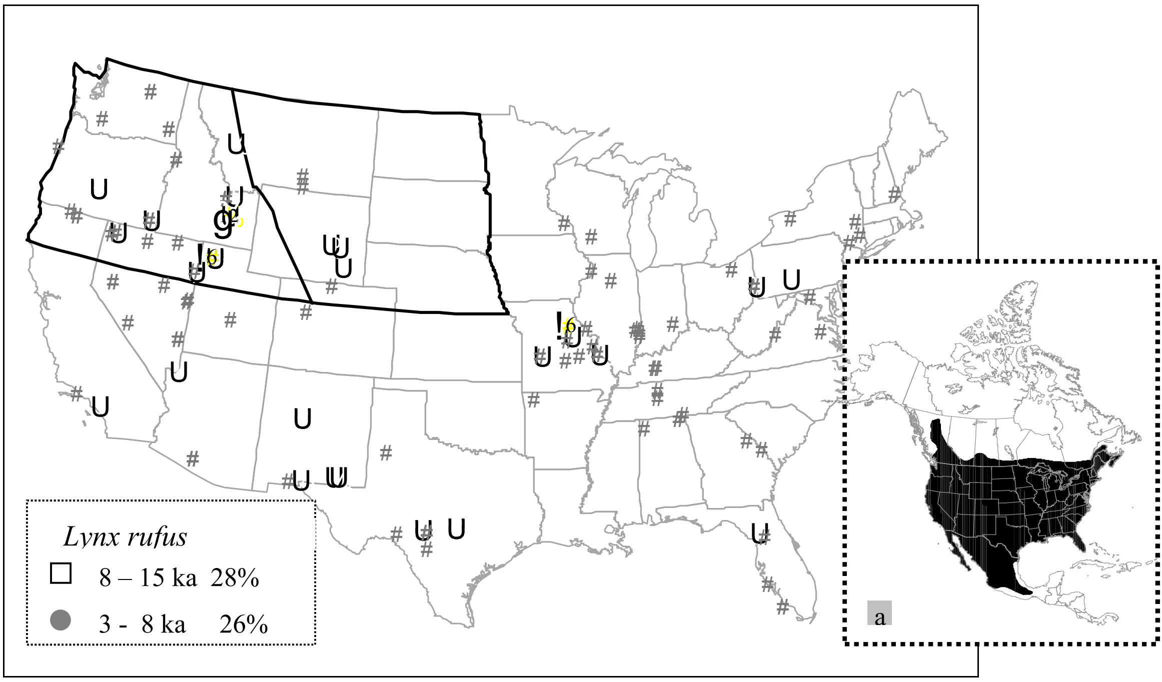


Fig. 54 The evolution of Arealsystem of *Lynx rufus* (15 – 3 ka)

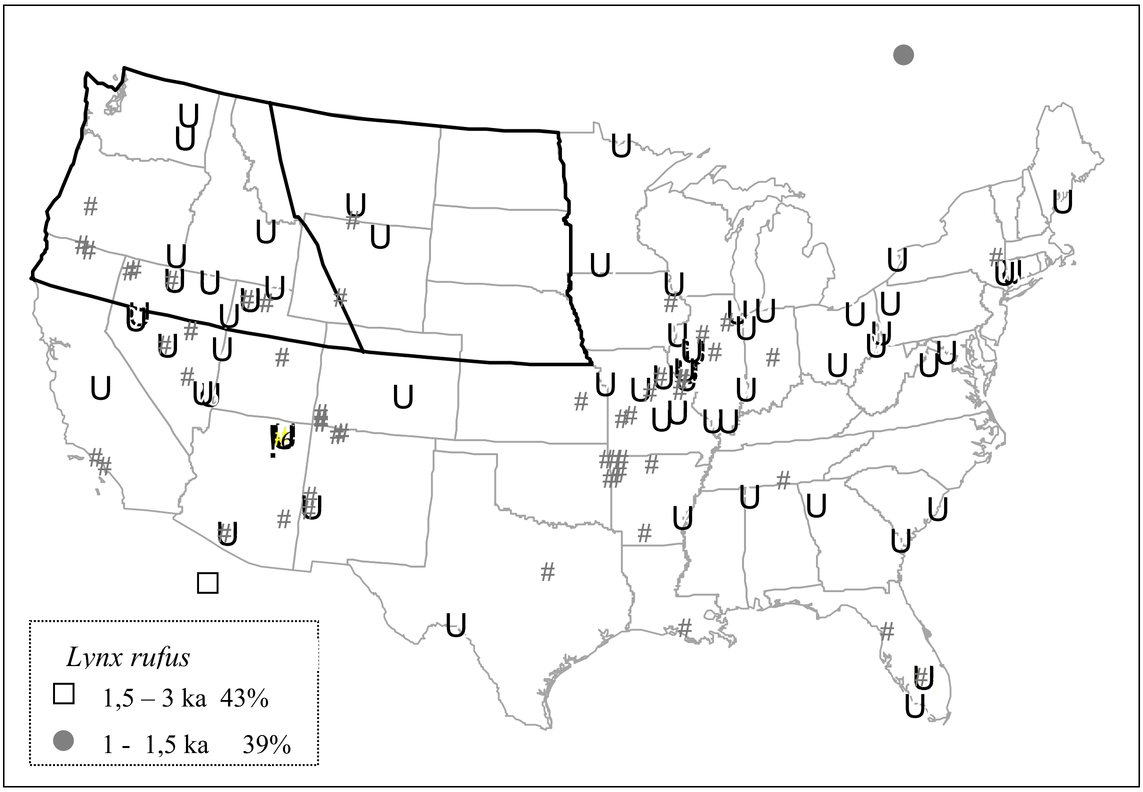


Fig. 55 The evolution of Arealsystem of *Lynx rufus* (3 - 1 ka)

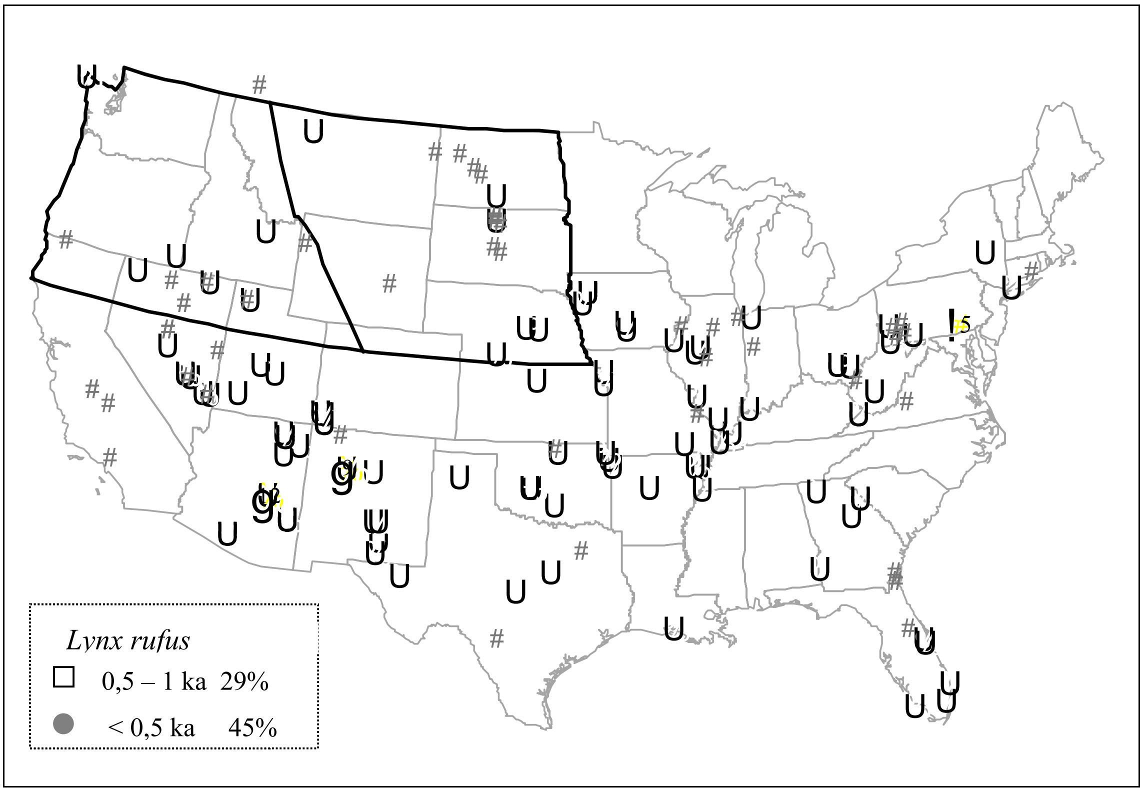


Fig. 56 The evolution of Arealsystem of *Lynx rufus* (the last 1 ka)

Lagomorpha

Leporidae

4. 1. 11 *Lepus townsendii* **White-tailed Jackrabbit**

The white-tailed Jackrabbit prefers sagebrush, barren, grazed, or cultivated lands and grasslands. It ranges from central Alberta and Saskatchewan east to extreme southwestern Ontario (Canada), south to southwestern Wisconsin, Iowa, northwestern Missouri, west through central Kansas to north central New Mexico, west to central Nevada, east central California (USA) and north to south central British Columbia (Canada) (Dig. Ref., Fig. 57a) .

Before 15 ka, it distributed mainly in the Great Basin and Rocky Mountain Refugium. From 15 to 8 ka, it once lived in Texas and southern New Mexico. About 8% of the records contained more than 50% of the total MNIs. The hot spots were located in southern Idaho (Fig. 57). From 3 to 1.5 ka it had disappeared from Texas and southern New Mexico. About 10% of the records contained more than 50% of the total MNIs. The hot spots were still in southern Idaho. During

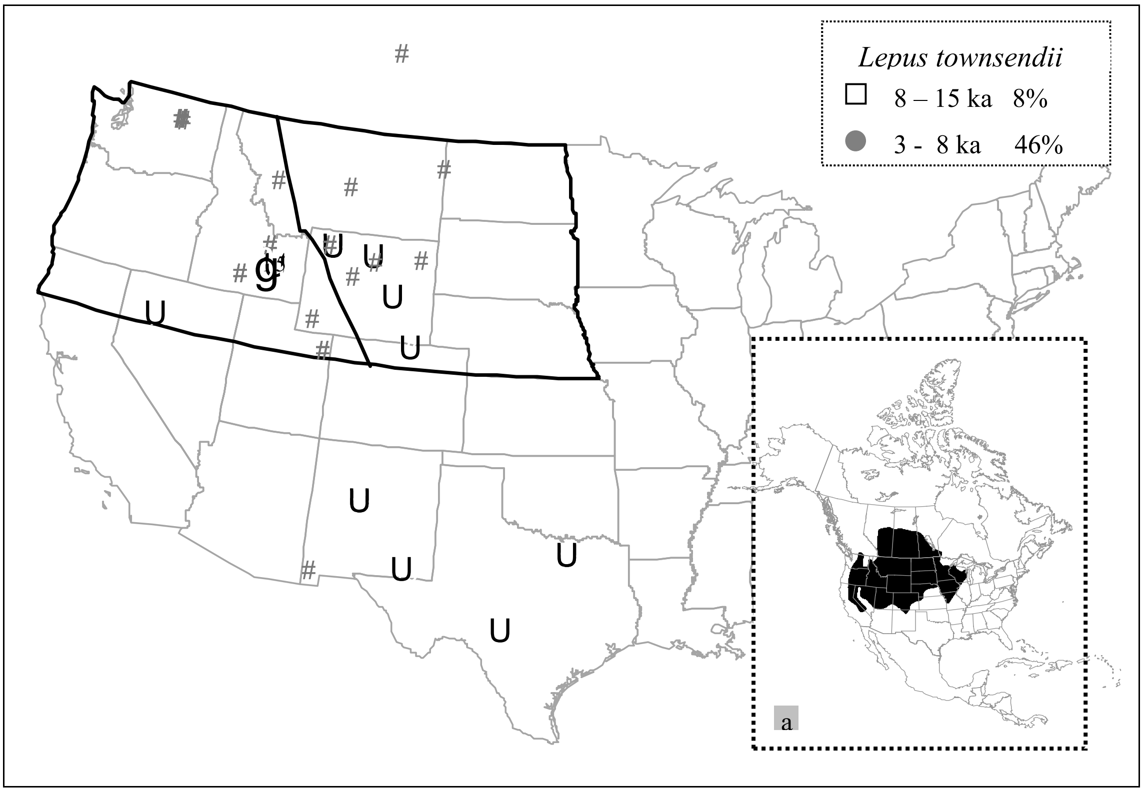


Fig. 57 The evolution of Arealsystem of *Lepus townsendii* (15 – 3 ka)

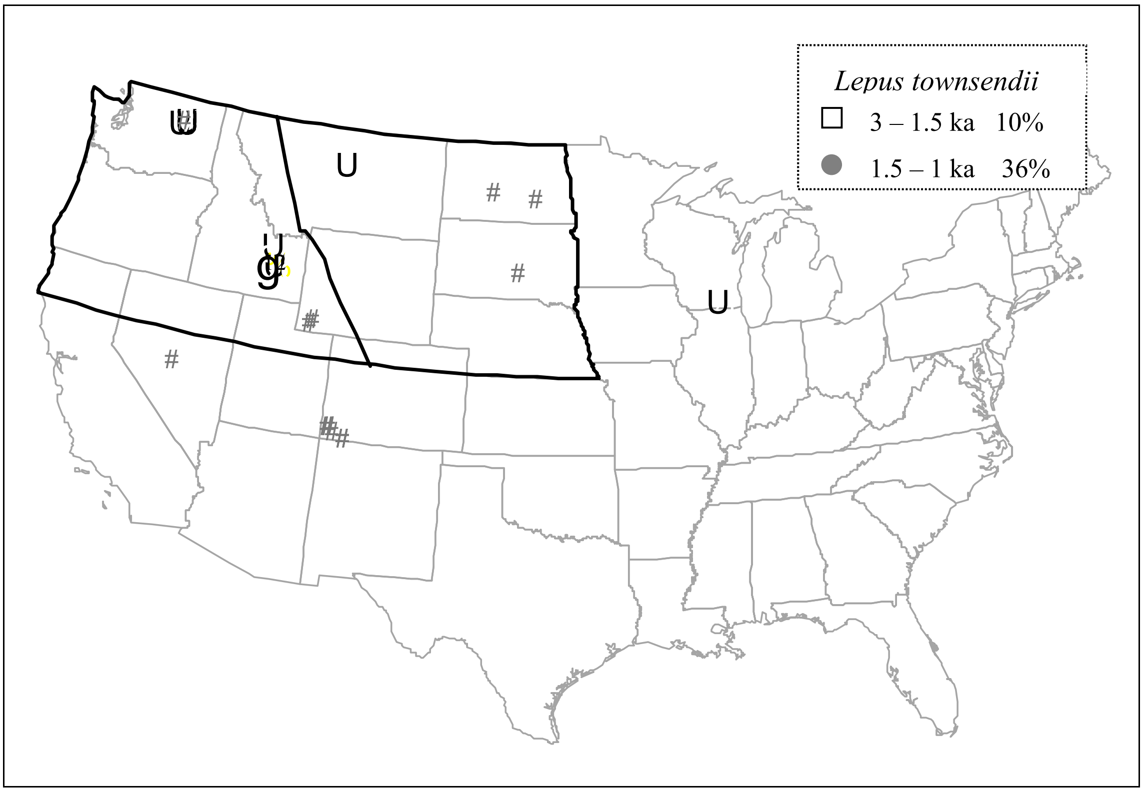


Fig. 58 The evolution of Arealsystem of *Lepus townsendii* (3 - 1 ka)

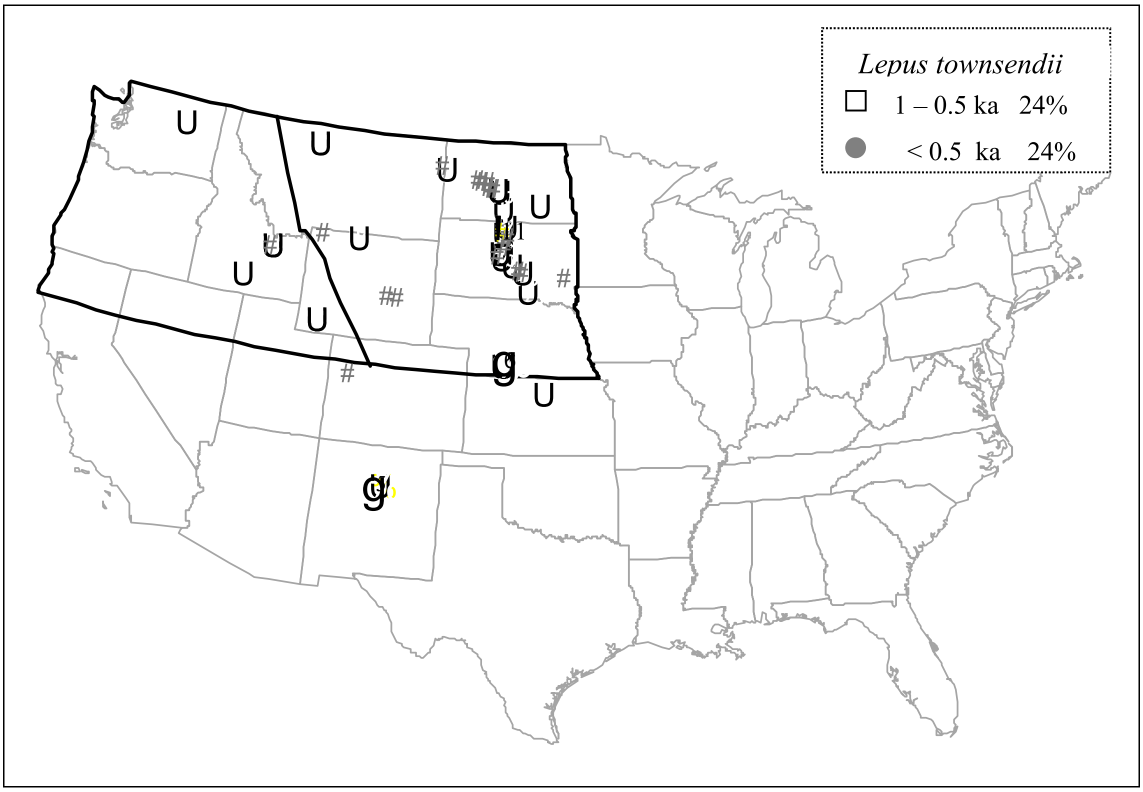


Fig. 59 The evolution of Arealsystem of *Lepus townsendii* (the last 1 ka)

1.5 and 1 ka, the fossil records started to appear in South and North Dakota. About 36% of the records contained more than 50% of the total MNIs. The hot spots had since then disappeared from the west side of the Rockies (Fig. 58). From 1 to 0.5 ka, about 24% of the records contained more than 50% of the total MNIs. The hot spots first appeared on the east side of the Rockies such as in Nebraska. In the last 500 years, about also 24% of the records contained more than 50% of the total MNIs. The hot spots were located in the upper Missouri River area (Dig. Ref., Fig. 59).

Rodentia

Heteromyidae

4. 1. 12 Dipodomys *ordii* **Ord's Kangaroo Rat**

Ord's Kangaroo Rats are common and widespread in the United States and Mexico but are becoming rare in Alberta and Saskatchewan of Canada (Fig. 62a). They prefers arid sandy areas with sagebrush and varied including sandy waste areas, sand dunes, sometimes hard-packed soil (Armstrong, 1979, Epp, 1980, Hallett, 1982).

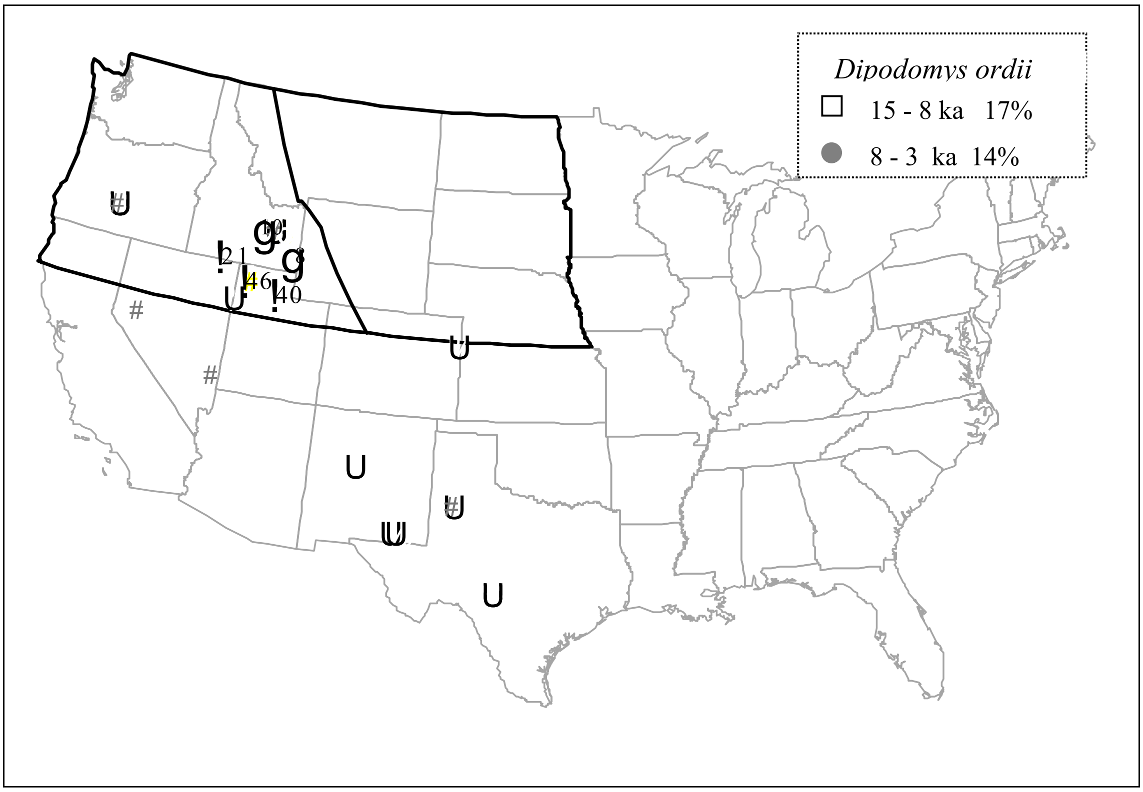


Fig. 60 The evolution of Arealsystem of *Dipodomys ordii* (15-3 ka)

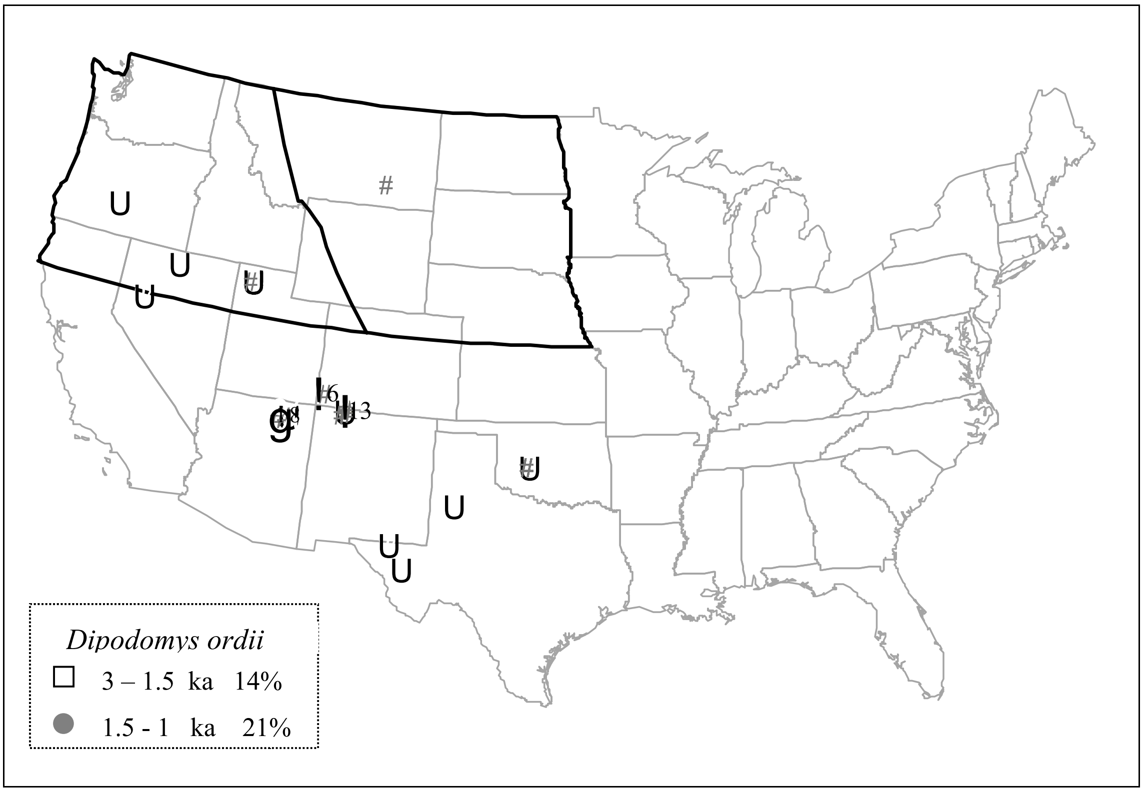


Fig. 61 The evolution of Arealsystem of *Dipodomys ordii* (3 – 1 ka)

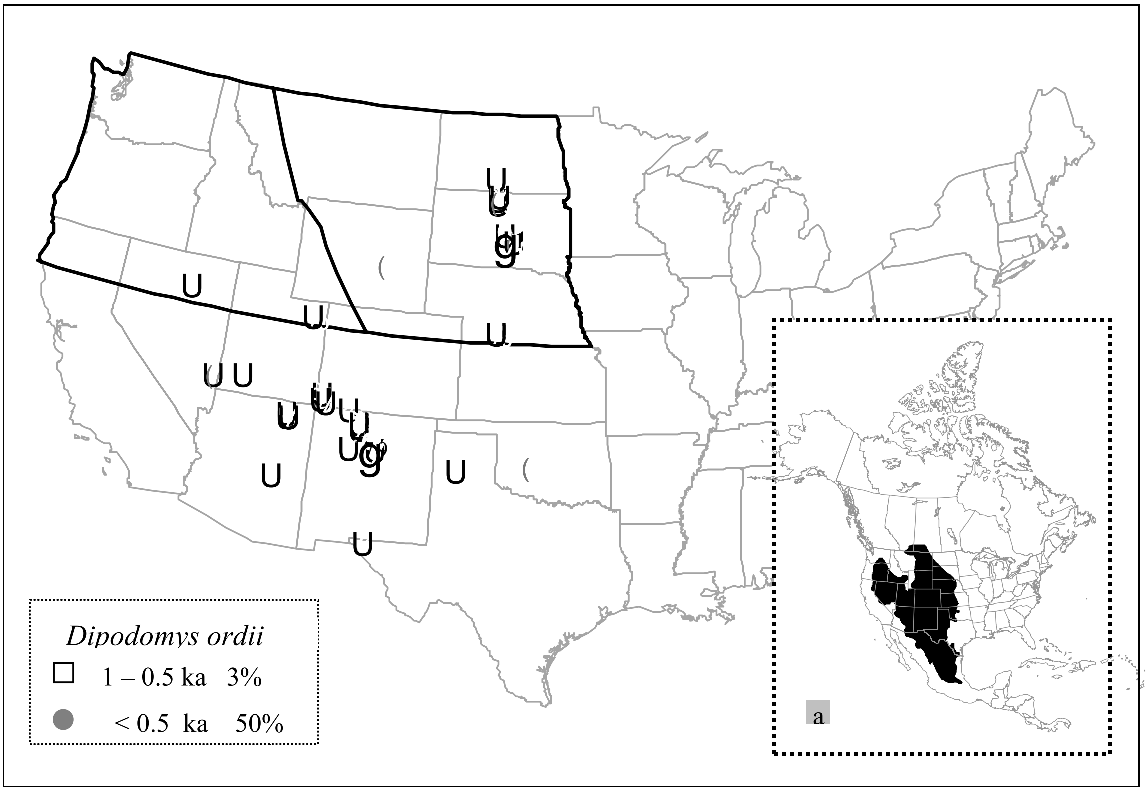


Fig. 62 The evolution of Arealsystem of *Dipodomys ordii* (the last 1 ka)

The Ord's Kangaroo Rat's fossil records were rare before 15 ka, which distributed mainly in the Great Basin and Mexico Refugium. From 15 to 3 ka, the hot spots were located in southern Idaho and northern Utah. About 17% and 14% of the records contained more than 50% of the total MNIs during 15-8 and 8-3 ka respectively. From 3 to 1.5 ka about 14% of records contained more than 50% of MNIs, and the hot spots started to appear in northern Arizona. During 1.5 to 1 ka the hot spots had disappeared from Idaho and northern Utah, and appeared in northern Mexico and southern Colorado. After 1 ka the hot spots were located in northern Mexico and also in South Dakota. About 3% of the records contained more than 50% of the total MNIs during 1 and 0.5 ka.

An average of 15.6 individuals/ha in Texas (Garner, 1974) and the maximum of 53 individuals/ha in New Mexico (Conley, 1977) were reported, while only an average density of 2.2 individuals/ha (Kenny, 1989) was estimated in Saskatchewan. This is coincident with the results above.

Rodentia

Geomyidae

4. 1. 13 *Thomomys talpoides* Northern **Pocket Gopher**

The northern pocket gopher prefers most open habitats, good soil in meadows or along streams. It ranges from southern British Columbia to southern Manitoba, and south to northeastern California and northern Nevada, through most of Colorado to isolated portions of northern Arizona and northern New Mexico, east to western Nebraska and through most of North and South Dakota (Fig. 63a).

Before 15 ka, it distributed mainly in the Rocky Mountain and Great Basin Refugium. About 6% and 2% of the records contained more than 50% of the total MNIs from 15 to 8 ka and during 8 and 3 ka respectively. The hot spots were located in southern Idaho (Fig. 63). During 3 and 1 ka it started to migrate to Montana, North and South Dakota. And the hot spots shifted from southern Idaho to western Washington. About 6% and 2% of the records contained more than 50% of the total MNIs from 3 to 1.5 ka and from 1.5 to 1 ka respectively (Fig. 64).

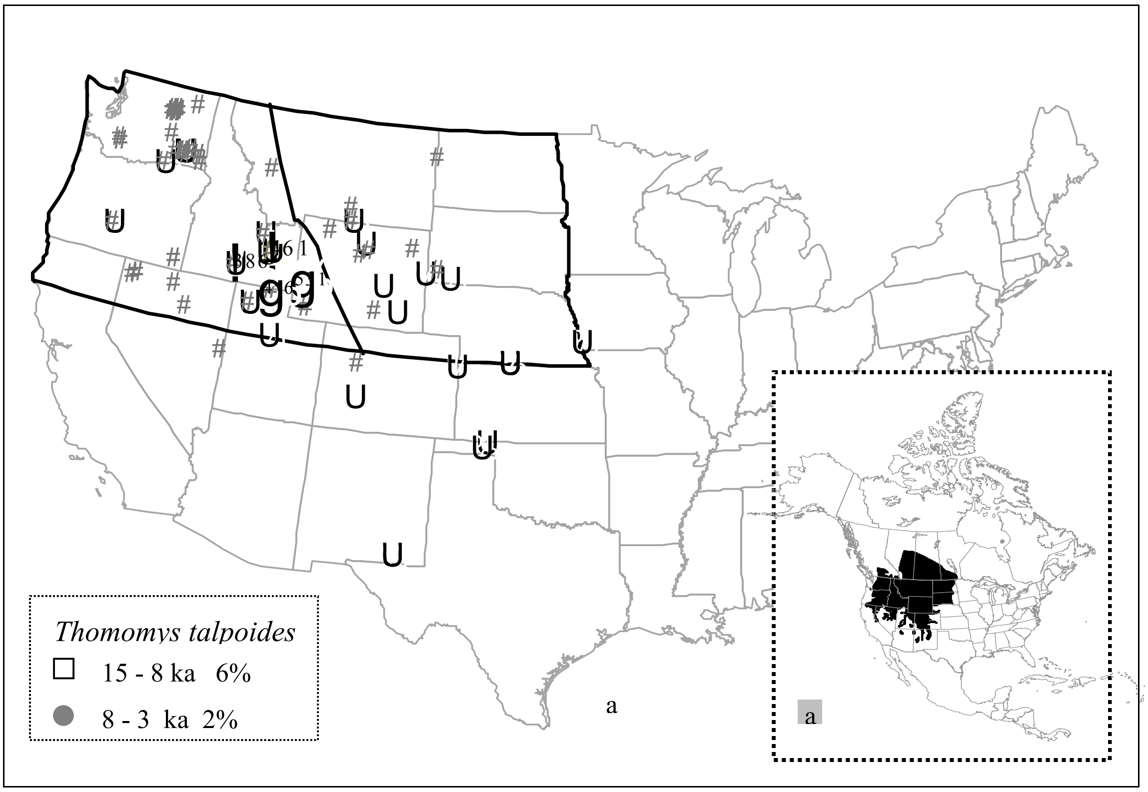


Fig. 63 The evolution of Arealsystem of *Thomomys talpoides* (15 – 3 ka)

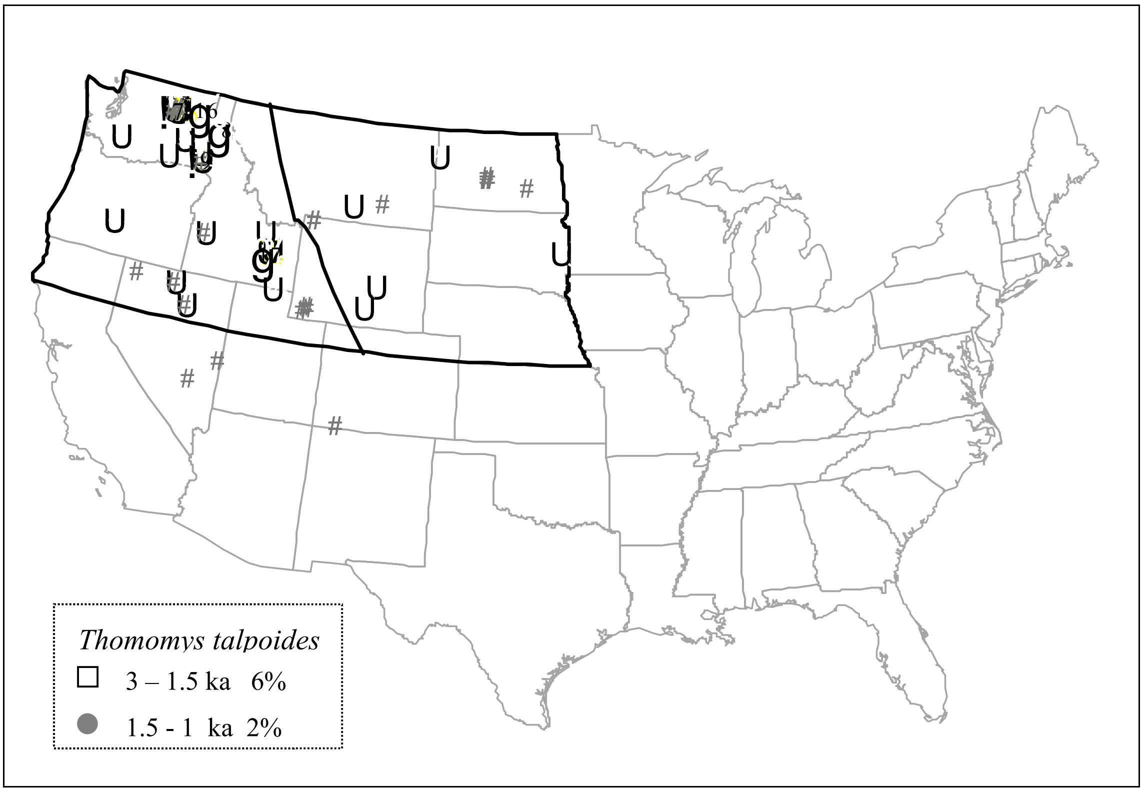


Fig. 64 The evolution of Arealsystem of *Thomomys talpoides* (3 - 1 ka)

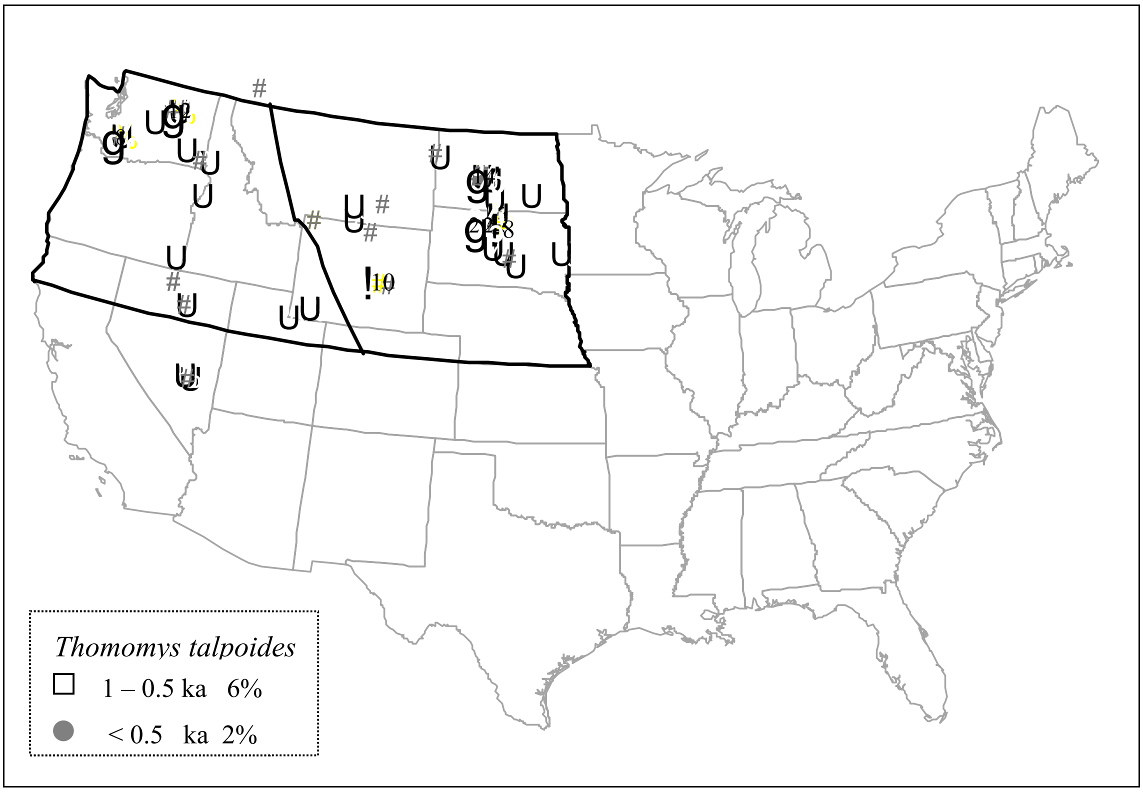


Fig. 65 The evolution of Arealsystem of *Thomomys talpoides* (the last 1 ka)

From 1 to 0.5 ka the hot spots were located in Washington, but also appeared in South and North Dakota. After about 500 year ago the hot spots might disappeared from the west side of the Rockies. About 6% and 2% of the records contained more than 50% of the total MNIs from 1 to 0.5 and in the last 500 years respectively.

Rodentia

Muridae

4. 1.14 Onychomys *leucogaster* **Northern Grasshopper Mouse**

The northern grasshopper mice prefer arid shortgrass prairies, sand dunes or sandy sagebrush. These are primarily areas with sandy soil in which they can build their burrows. Its range covers much of western North America from southeastern Washington, southern Alberta, Saskatchewan, and southwestern Manitoba south to northeastern California, eastern Arizona, and western Texas (Dig. Ref., Fig. 66a)

Before 15 ka it distributed mainly in the southern parts of the Great Plains. From 15 to 8 ka about 8% of the records contained more than 50% of the total MNIs, and the hot spots were

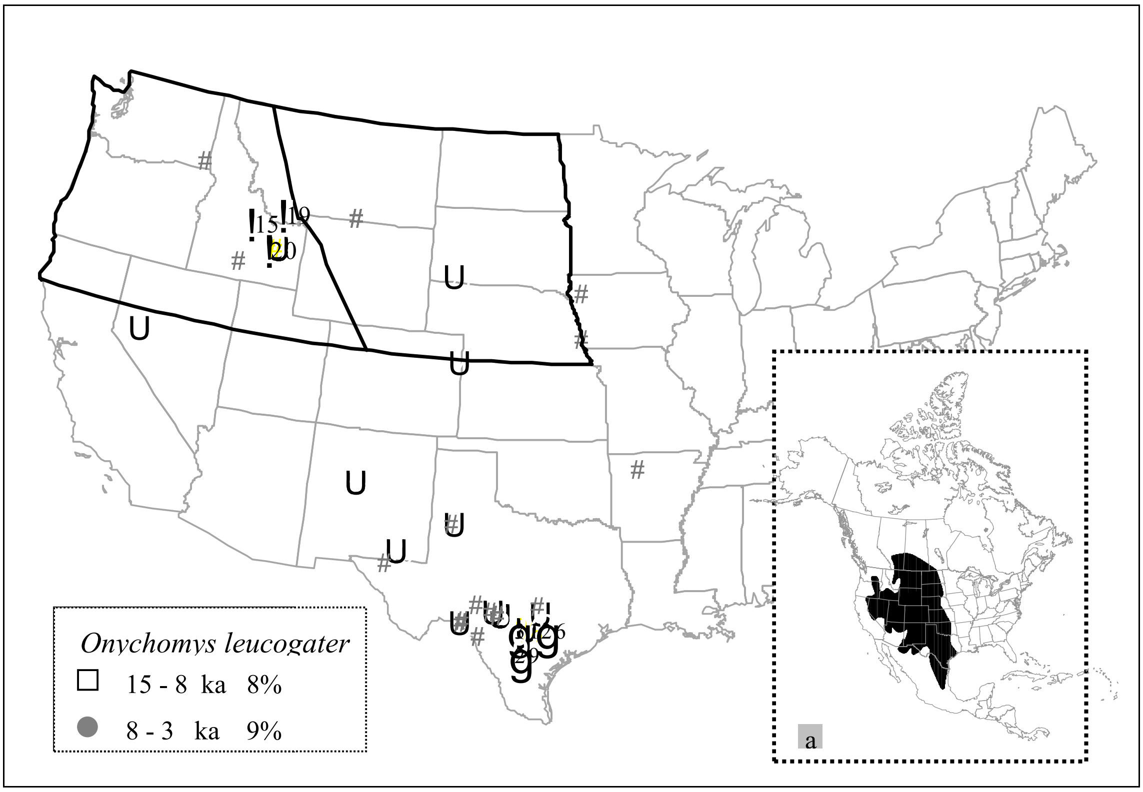


Fig. 66 The evolution of Arealsystem of *Onychomys leucogaster* (15 – 3 ka)

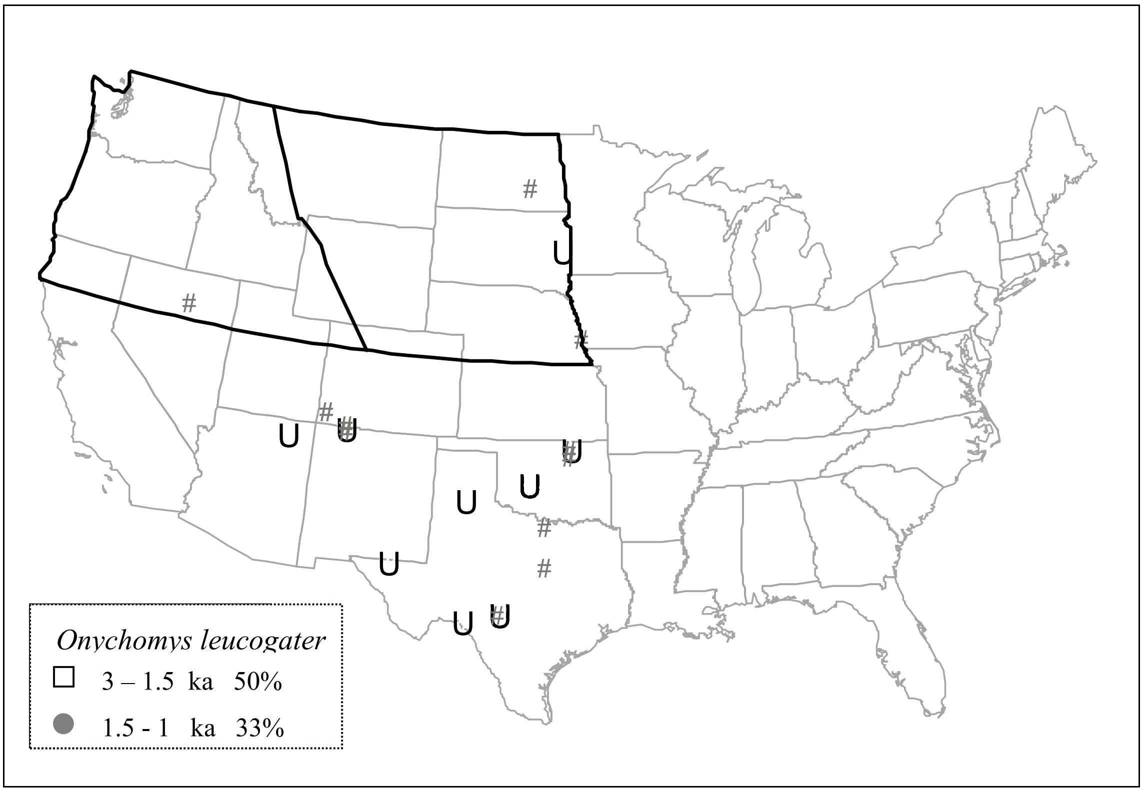


Fig. 67 The evolution of Arealsystem of *Onychomys leucogaster* (3-1 ka)

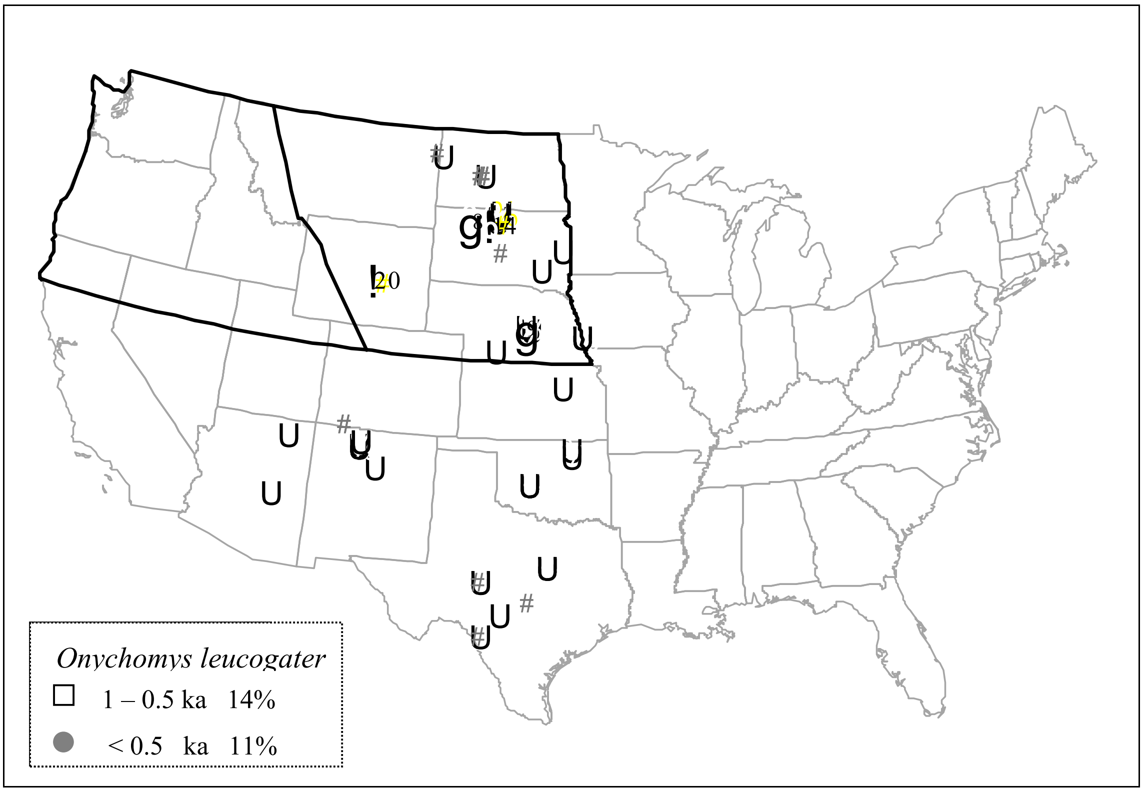


Fig. 68 The evolution of Arealsystem of *Onychomys leucogaster* (the last 1 ka)

located in southern Texas. During 8 and 3 ka the hot spots also appeared in southern Idaho. About 9% of the records comprised more than 50% of the total MNIs in this period (Fig. 66). But after 3 ka, its hot spots disappeared from Idaho. And it started to disperse northward to South and North Dakota. After 1 ka its hot spots had appeared in South and North Dakota, Wyoming. About 14% and 11% of the records contained more than 50% of the total MNIs from 1 to 0.5 and in the last 500 years respectively (Fig. 67)

Rodentia
Muridae
Sigmodontinae

4. 1. 15 *Peromyscus maniculatus* **Deer Mouse**

The range of deer mouse covers from southern Yukon and Northwest Territories to Mexico in West, and from Hudson Bay to Pennsylvania and southern Appalachians, and across northern tier of states and south into central Arkansas and eastern Texas in East (Fig. 70a). Its most common habitats are prairies, bushy areas, and woodlands (Dig. Ref.).

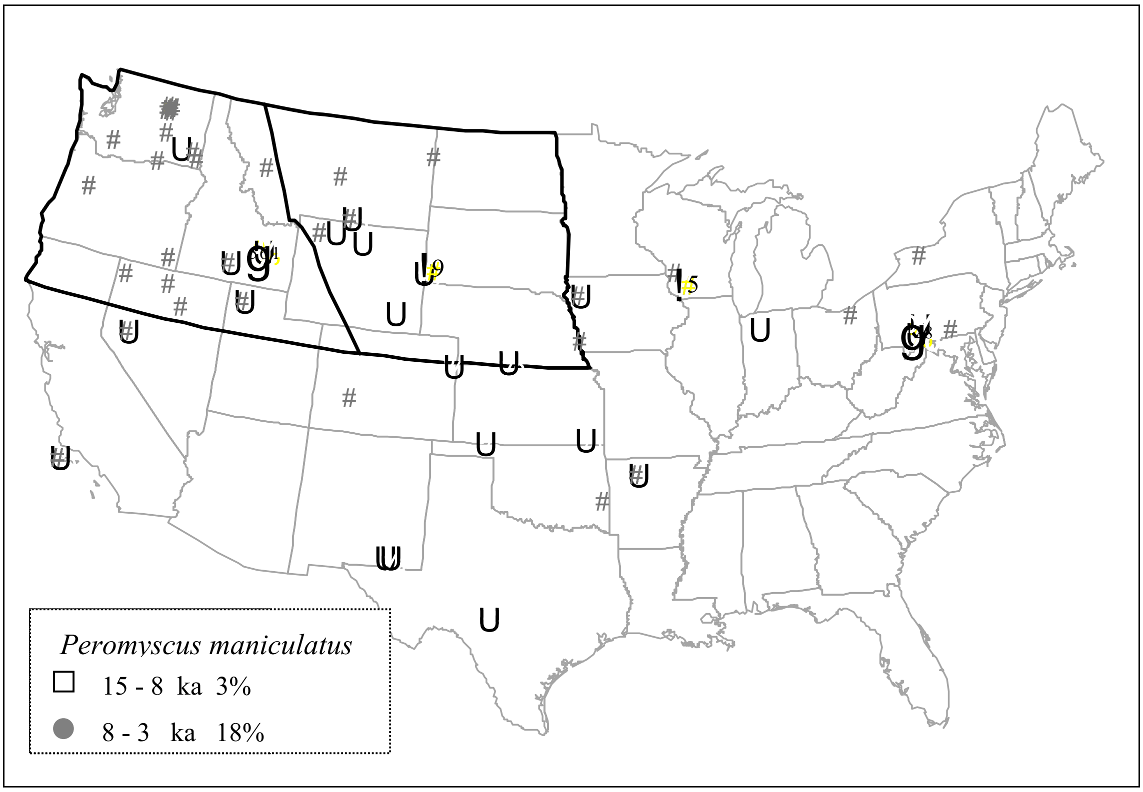


Fig. 69 The evolution of Arealsystem of *Peromyscus maniculatus* (15-3 ka)

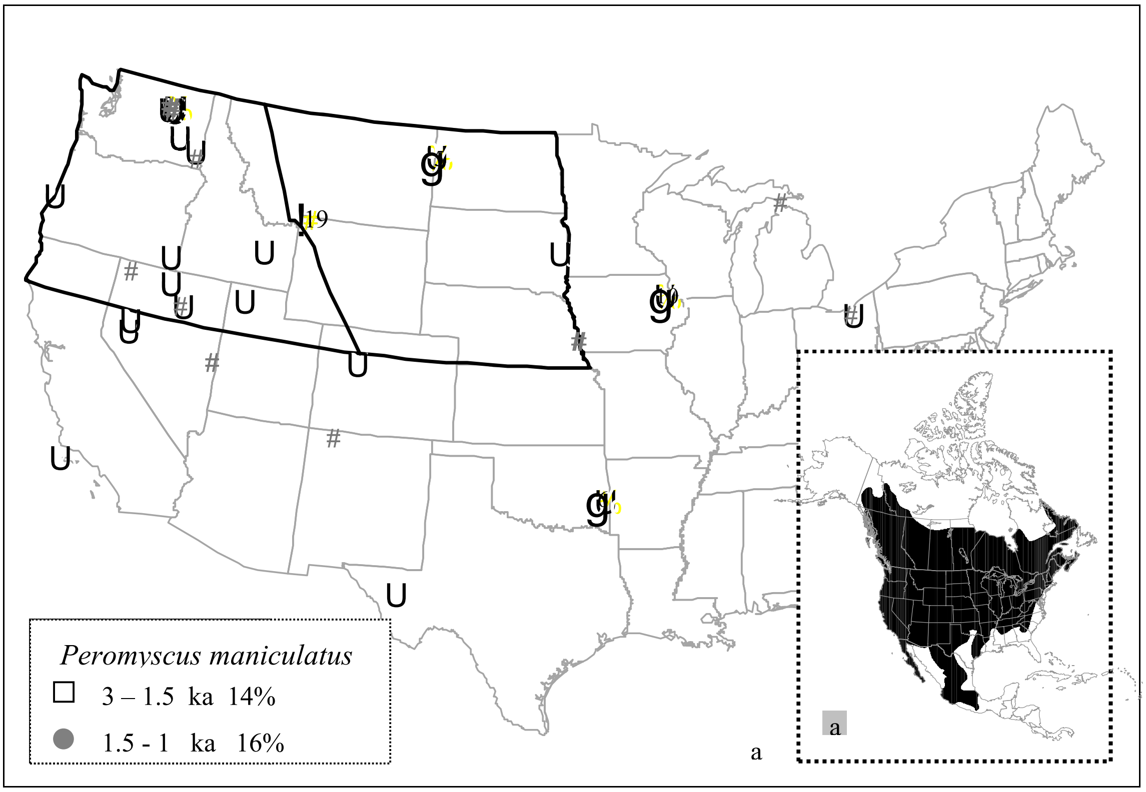


Fig. 70 The evolution of Arealsystem of *Peromyscus maniculatus* (3-1 ka)

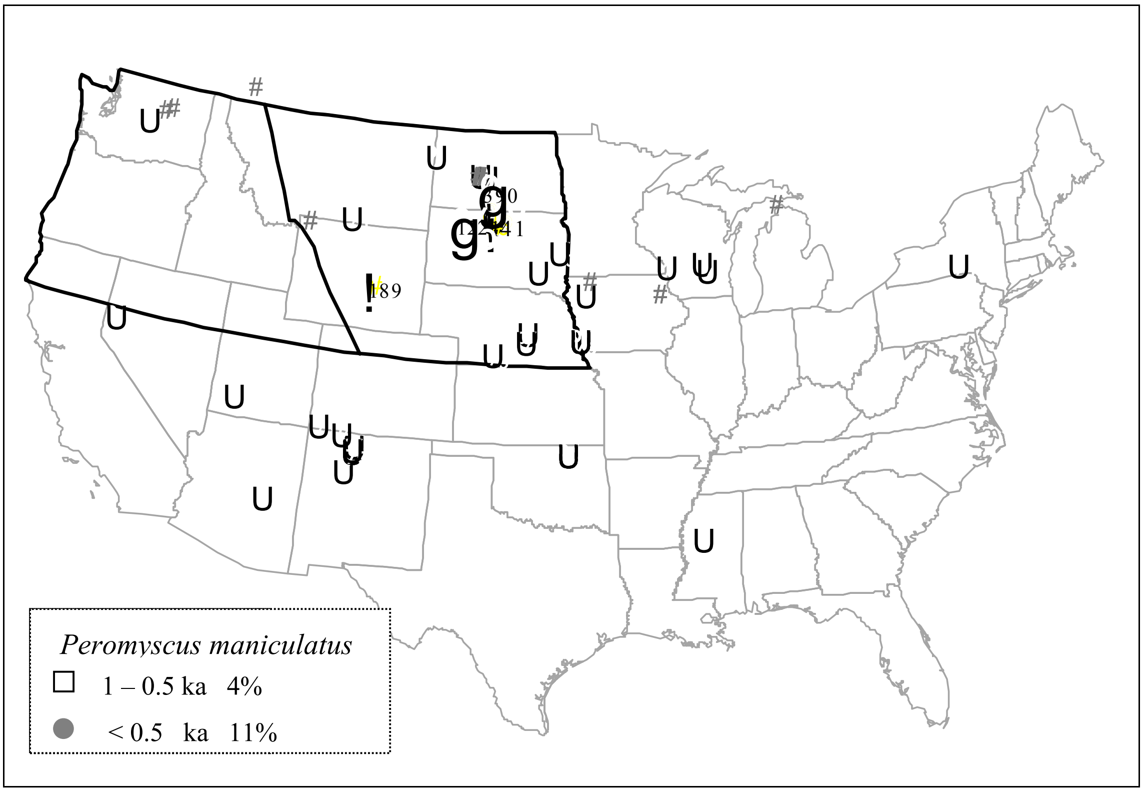


Fig. 71 The evolution of Arealsystem of *Peromyscus maniculatus* (the last 1 ka)

Before 15 ka the deer mouse distributed widely in USA. From 18 to 8 ka about 3% of the records contained more than 50% of MNIs, and the hot spots were located in southern Idaho and Pennsylvania. During 8 and 3 ka about 18% of the records comprised more than 50% of the total MNIs, and the hot spots might shift to southwestern Wisconsin and South Dakota (Fig. 69). After 3 ka, the hot spots disappeared from the west side of the Rockies, and started to appear on the east side of the Rockies. About 14% and 16% of the records contained more than 50% of the total MNIs from 3 to 1.5 ka and from 1.5 to 1 ka respectively. In the last 1 ka the hot spots were located on the east side of the Rockies. About 4% and 11% of the records contained more than 50% of the total MNIs from 1 to 0.5 ka and in the last 500 years respectively.

Rodentia

Erethizontidae

4. 1. 16 *Erethizon dorsatum* **Common Porcupine**

Highly adaptable, *Erethizon dorsatum* may be found in open tundra, rangeland, and deserts. When away from forests, the common porcupine usually remains in vegetated riparian areas (Sweitzer, 1992). The porcupine distributes most of Canada (Anderson, 1943) and western U.S. south to Mexico, in the East, south to Wisconsin, northern half of Michigan, and most of Pennsylvania, New York, and New England, central Alaska (USA), most of Canada to S Hudson Bay and Labrador, south to E Tennessee, C Iowa, and C Texas (USA), N Coahuila, Chihuahua, and Sonora (Mexico), and S California (USA) (Woods, 1973) (Fig. 74a).

The porcupine was a polycentric species, which distributed nearly in all refugium before 15 ka. From 8 to 3 ka about 15% of the records contained more than 50% of the total MNIs. The hot spots might be located in southern Idaho and Illinois (Fig. 72). From 3 to 1.5 ka about 40% of the records contained more than 50% of the total MNIs. The records with highest MNIs were found still in southern Idaho. After 1.5 ka the ISVAs were all over 25%. But fossil records started to appear in the upper Missouri River area during 1-0.5 ka (Fig. 73, 74).

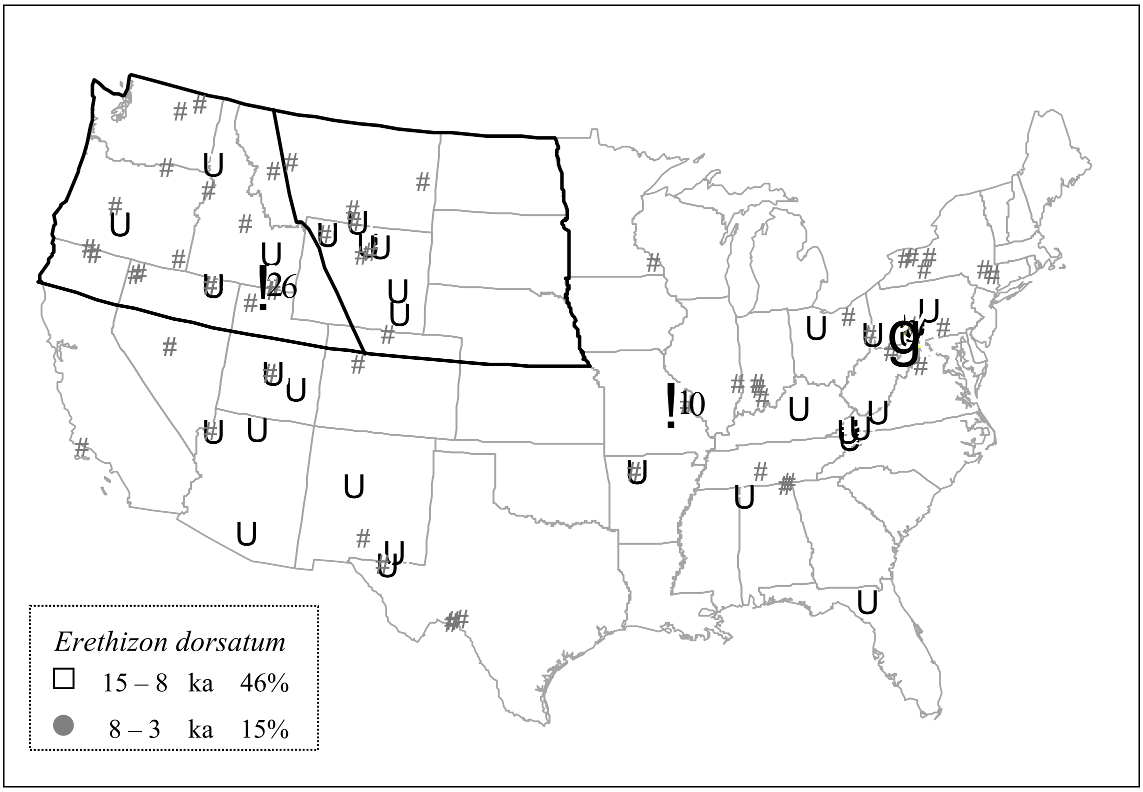


Fig. 72 The evolution of Arealsystem of *Erethizon dorsatum* (15 – 3 ka)

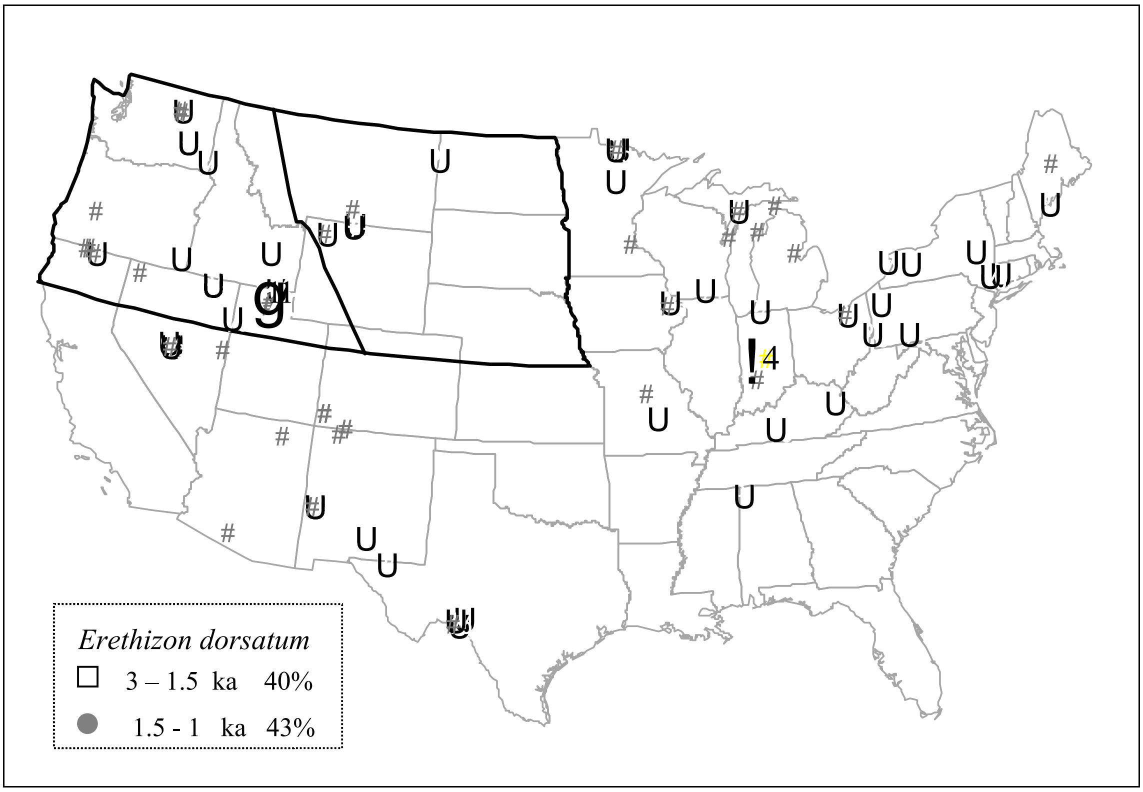


Fig. 73 The evolution of Arealsystem of *Erethizon dorsatum* (3 - 1 ka)

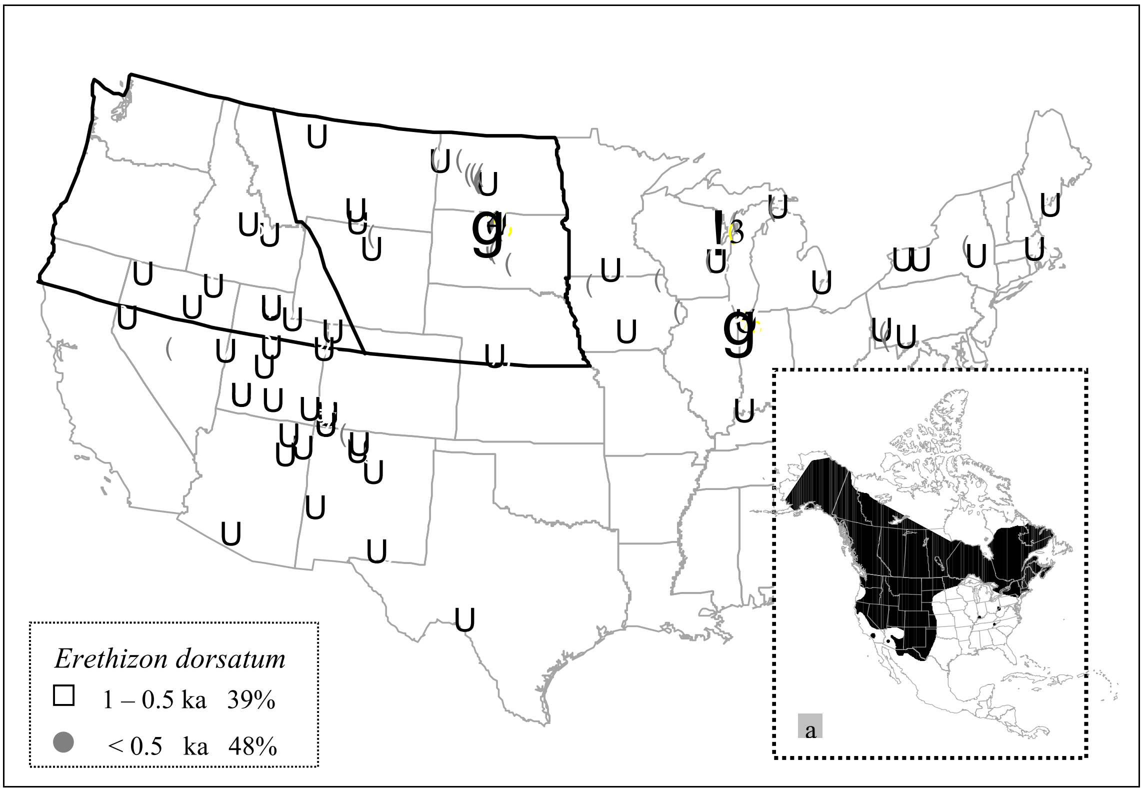


Fig. 74 The evolution of Arealsystem of *Erethizon dorsatum* (the last 1 ka)

4. 2 MOVEMENT FROM THE EAST OF USA TO THE EAST SIDE OF THE ROCKIES

Artiodactyla

Cervidae

4. 2. 1 *Odocoileus virginianus* **White-tailed Deer**

The whitetail deer inhabit most of southern Canada and the entire mainland United States except California, Nevada and Utah. Their range reaches throughout Central America to Bolivia (Fig. 75a). Whitetail deer are able to survive in a variety of terrestrial habitats, from the big woods of northern Maine to the deep saw grass and hammock swamps of Florida. They also inhabit farmlands, brushy areas and such desolate areas of the west such as the cactus and thornbrush deserts of southern Texas and Mexico. Ideal whitetail deer habitat would contain dense thickets (Dig. Ref.).

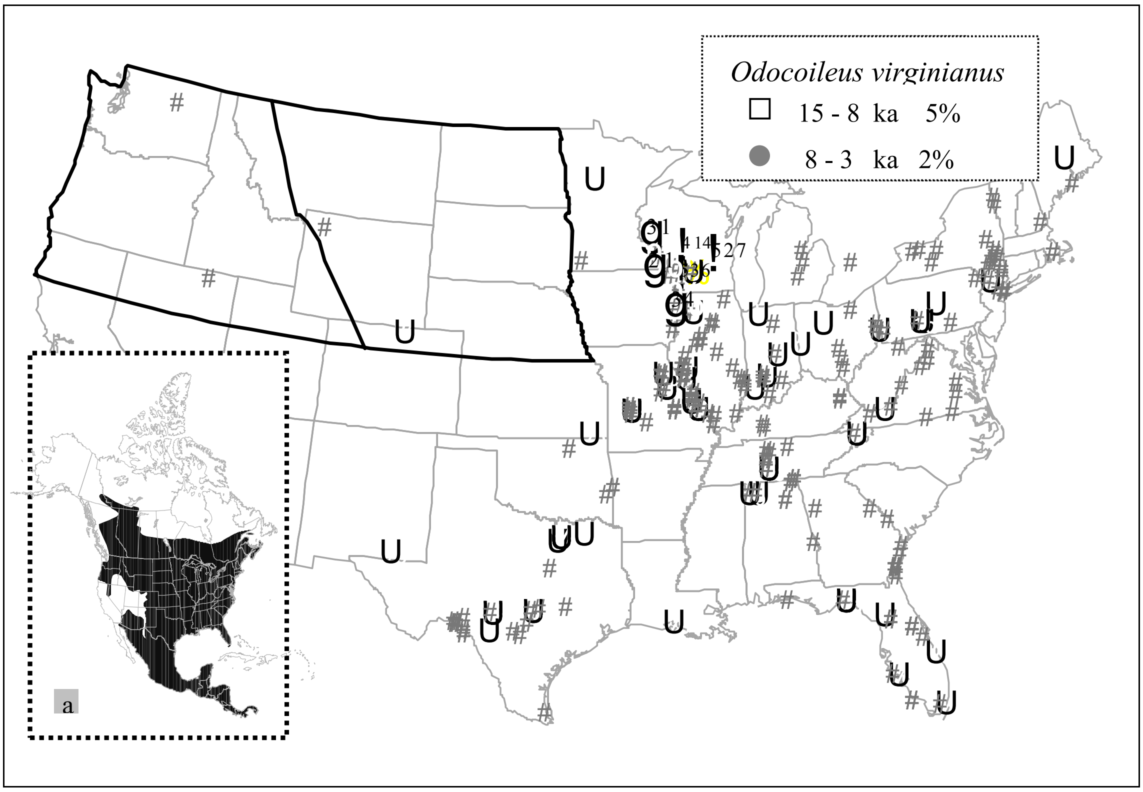


Fig. 75 The evolution of Arealsystem of *Odocoileus virginianus* (15-8 ka)

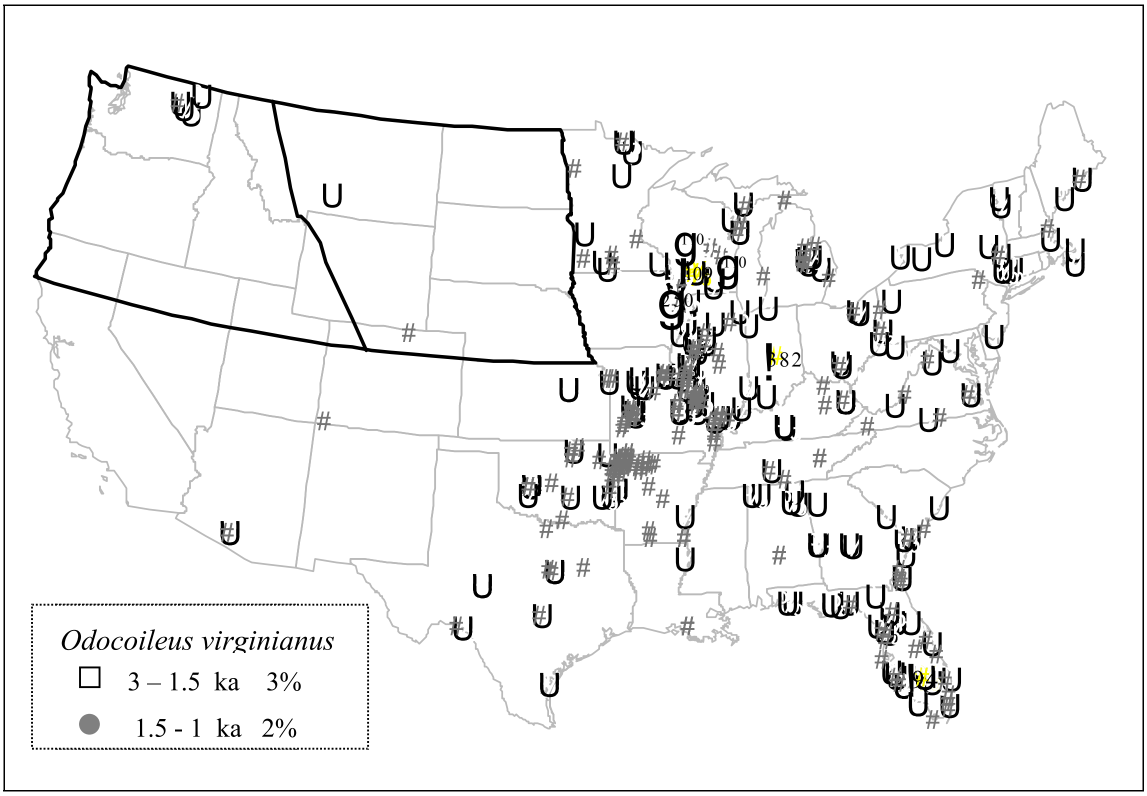


Fig. 76 The evolution of Arealsystem of *Odocoileus virginianus* (3-1 ka)

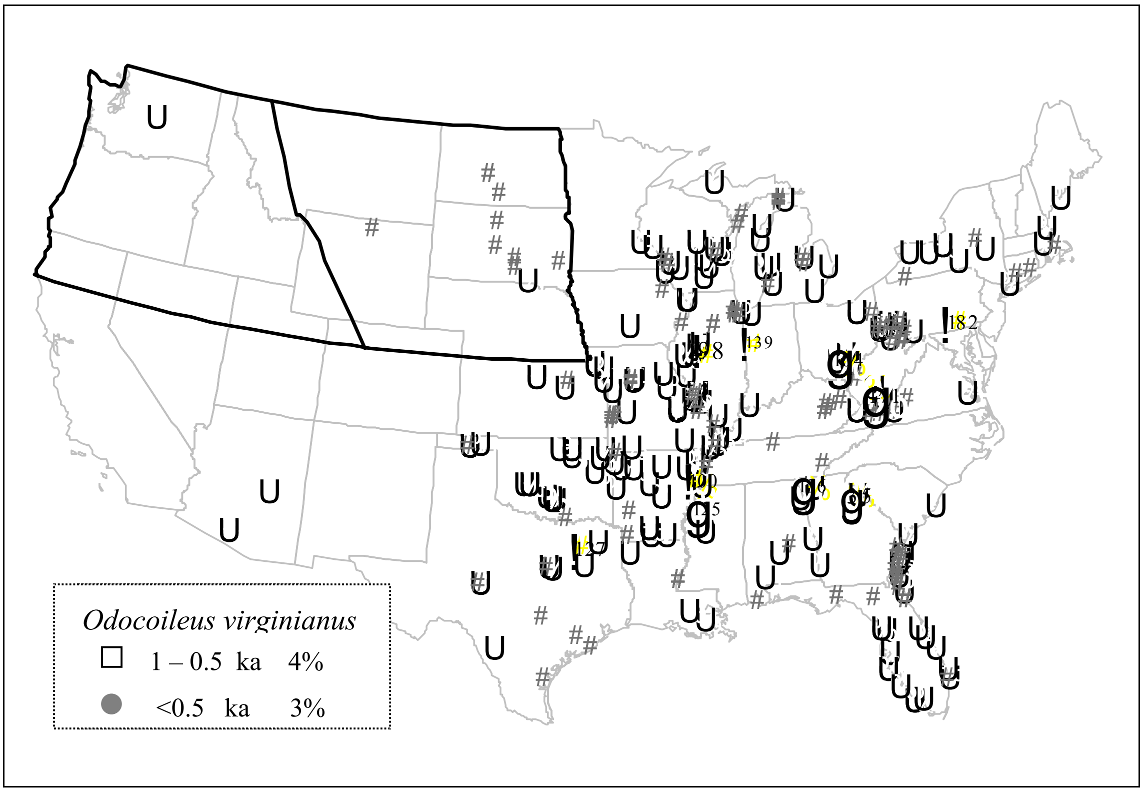


Fig. 77 The evolution of Arealsystem of *Odocoileus virginianus* (the last 1 ka)

Before 15 ka it distributed mainly in the Florida and Appalachia Refugium. Since 15 ka it started to migrate northward and northwestward. During 8 and 3 ka it had reached Maine and New York. The ISVA equals 5% from 15 to 8 ka and 2% from 8 to 3 ka, the hot spots remained to be in Wisconsin (Fig. 75). From 3 to 1.5 ka the ISVA equals 3%, the hot spots were still in Wisconsin. But during 1.5 and 1 ka the hot spots first appeared in Indiana (Fig. 76). After 1 ka, the hot spots were mainly located in the Appalachians. In the last 500 years it appeared on the east side of the Rockies (Fig. 77).

Lagomorpha

Leporidae

4. 2. 2 *Sylvilagus floridanus* **Eastern Cottontail**

The eastern cottontail is found in a variety of habitats including old fields, brushy clearings, brier patches, hedgerows, orchards, and along the edges of woodlands. It ranges from Costa

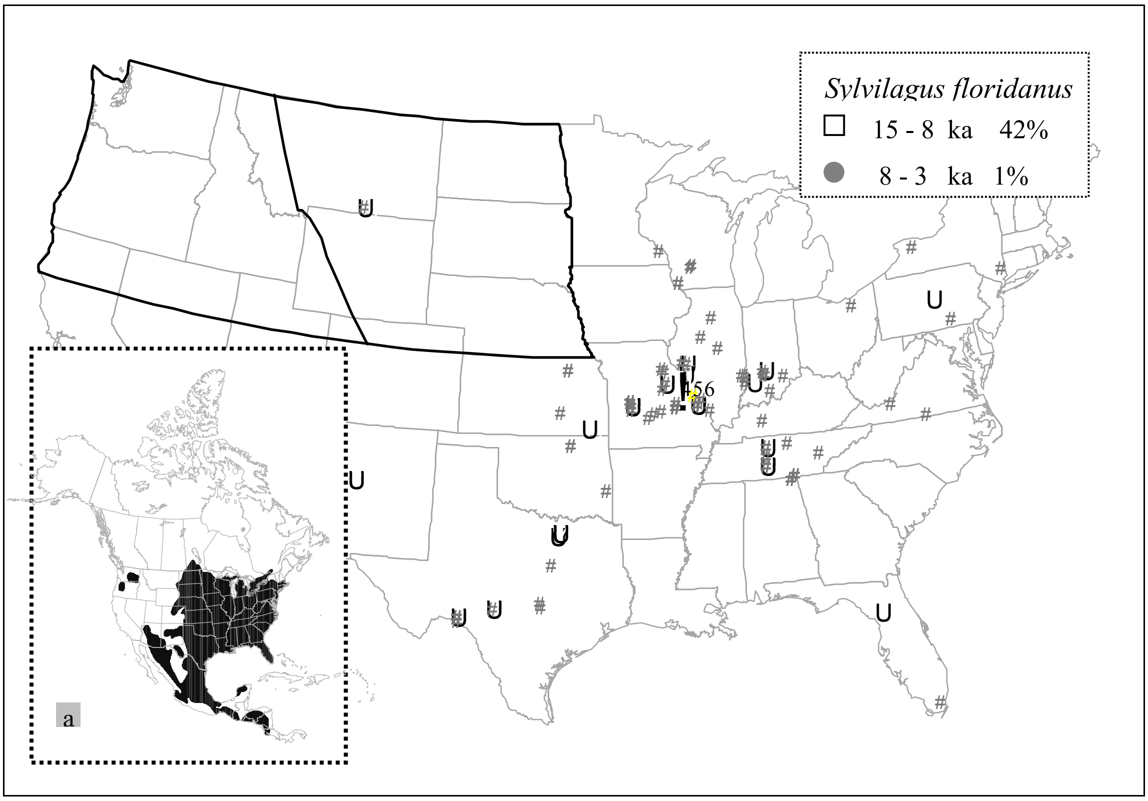


Fig. 78 The evolution of Arealsystem of *Sylvilagus floridanus* (15-3 ka)

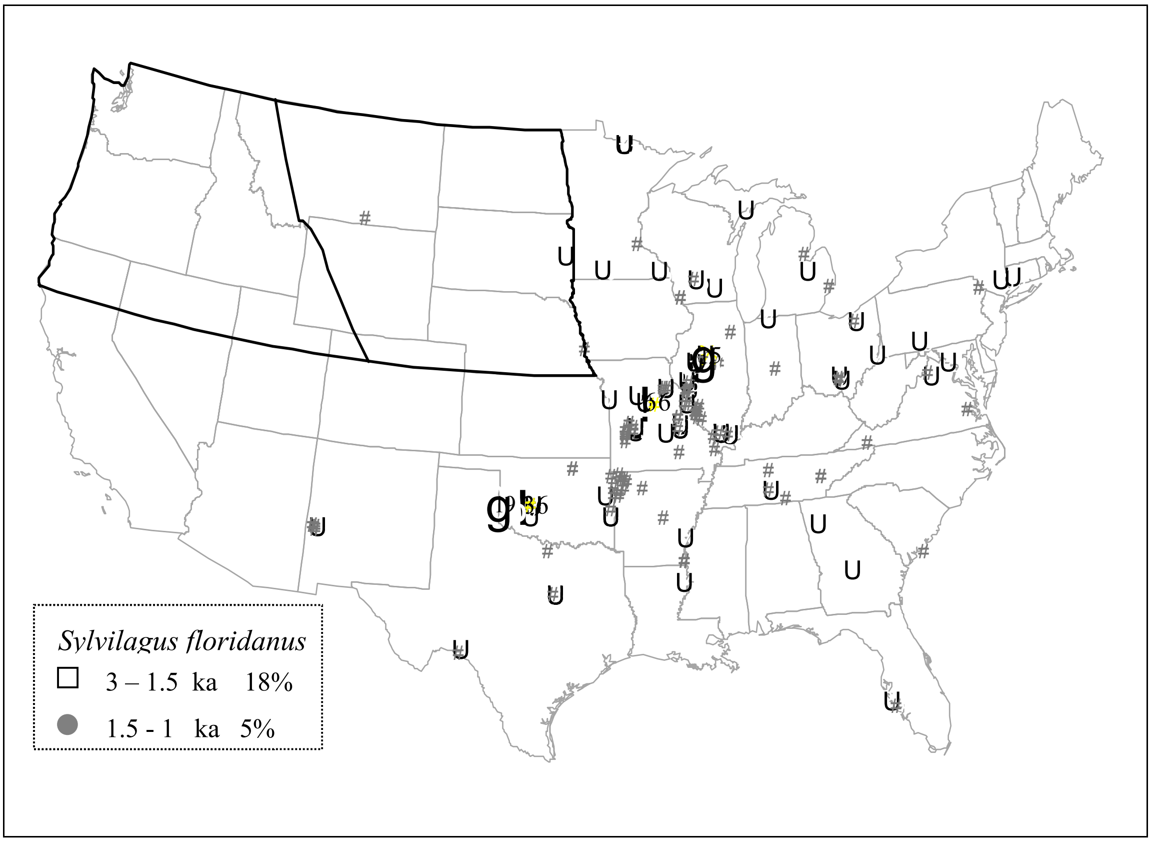


Fig. 79 The evolution of Arealsystem of *Sylvilagus floridanus* (3-1 ka)

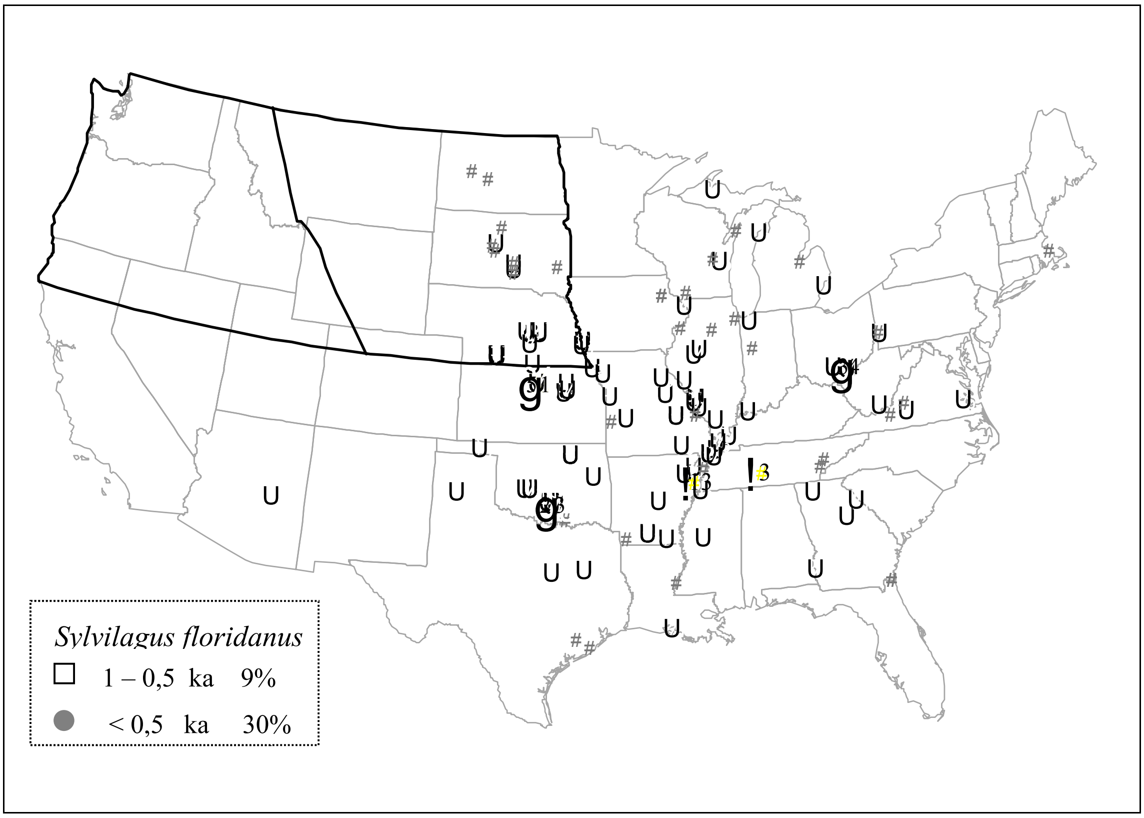


Fig. 80 The evolution of Arealsystem of *Sylvilagus floridanus* (the last 1 ka)

Rica through Mexico to Arizona and New Mexico and throughout most of the United States east of the Rocky Mountains (Dig. Ref., Fig. 78a).

Before 15 ka it distributed mainly in the Florida and Appalachia Refugium. During 15 and 8 ka it was still restricted to these areas. But from 8 to 3 ka it had extended its range northward. Only about 1% of the records contained more than 50% of the total MNIs, and the hot spots were located in the southern Illinois (Fig. 78). From 3 to 1.5 ka about 18% of the records contained more than 50% of the total MNIs. The hot spots were located in northern Illinois and Oklahoma. During 1.5 and 1 ka about 5% of the records contained more than 50% of the total MNIs. The hot spots were still in Oklahoma but also in Missouri (Fig. 79). From 1 and 0.5 ka it started to enter the upper Missouri River basin. About 9% of the records contained more than 50% of the total MNIs. The hot spots were still in Oklahoma, but also appeared in northern Kansas and southern Ohio (Fig. 80).

Rodentia

Sciuridae

4. 2. 3 *Spermophilus tridecemlineatus* **Thirteen-Lined Ground Squirrel**

Spermophilus tridecemlineatus is found in central North America. Originally confined to the prairie, it has extended its range northward and eastward over the past two centuries as land has been cleared. Currently *S. tridecemlineatus* can be found as far east as Ohio and as far west as Montana and Arizona. It reaches its northern limit in central Alberta and Saskatchewan and is found as far south as the Texas coast (Fig. 81a). It prefers open areas with short grass and well-drained sandy or loamy soils for burrows (Dig. Ref.).

It distributed mainly in the Appalachia Refugium before 15 ka. During 15 and 8 ka about 8% of the records contained more than 50% of the total MNIs. The hot spots were located in the Appalachia Refugium. From 8 to 3 ka it had migrated northward to Wisconsin and might start to disappear from the Appalachia Refugium (Fig. 81). Since 3 ka it might have disappeared from the Appalachia area and started to enter the upper Missouri River area (Fig. 82). From 1

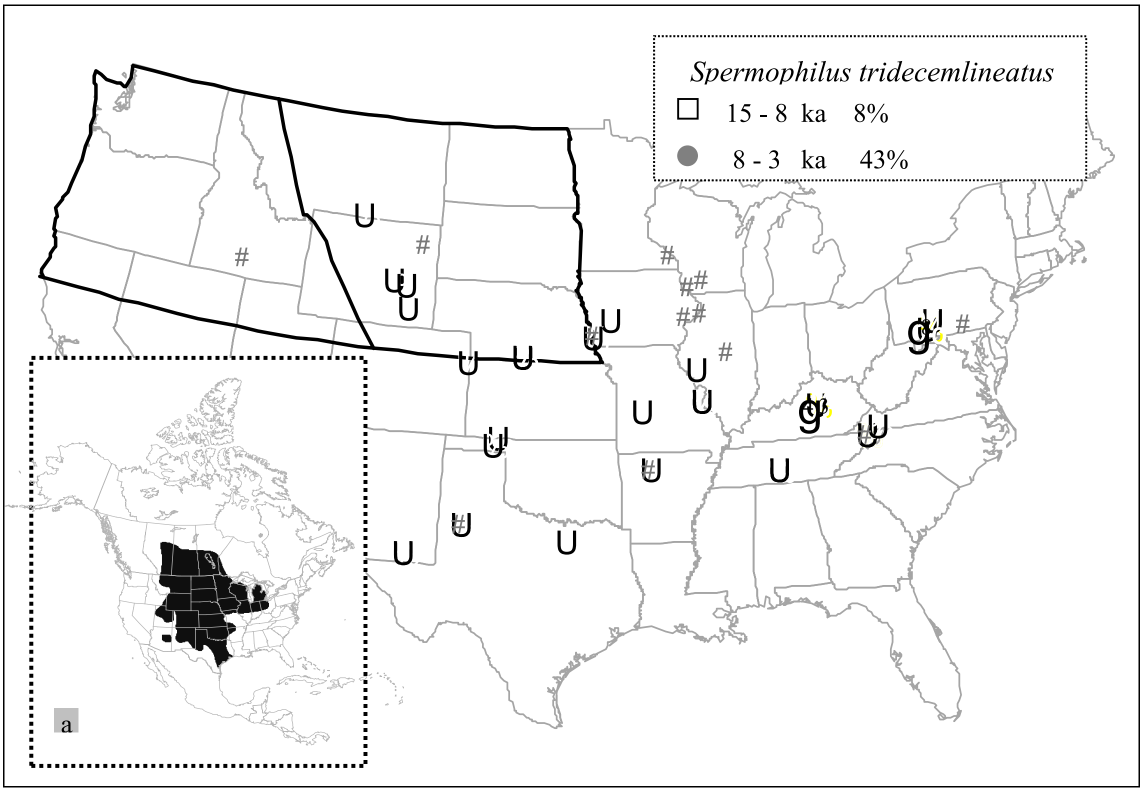


Fig. 81 The evolution of Arealsystem of *Spermophilus tridecemlineatus* (15-3 ka)

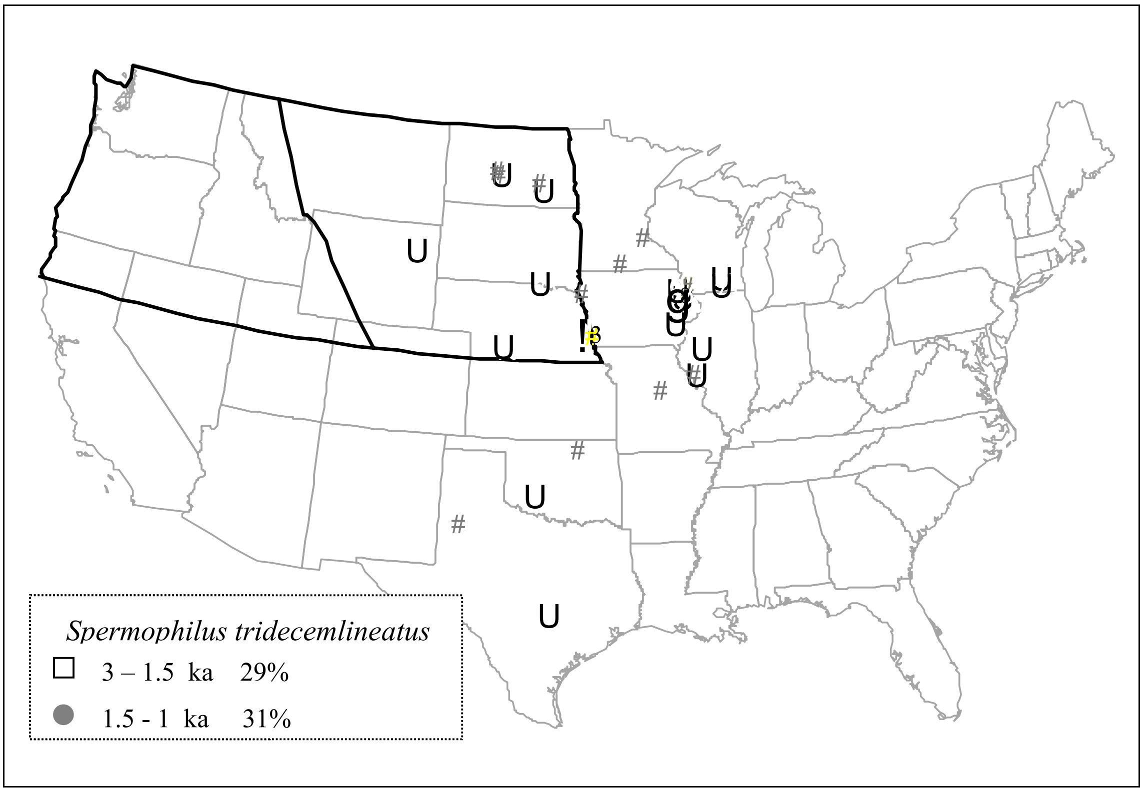


Fig. 82 The evolution of Arealsystem of *Spermophilus tridecemlineatus* (3-1 ka)

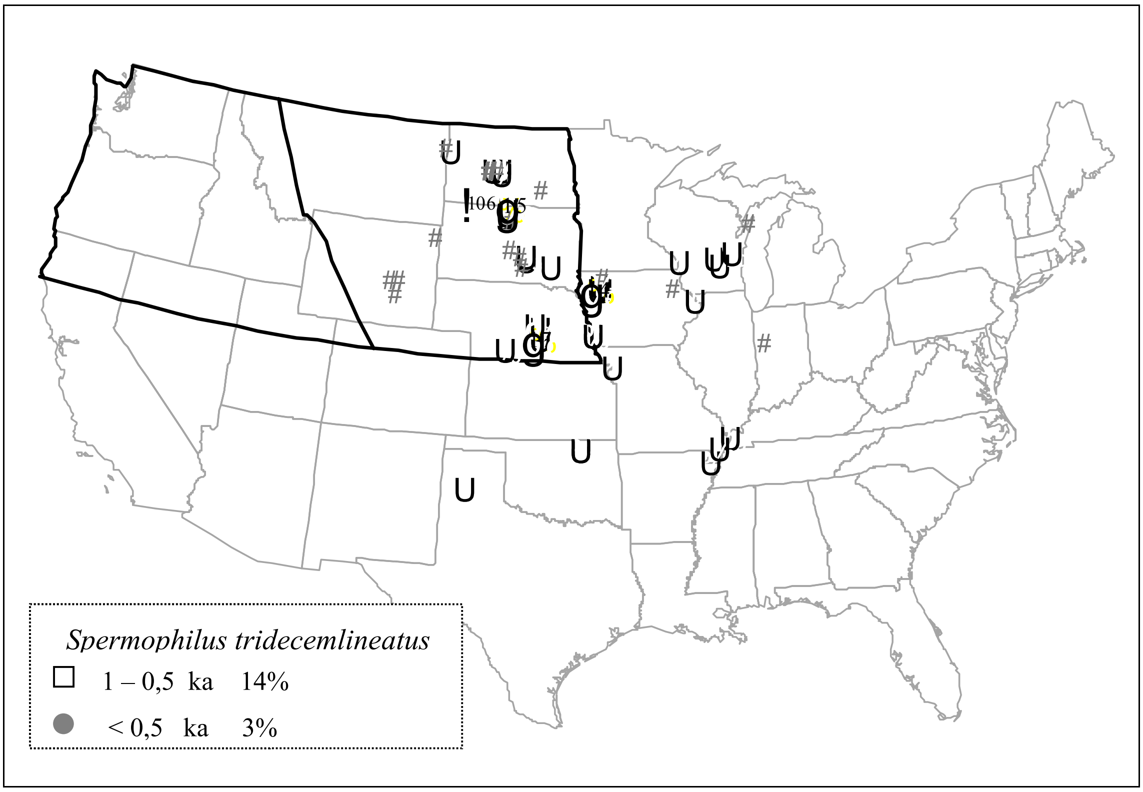


Fig. 83 The evolution of Arealsystem of *Spermophilus tridecemlineatus* (the last 1 ka)

to 0.5 ka about 14% of the records contained more than 50% of the total MNIs, and in the last 500 years about 3% of the records contained more than 50% of the total MNIs. The hot spots first appeared in Nebraska, and then in the upper Missouri River basin (Fig. 83).

Rodentia

Castoridae

4. 2. 4 *Castor canadensis* **American Beaver**

American Beaver's current range covers most of Canada and America, except for most of Florida, much of Nevada, and southern California. However, it once distributed in Florida and did not disappeared from Florida till about 500 years ago (Dig. Ref., Fig. 84a).

Before 15 ka it distributed mainly in the Appalachia and Rocky Mountain Refugium. From 15 to 8 ka about 48% of the records contained more than 50% of the total MNIs. In the east it started to migrate northward around 8 ka. During 8 and 3 ka about 28% of the records comprised more than 50% of the total MNIs, and records with the highest MNIs were found in Tennessee and Illinois. From 3 to 1.5 ka it started to appear in the upper Missouri River basin. About 35% of the records contained more than 50% of the total MNIs. Records with the highest MNIs were

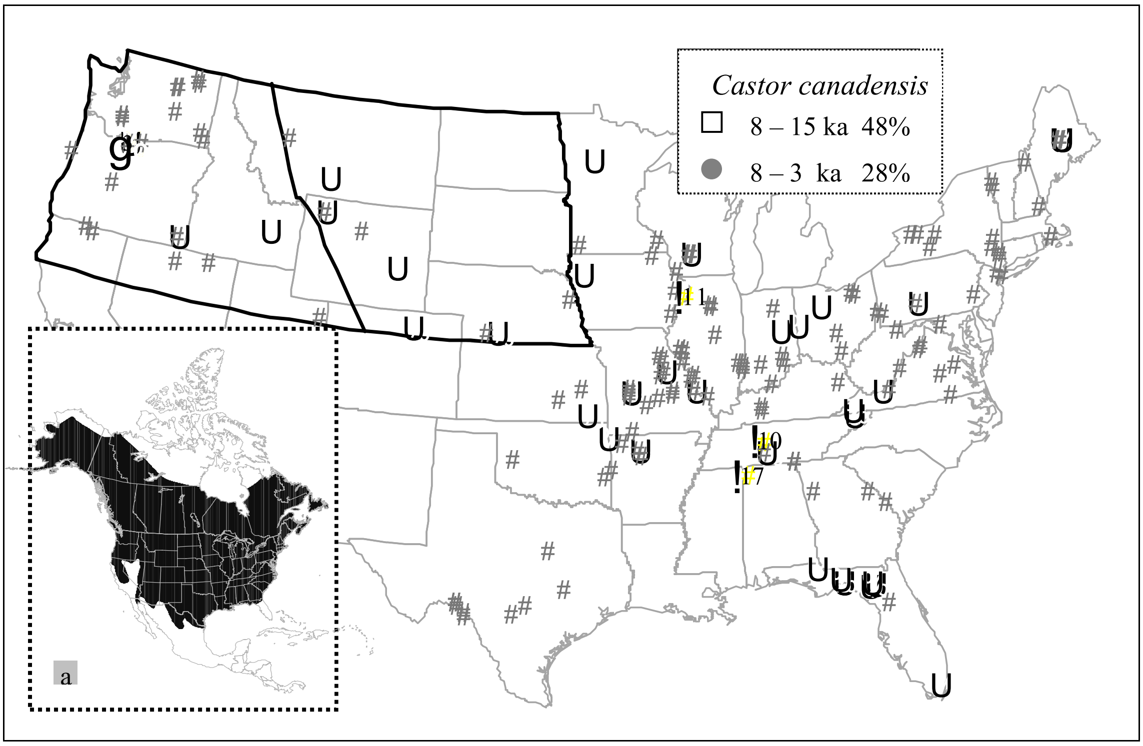


Fig. 84 The evolution of Arealsystem of *Castor canadensis* (15 – 3 ka)

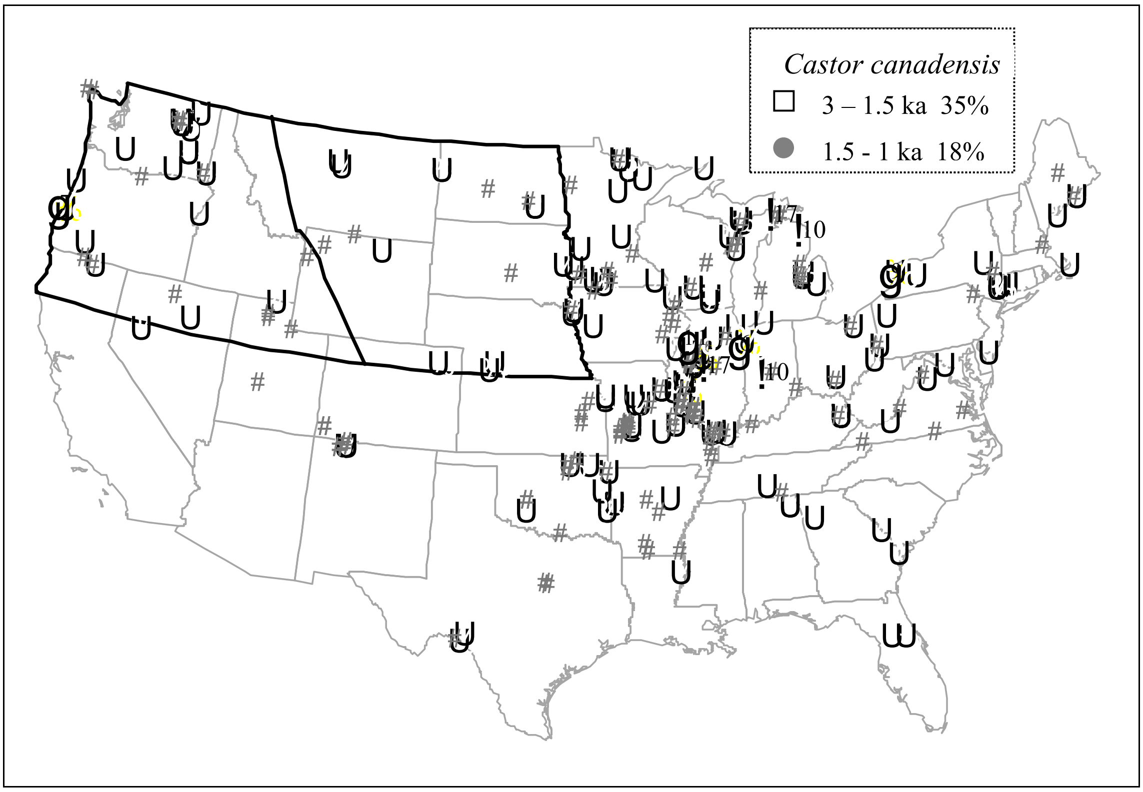


Fig. 85 The evolution of Arealsystem of *Castor canadensis* (3 - 1 ka)

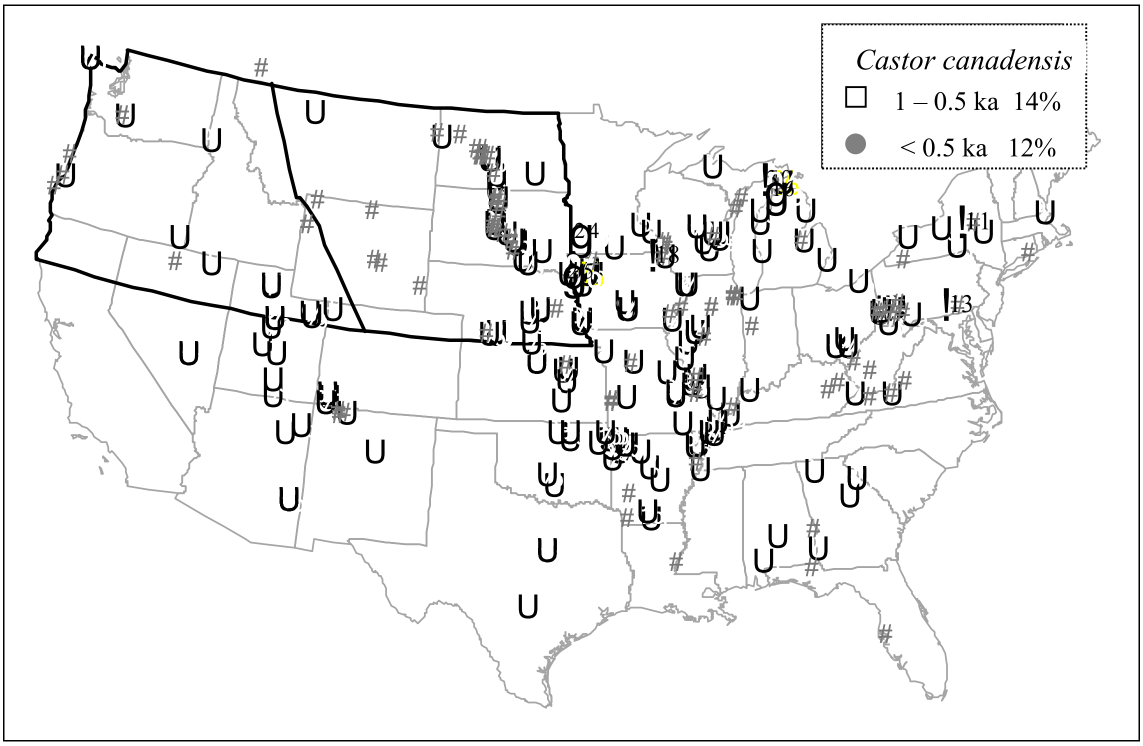


Fig. 86 The evolution of Arealsystem of *Castor canadensis* (the last 1 ka)

found in northern Illinois and Ohio. During 1.5 and 1 ka about 18% of the records comprised more than 50% of the total MNIs. Some hot spots appeared even in northern Michigan. In the West its distribution started to expand southward to Colorado and New Mexico. After 1 ka the hot spots appeared in Minnesota and Wisconsin. About 14% and 12% of the records contained more than 50% of the total MNIs during 1 and 0.5 ka and in the last 500 years respectively. At the same time, much more records were found in Colorado and New Mexico than on the west side of the Rockies. The conservation status differs with respect to source, but there have been significant threats to the survival of the beaver. Beavers have been hunted and trapped extensively in the past and by about 1900, the animals were almost gone in many of their original habitats. Pollution and habitat loss have also effected the survival of the beaver. In the last century, however, beavers have been successfully reintroduced to many of their former habitats (Dig. Ref., Frazier, 1996, Sevilleta LTER, 1998).

Rodentia

Muridae

4. 2. 5 *Ondatra zibethicus* **Muskrat**

Muskrat lives in wet environments, with a favorite of marshes and swamps. It distributes north to the treeline, including Newfoundland, Alaska; south to the Gulf of Mexico, Rio Grande and lower Colorado River valleys (Fig. 87a), often reaching high population densities in areas with emergent cattails, and abundant aquatic vegetation (Baker, 1983, Pietsch, 1982)

Before 15 ka the muskrat's fossil records were found widely in USA, but mainly distributed in the Appalachia Refugium. From 15 to 8 ka the hot spots might not have developed. Like American Beaver, Muskrat dispersed northward during 8 and 3 ka in the East. About 12% of the records contained more than 50% of the total MNIs, and the hot spots were located in Tennessee and northern Illinois (Fig. 87). During 3 and 1 ka the hot spots moved further northward. From 1.5 to 1 ka the hot spots already appeared in Michigan and Minnesota. At the same time it started to extend westward to the upper Missouri River area. The hot spots were also in Louisiana in this period (Fig 88). After 1 ka Muskrat's fossil records were found widely in the upper Missouri River area such as in North and South Dakota, and Nebraska. Muskrat distributed on the west side of the Rockies since 15ka, but the hot spots never seemed to developed in this area. The hot spots appeared in Utah during 1 and 0.5 ka (Fig 89).

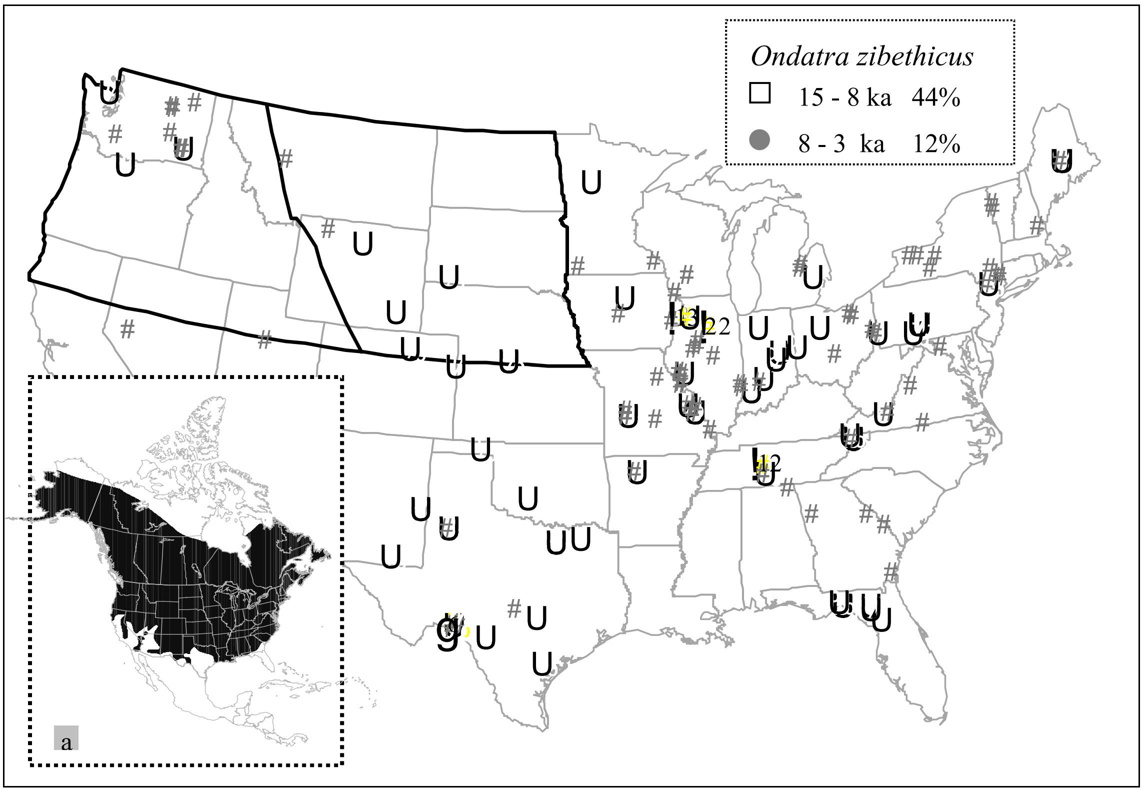


Fig. 87 The evolution of Arealsystem of *Ondatra zibethicus* (15 – 3 ka)

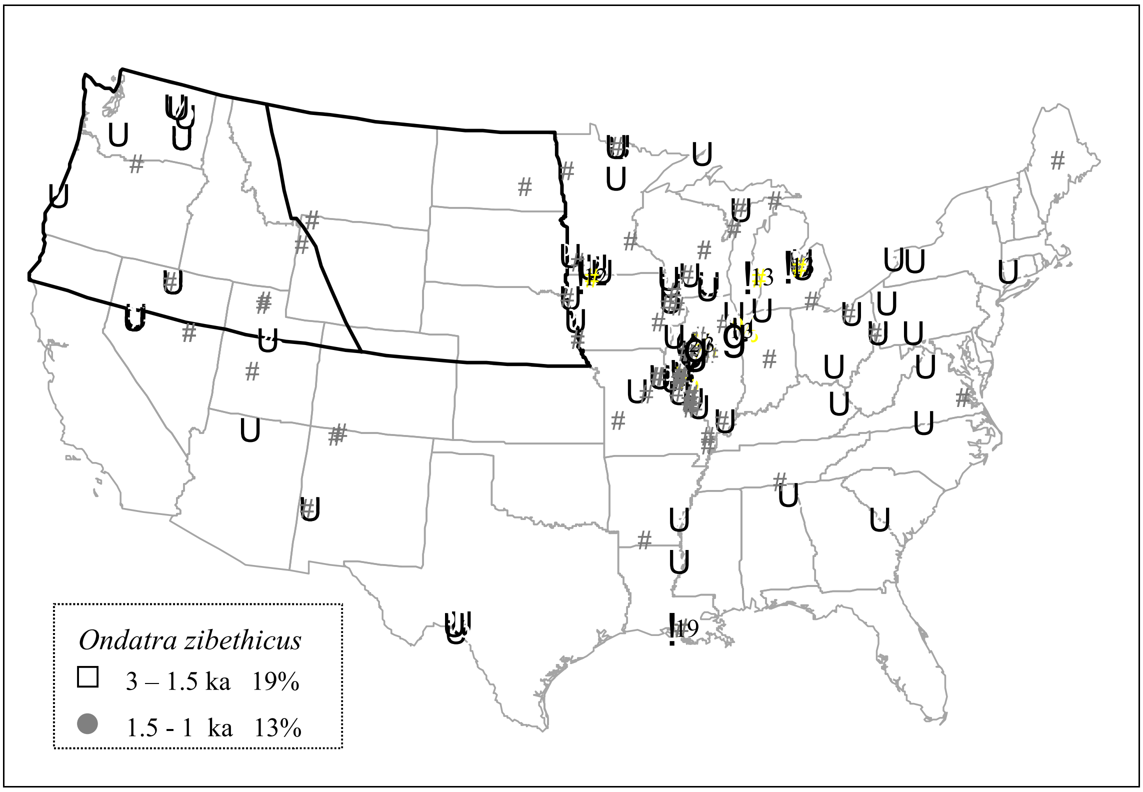


Fig. 88 The evolution of Arealsystem of *Ondatra zibethicus* (3 - 1 ka)

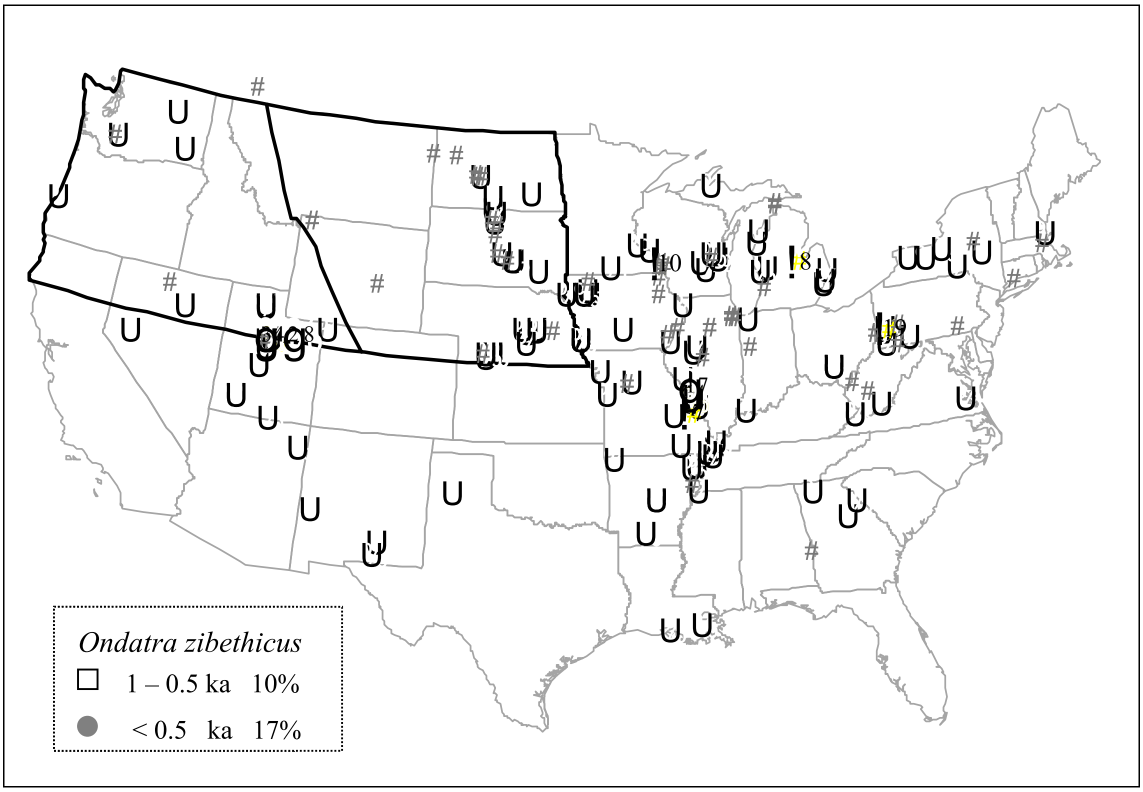


Fig. 89 The evolution of Arealsystem of *Ondatra zibethicus* (the last 1 ka)

Rodentia

Muridae

4. 2. 6 *Clethrionomys gapperi* **Red-Backed Vole**

Red-backed voles range from British Columbia to mainland Newfoundland and throughout the northern United States from the Rocky Mountains to the Appalachians (Fig. 90a). Red-backed voles inhabit cool, mossy and rocky boreal forests in both dry and moist areas. They also inhabit tundra and bogs. Coniferous forests are preferred habitat, although deciduous or mixed coniferous/deciduous woods are also accepted (Dig. Ref.).

Before 15 ka its distribution is like a narrow band extending from the Rockies southeast through Nebraska, Iowa, and Missouri to the Appalachians. From 15 to 8 ka about 7% of the records contained more than 50% of the total MNIs. The hot spots were mainly located in the Appalachia Refugium. During 8 and 3 ka about 27% of the records contained more than 50% of the total MNIs. Records with the highest MNIs were still found in the Appalachia area (Fig. 90). From 3 to 1.5 ka about 17% of the records contained more than 50% of the total MNIs.

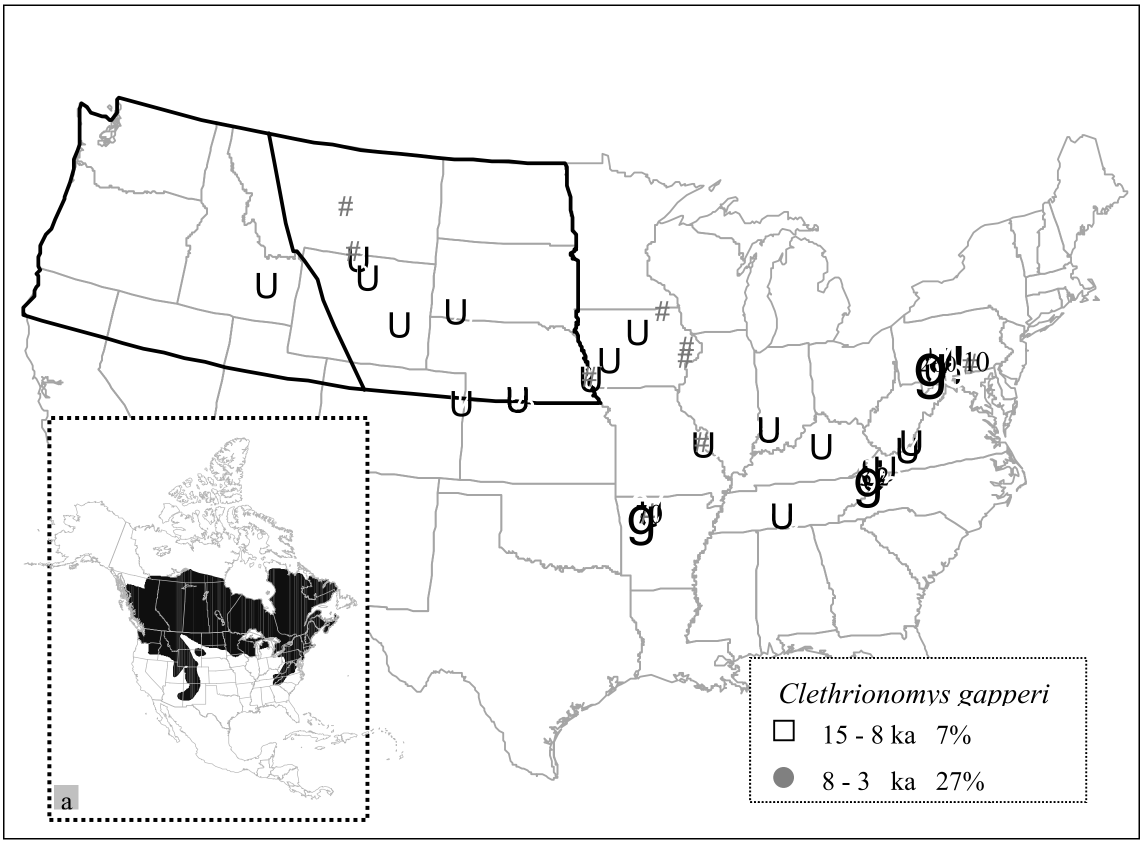


Fig. 90 The evolution of Arealsystem of *Clethrionomys gapperi* (15-3 ka)

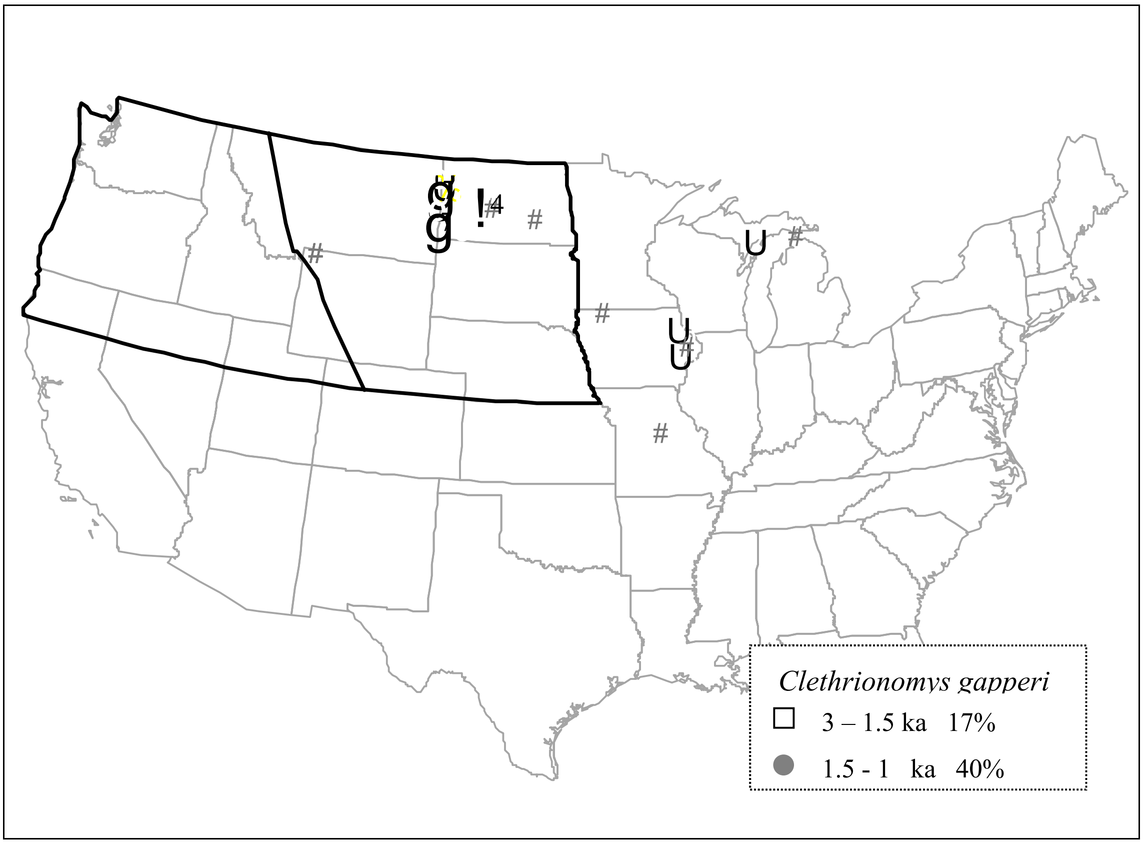


Fig. 91 The evolution of Arealsystem of *Clethrionomys gapperi* (3-1 ka)

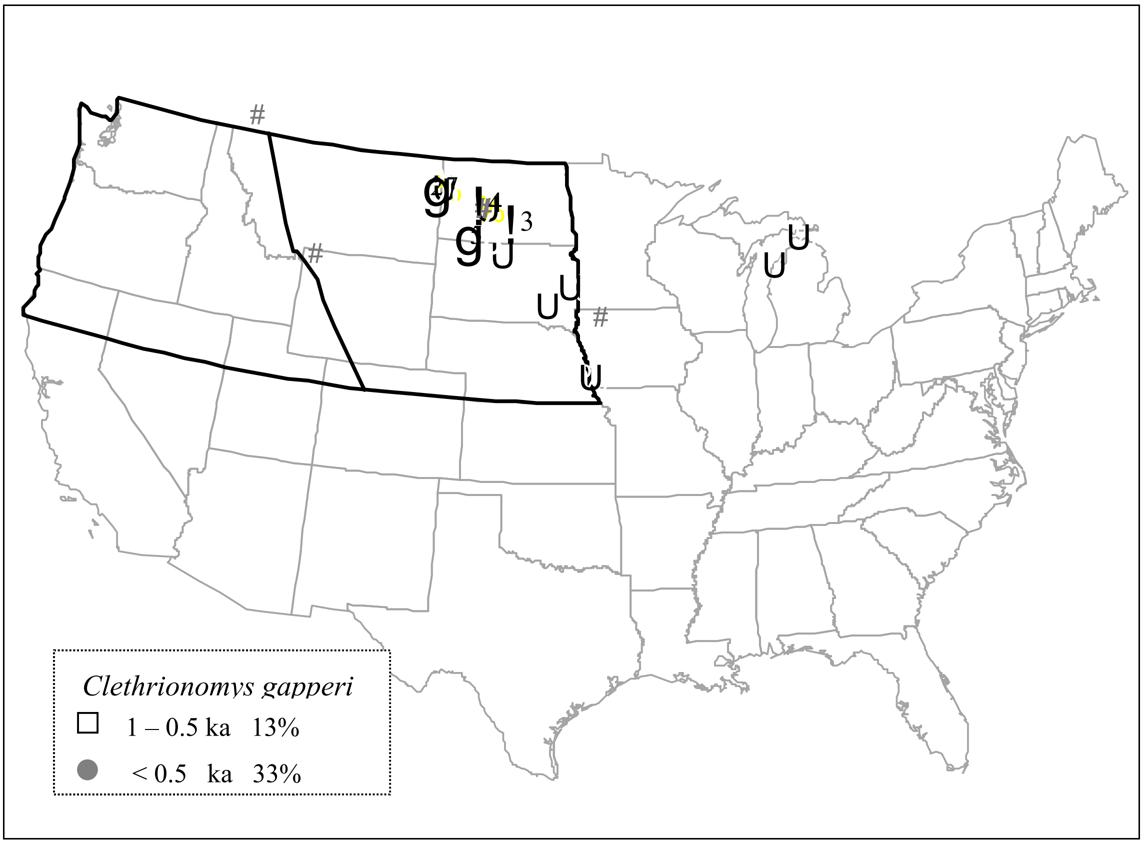


Fig. 92 The evolution of Arealsystem of *Clethrionomys gapperi* (the last 1 ka)

The hot spots first appeared in the upper Missouri River area, and its distribution started to disappear from most of the Appalachia Refugium (Fig. 91, 92).

Rodentia

Muridae

4. 2. 7 *Microtus ochrogaster* ***Prairie Vole***

Prairie voles occur from northeastern New Mexico to northern Alabama, western West Virginia, and northwest to central Alberta (Fig. 93a). Prairie voles are common in prairies, ungrazed pastures, fallow fields, weedy areas, road right-of-ways, and sometimes in soybean or alfalfa fields (Dig. Ref.).

It distributed mainly in the Great Plains before 15 ka. From 15 to 8 ka about 3% of the records contained more than 50% of the total MNIs. The hot spots might be located in northern Arkansas. During 8 and 3 ka it dispersed northward, but still lived in southern Texas. And about 15% of the records contained more than 50% of the total MNIs. The hot spots were

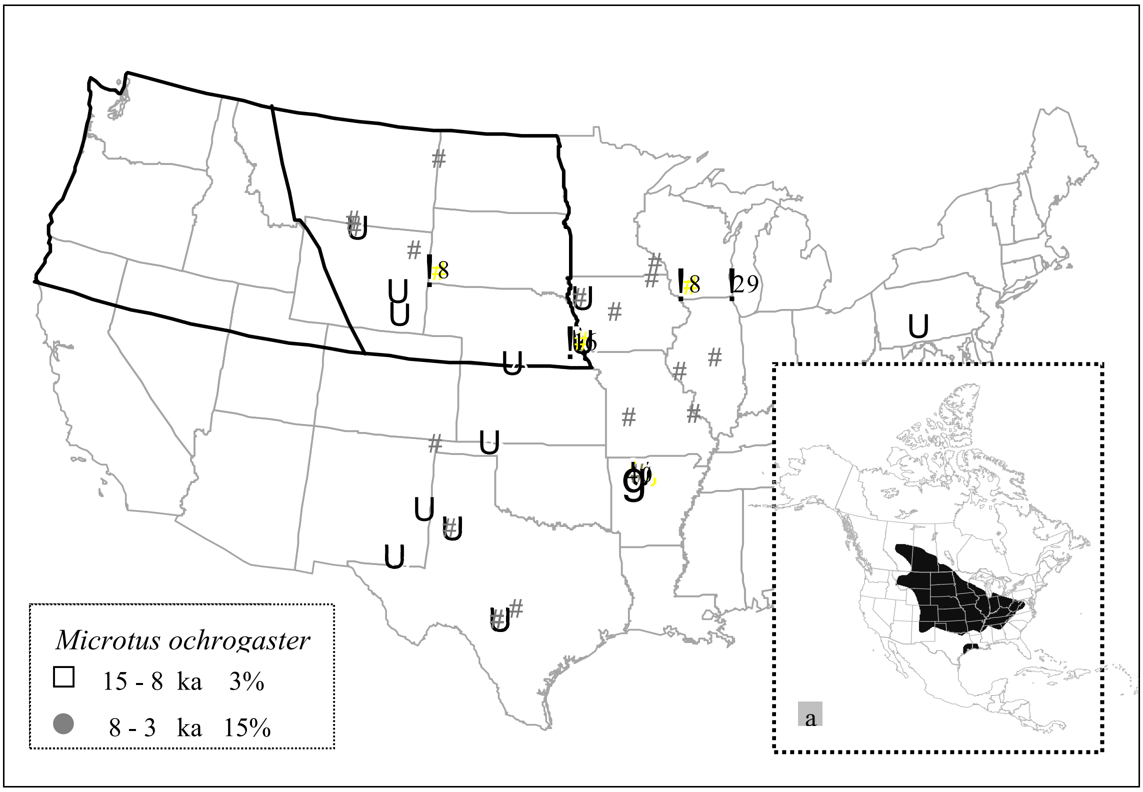


Fig. 93 The evolution of Arealsystem of *Microtus ochrogaster* (15-3 ka)

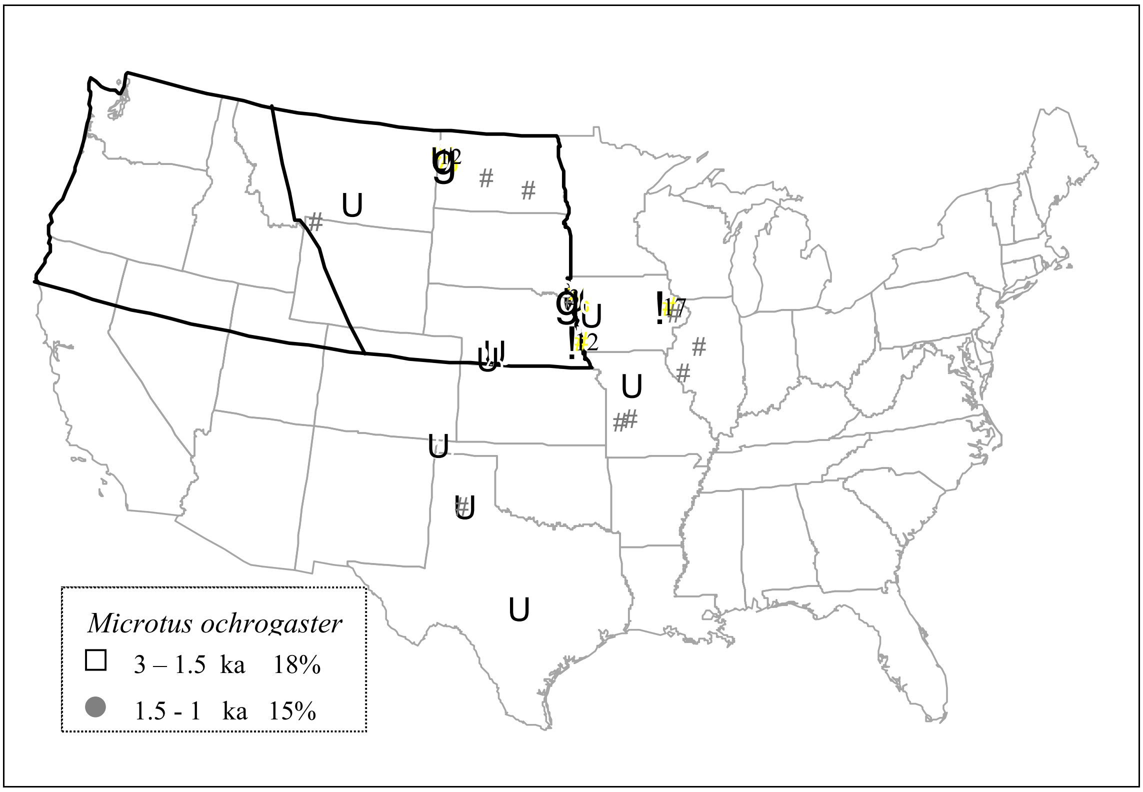


Fig. 94 The evolution of Arealsystem of *Microtus ochrogaster* (3-1 ka)

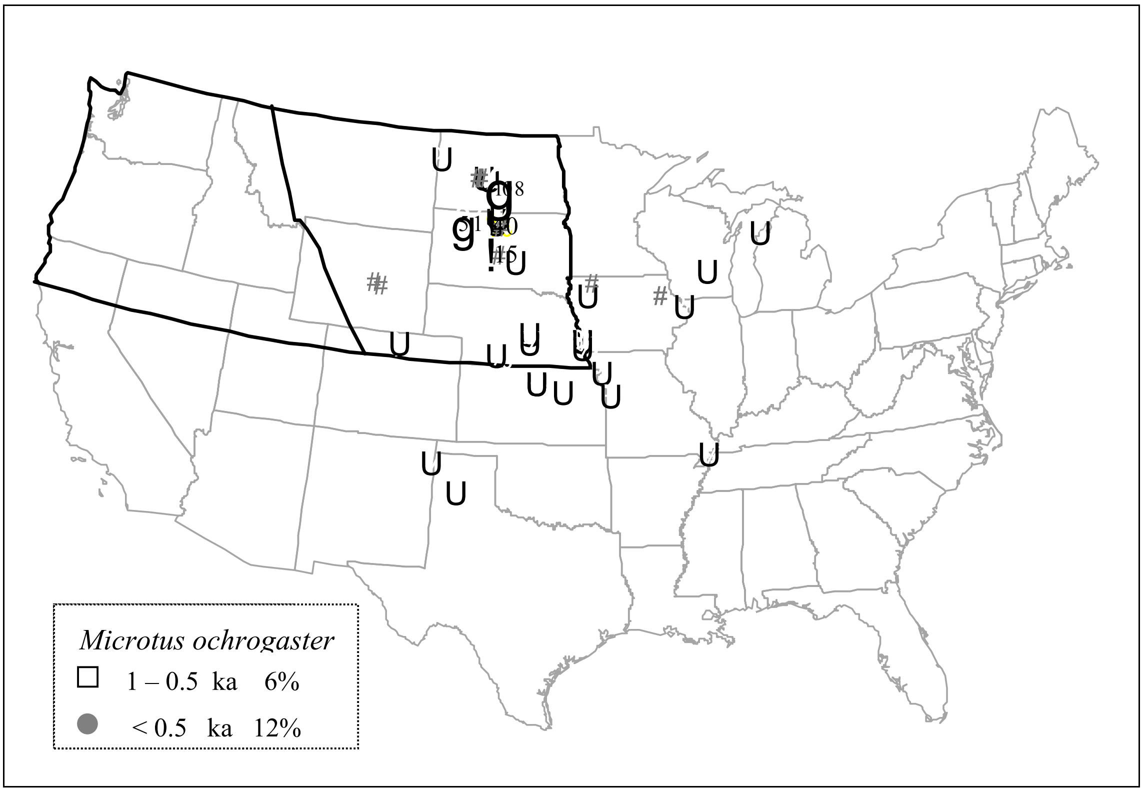


Fig. 95 The evolution of Arealsystem of *Microtus ochrogaster* (the last 1 ka)

located in Iowa and Wisconsin (Fig. 93). From 3 to 1.5 ka about 18% of the records contained more than 50% of the total MNIs, and the hot spots first appeared in the upper Missouri River area. After about 1 ka it disappeared from the southern Texas and the hot spots were located mainly in the upper Missouri River basin. (Fig. 94, 95)

Rodentia

Muridae

4. 2. 8 *Microtus pennsylvania* **Meadow Vole**

Meadow voles can be found mainly in meadows, lowland fields, grassy marshes, and along rivers and lakes. *Microtus pennsylvanicus* is the most widespread vole in North America. Its east to west range is continuous from central Alaska to the Atlantic coast. South of the Canadian border, its western limit is the Rocky Mountains. The meadow vole is found as far south as New Mexico and Georgia (Dig. Ref., Fig. 97a).

Meadow vole was a polycentric species, which distributed mainly in the Appalachia Refugium before 15 ka. The ISVAs from 15 to 8 ka and from 8 to 3 ka are 3% and 8% respectively.

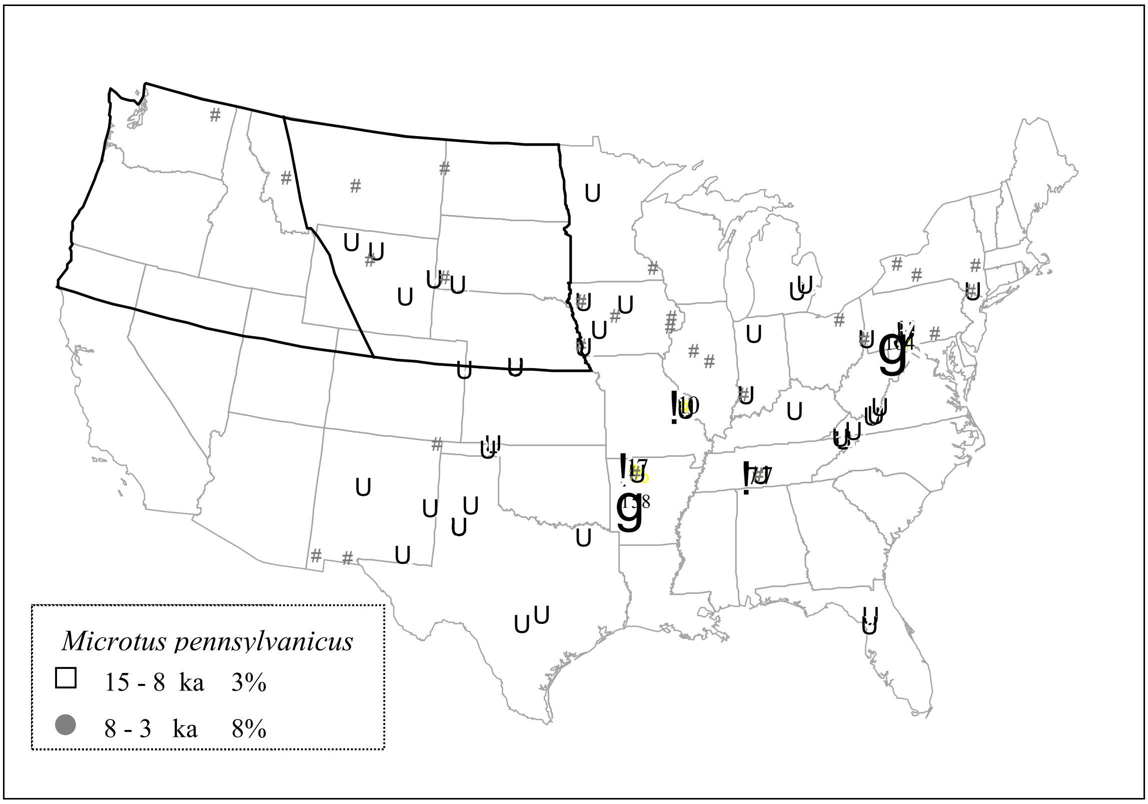


Fig. 96 The evolution of Arealsystem of *Microtus pennsylvanicus* (15-3ka)

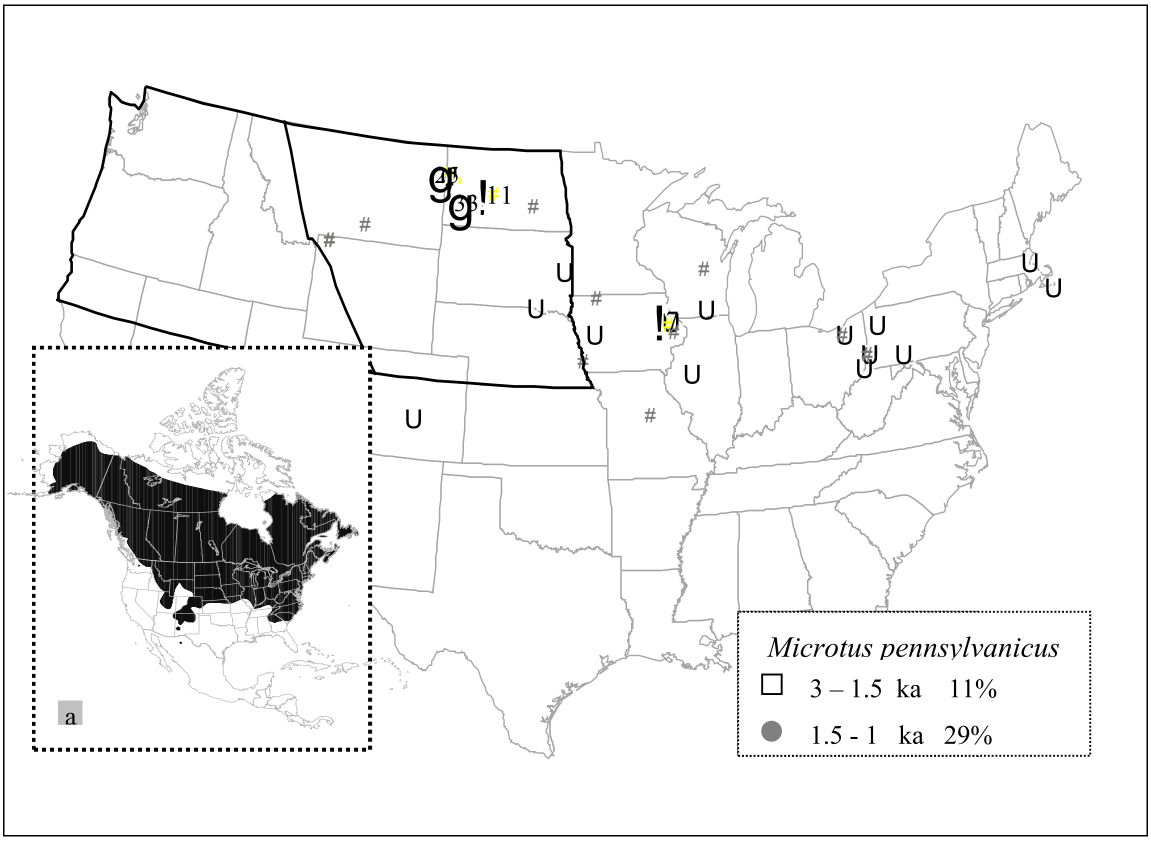


Fig. 97 The evolution of Arealsystem of *Microtus pennsylvanicus* (3-1 ka)

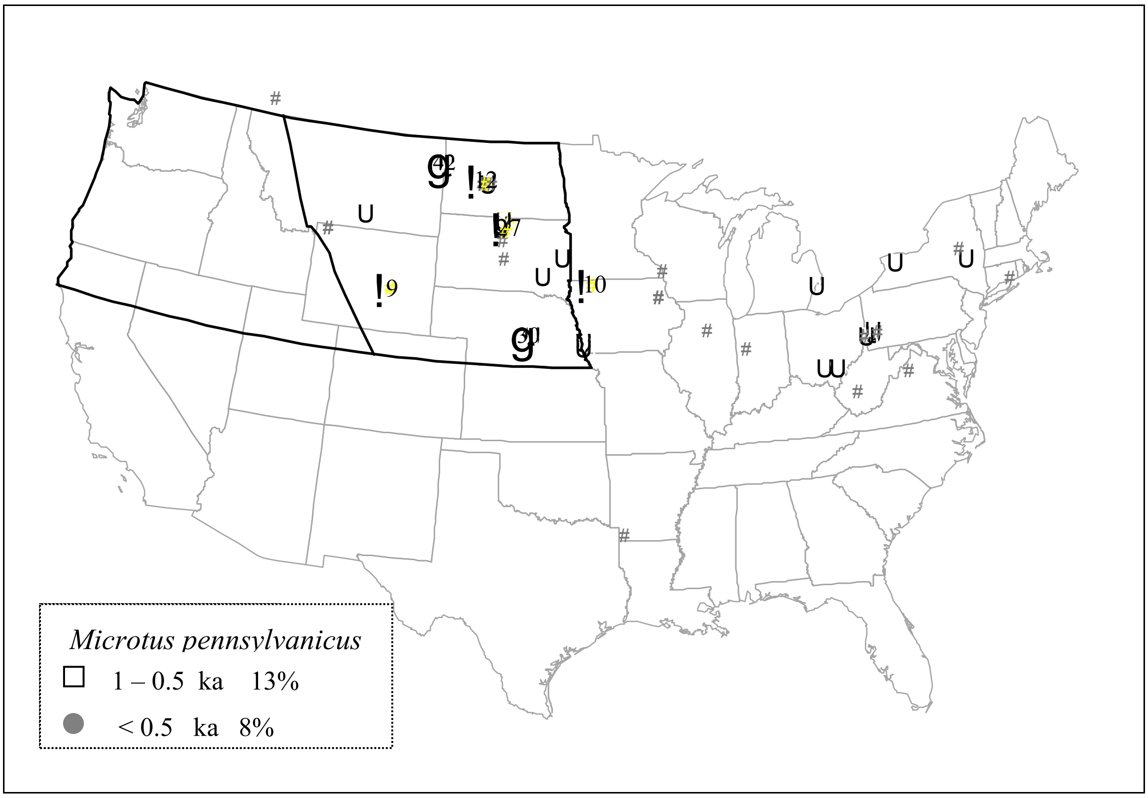


Fig. 98 The evolution of Arealsystem of *Microtus pennsylvanicus* (the last 1 ka)

The hot spots were located in the Appalachia area. From 15 to 8 ka it still lived in Texas (Fig. 96). But during 3 and 1.5 ka it disappeared from most of the Appalachia Refugium and Texas. About 11% of the records contained more than 50% of the total MNIs. The hot spots first appeared in the upper Missouri River (Fig. 97). After 1 ka the ISVAs are 13% and 8%. The hot spots were still in the upper Missouri River basin (Fig. 98).

Carnivora

Canidae

4. 2. 9 *Canis familiaris* **Dog**

Dog is a subspecies of *Canis lupus*, which distributes now throughout the world.

Dog distributed only in the Appalachia and Florida Refugium during the glacial time. From 15 to 8 ka, the hot spots did not seemed to be apparent, and 38% of the records contained more than 50% of the total MNIs. But during 8 and 3 ka, about 22% of the records contained more than 50% of the total MNIs. The hot spots were located in Illinois (Fig. 99).

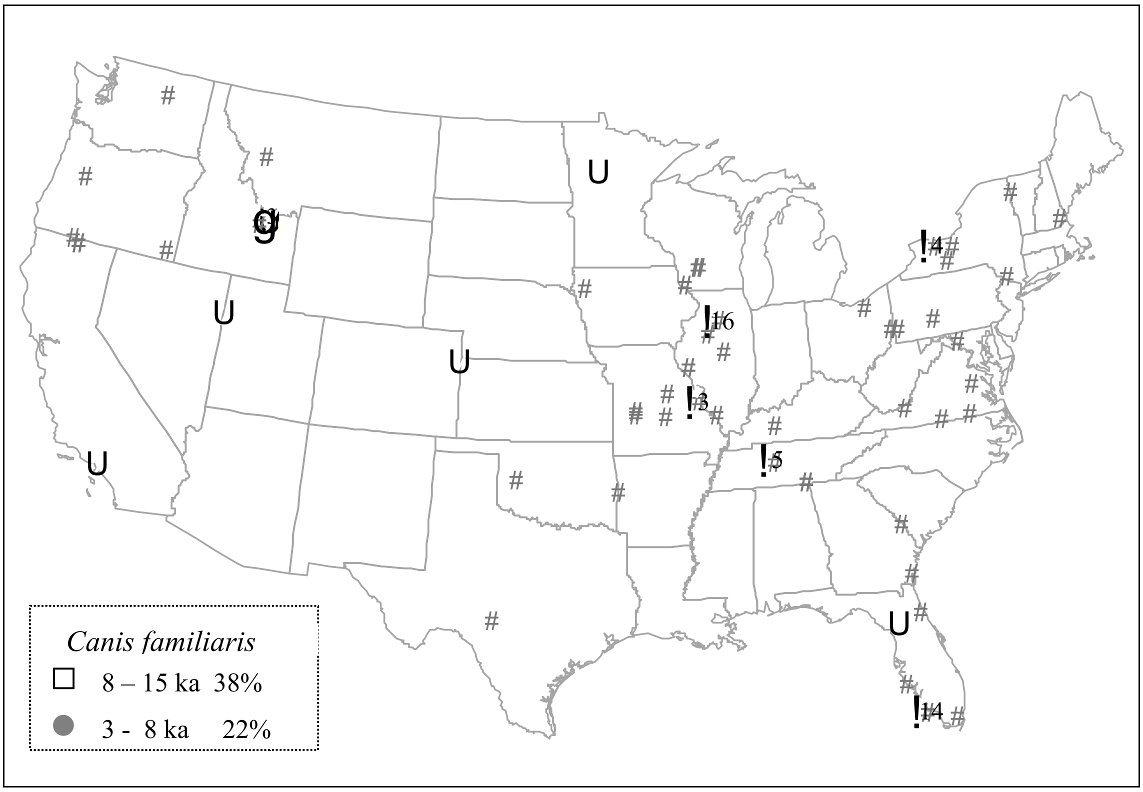


Fig. 99 The evolution of Arealsystem of *Canis familiaris* (15-3 ka)

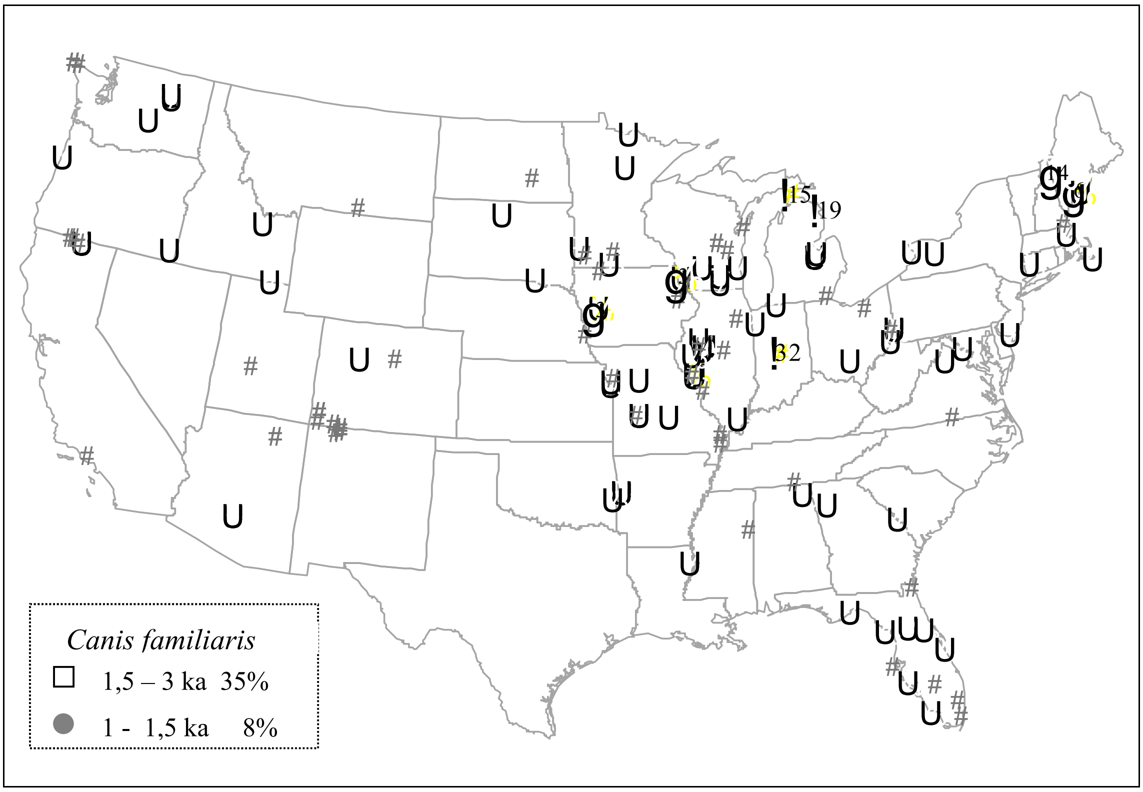


Fig. 100 The evolution of Arealsystem of *Canis familiaris* (3 - 1 ka)

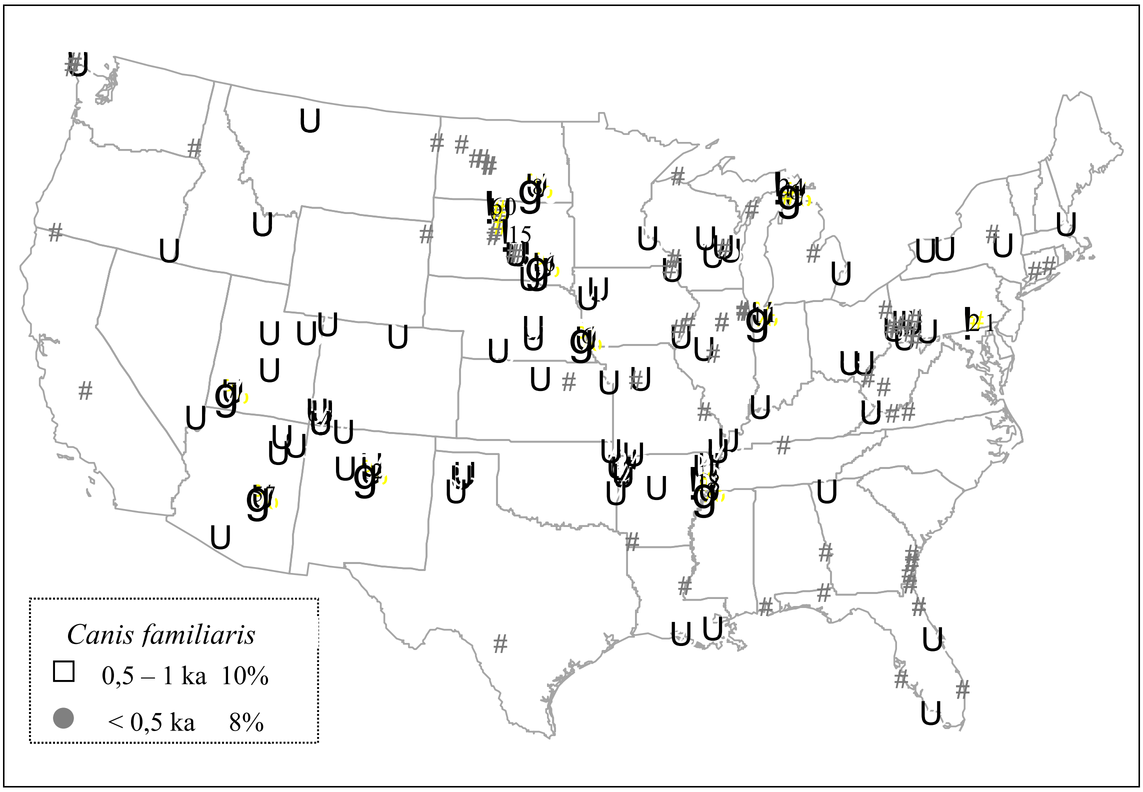


Fig. 101 The evolution of Arealsystem of *Canis familiaris* (the last 1 ka)

During 1.5 and 3 ka it started to enter the east side of the Rockies. From 1 to 1.5 ka the ISVA equals 8%, and the hot spots were located in Indiana and Michigan (Fig. 100). From 1 to 0.5 ka, the ISVA equals 10%. The hot spots started to appear on the west side of the Rockies. And in the last 500 years, the ISVA equals 8%. The hot spots were still in the upper Missouri basin, but also in northern Michigan (Fig. 101).

Carnivora

Canidae

4. 2. 10 *Urocyon cinereoargenteus* **Grey Fox**

The gray fox occurs throughout most of the southern half of North America from southern Canada to northern Venezuela and Colombia. It does not occur in portions of the mountainous northwestern United States, the Great Plains and eastern Central America (Fig. 102a). Grey foxes are found in deciduous woodlands, but are occasionally seen in old fields foraging for fruits and insects (Dig. Ref.).

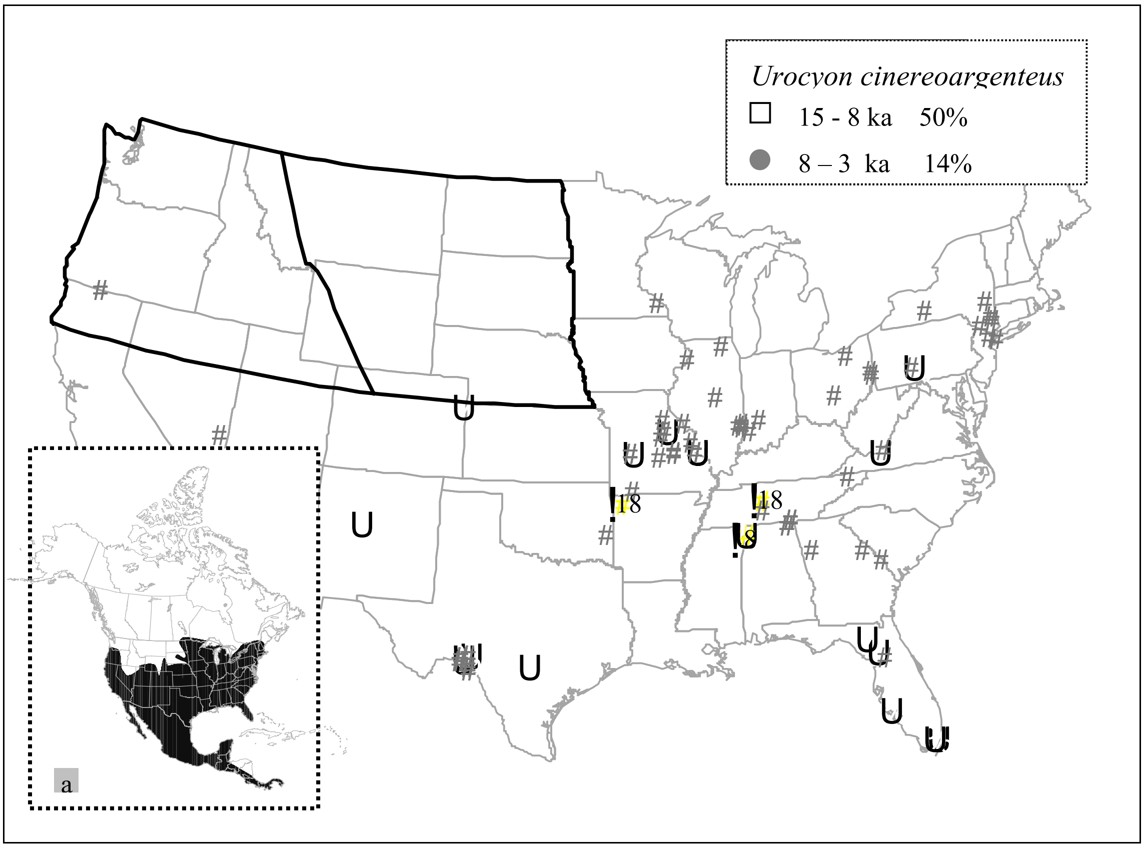


Fig. 102 The evolution of Arealsystem of *Urocyon cinereoargenteus* (15-8 ka)

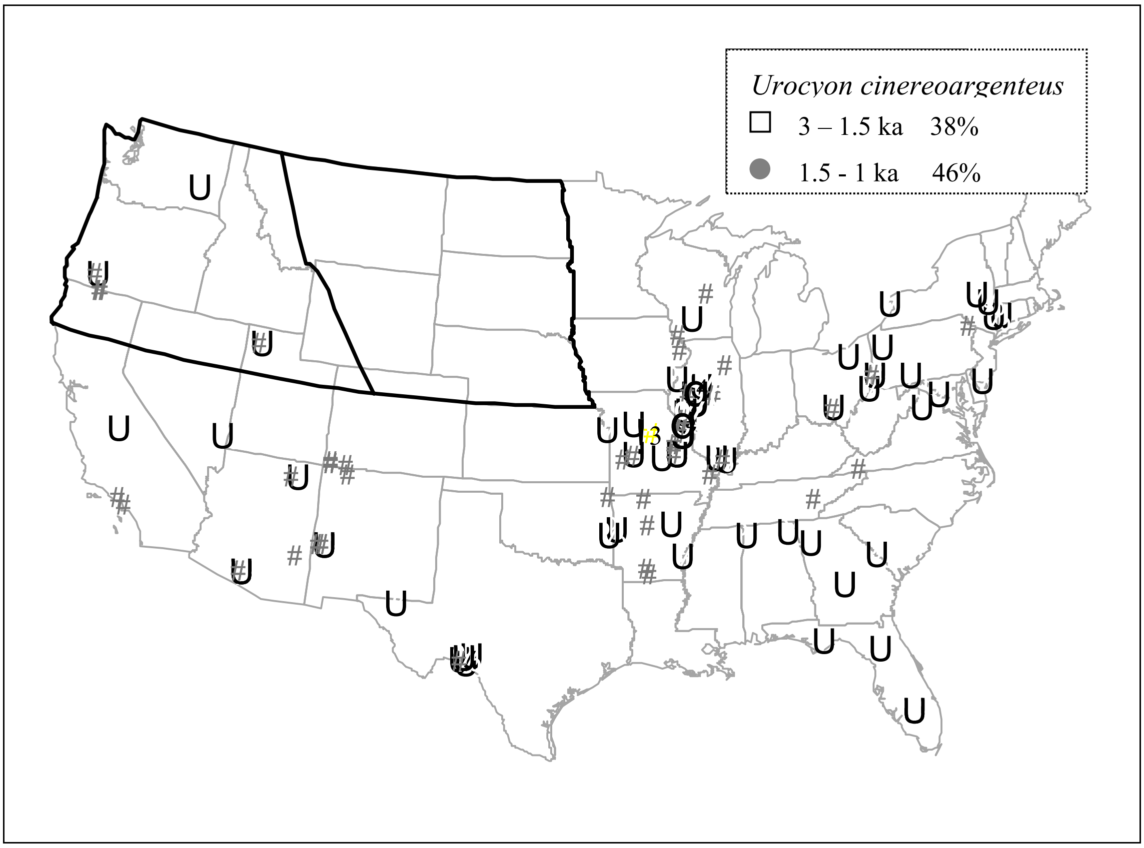


Fig. 103 The evolution of Arealsystem of *Urocyon cinereoargenteus* (3-1 ka)

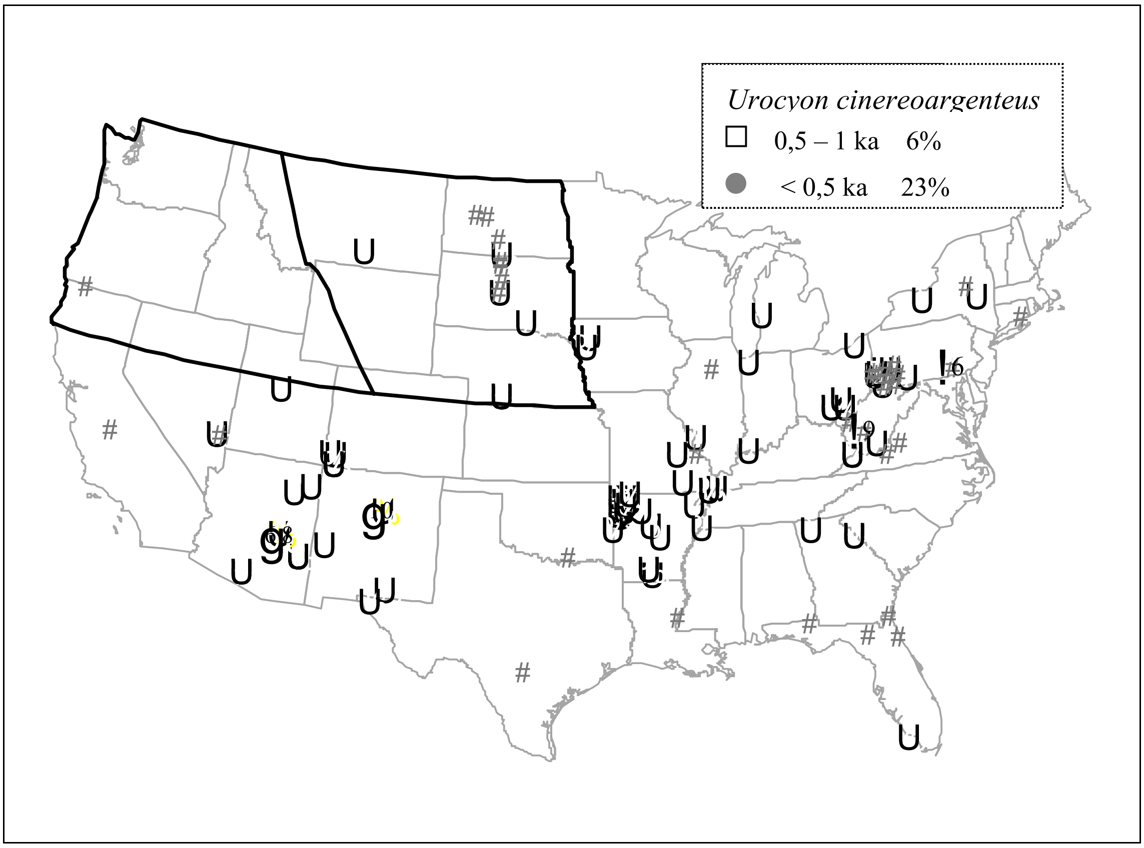


Fig. 104 The evolution of Arealsystem of *Urocyon cinereoargenteus* (the last 1 ka)

Before 15 ka only a few fossil records were found in the Appalachia and Florida Refugium. During 15 and 8 ka its range was still restricted to a small area. But from 8 to 3 ka it had reached Wisconsin and New York in the east and Oregon in the west. About 14% of the records contained more than 50% of the total MNIs. The hot spots were still located in the Appalachia Refugium such as in Tennessee, northern Kansas (Fig. 102). From 3 to 1 ka the hot spots were not obvious. The ISVAs are 38% and 46% for 3-1.5 ka and 1.5-1 ka respectively. But it had distributed widely in the southwest of USA (Fig. 103). During 1 and 0.5 ka it had entered the upper Missouri River basin. The ISVA equals 6%. The hot spots were in northern Arizona and New Mexico (Fig. 104).

Carnivora

Mustelidae

4. 2. 11 *Lutra canadensis* **North American River Otter**

North American river otters are found from Alaska in the west across northern Canada and the United States to Nova Scotia in the east and south to California and sections of Arizona. They

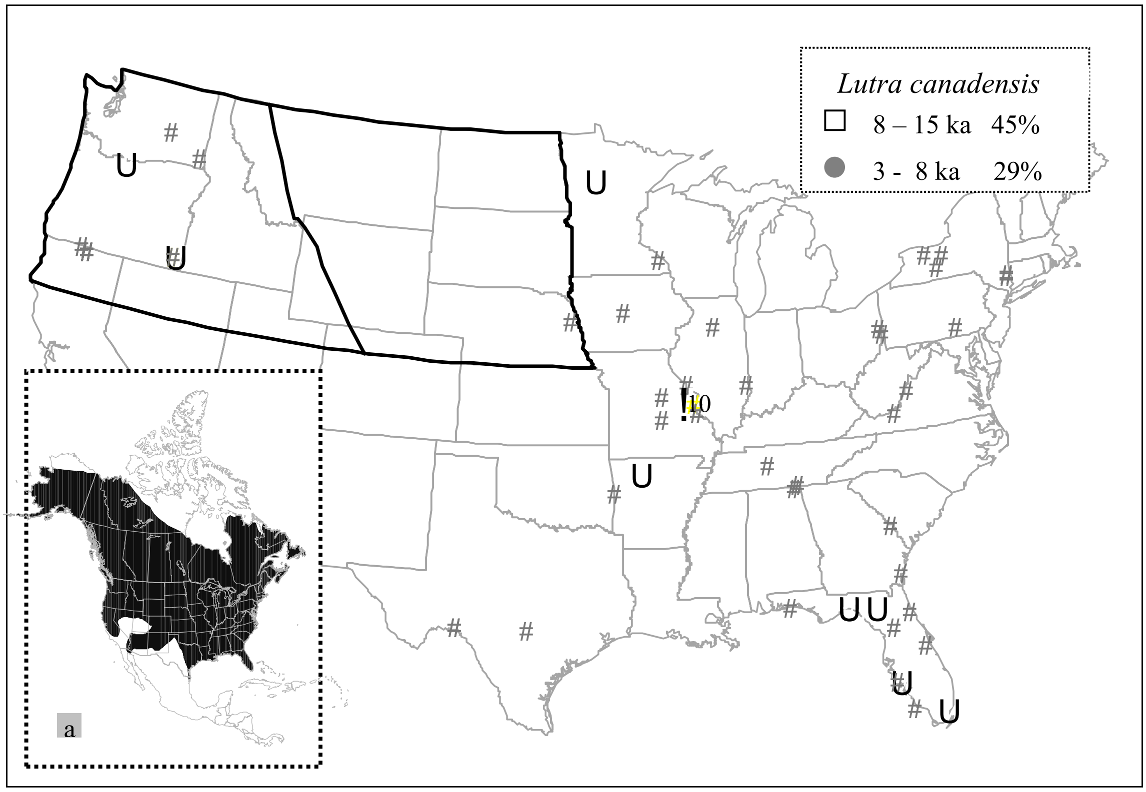


Fig. 105 The evolution of Arealsystem of *Lutra canadensis* (15-8 ka)

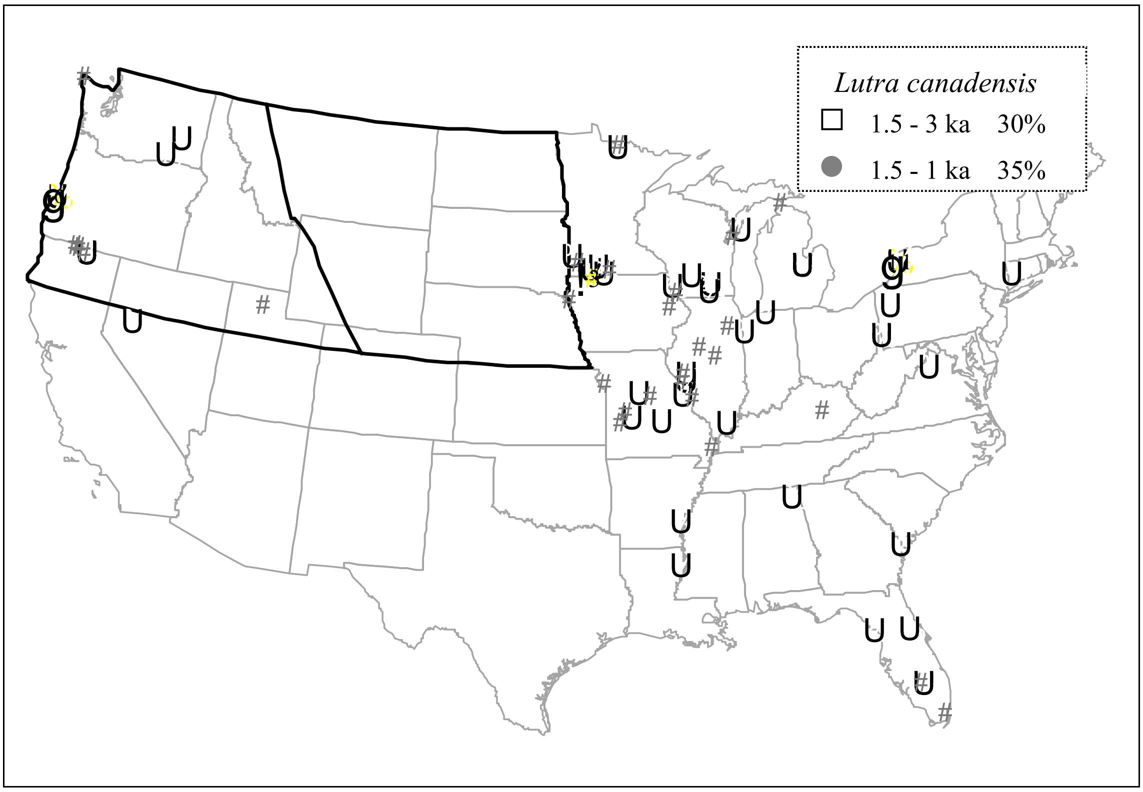


Fig. 106 The evolution of Arealsystem of *Lutra canadensis* (3-1 ka)

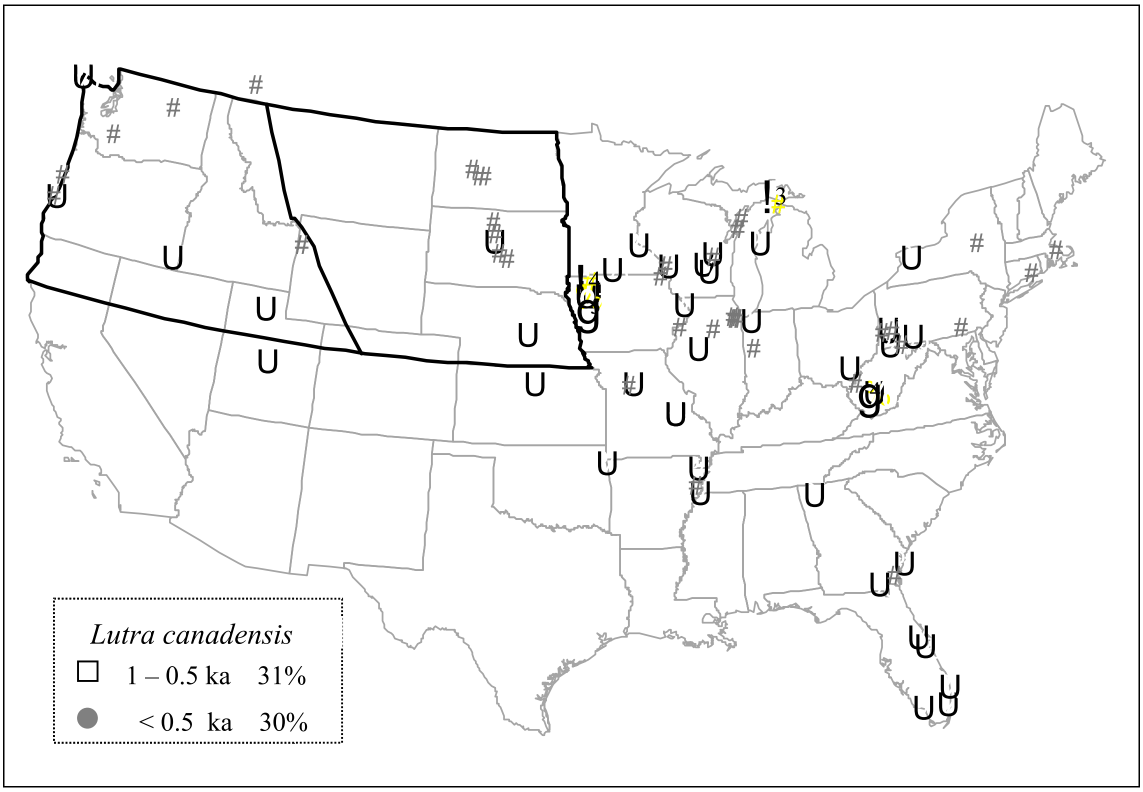


Fig. 107 The evolution of Arealsystem of *Lutra canadensis* (the last 1 ka)

occur as far east as the Atlantic coast (Fig. 105a). They prefer riparian zones, usually no more than a few hundred meters from water unless they are moving between rivers or lakes.

Before 15 ka it distributed mainly in the Appalachia and Florida Refugium. All ISVAs are more than 25%. It seems that the river otter has no hot spots. During 8 and 3 ka it had migrated northward to Minnesota and New York. From 1 to 0.5 ka it had entered the upper Missouri River area. There are no fossil records found in the southern and midwestern United States. This is coincident with the ecological finding that the river otter has been, until recently, rare throughout the southern and midwestern United States. River otters may be increasing in number in these areas (Digital Ref.).

Carnivora

Mustelidae

4. 2. 12 *Mephitis mephitis* **Striped Skunk**

Striped skunks occur from central Canada south to northern Mexico (Fig. 108a). *Mephitis mephitis* prefers somewhat open areas with a mixture of habitats such as woods, grasslands,

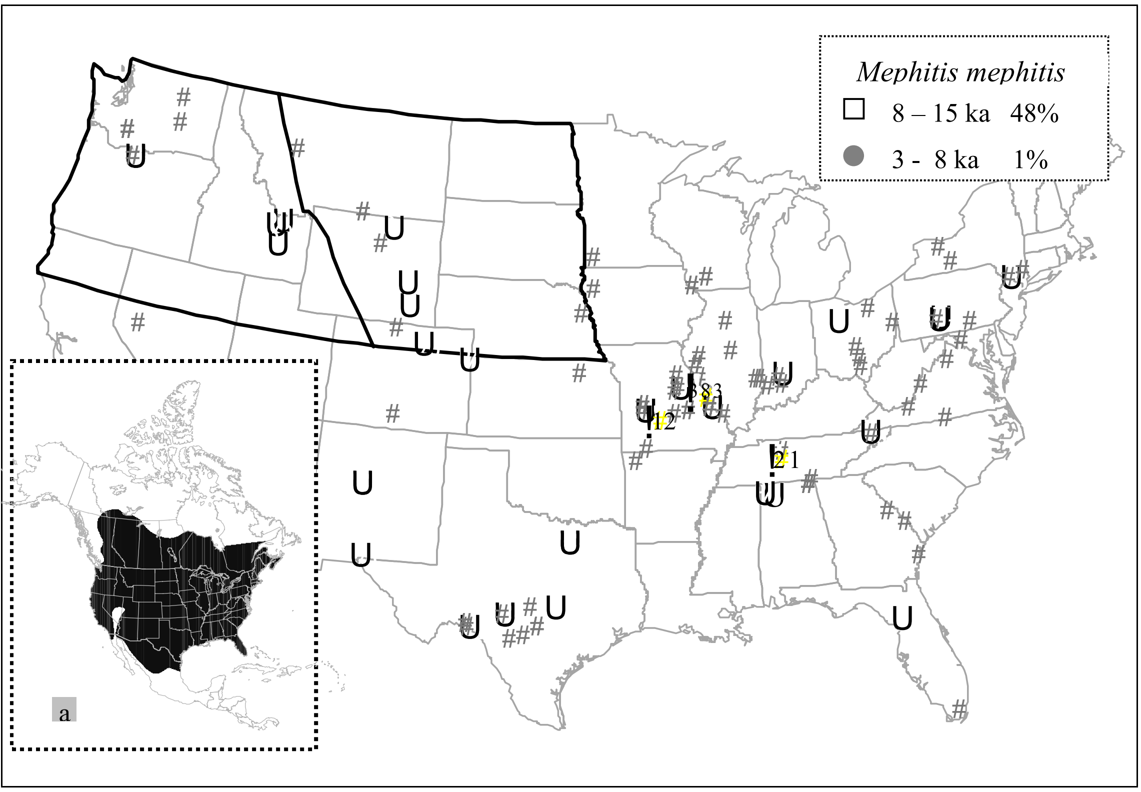


Fig. 108 The evolution of Arealsystem of *Mephitis mephitis*(15 – 3 ka)

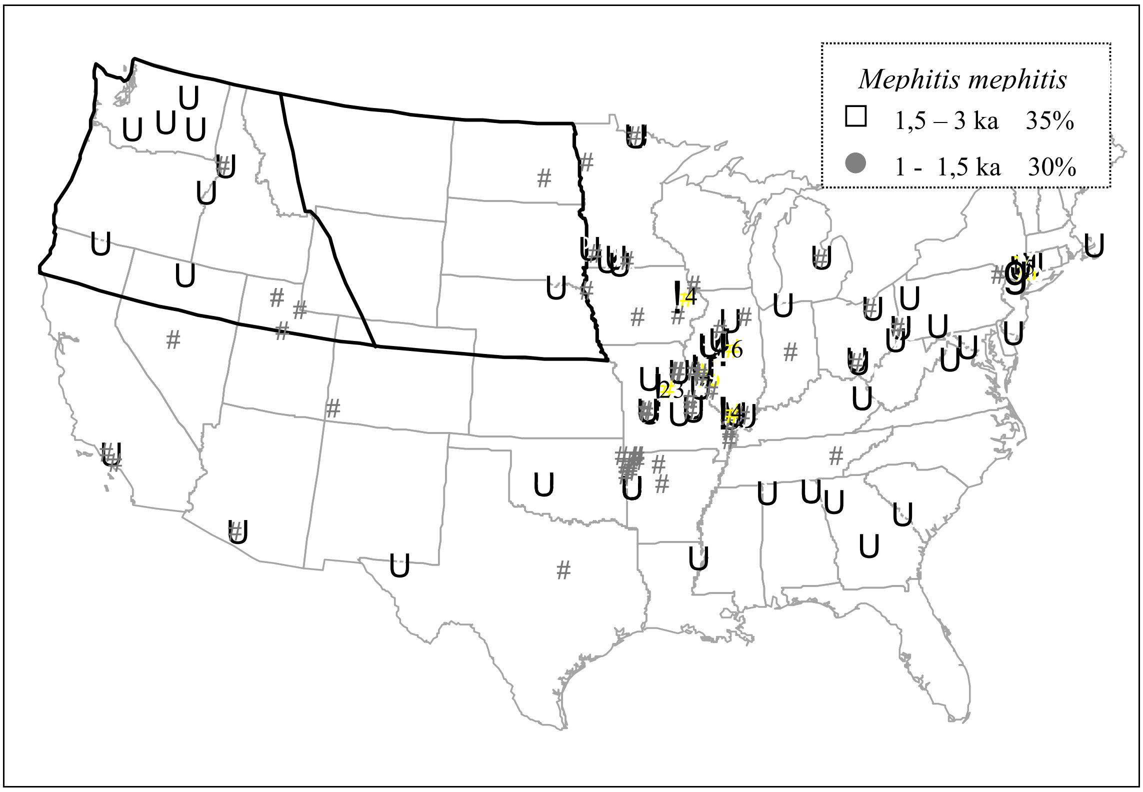


Fig. 109 The evolution of Arealsystem of *Mephitis mephitis* (3 - 1 ka)

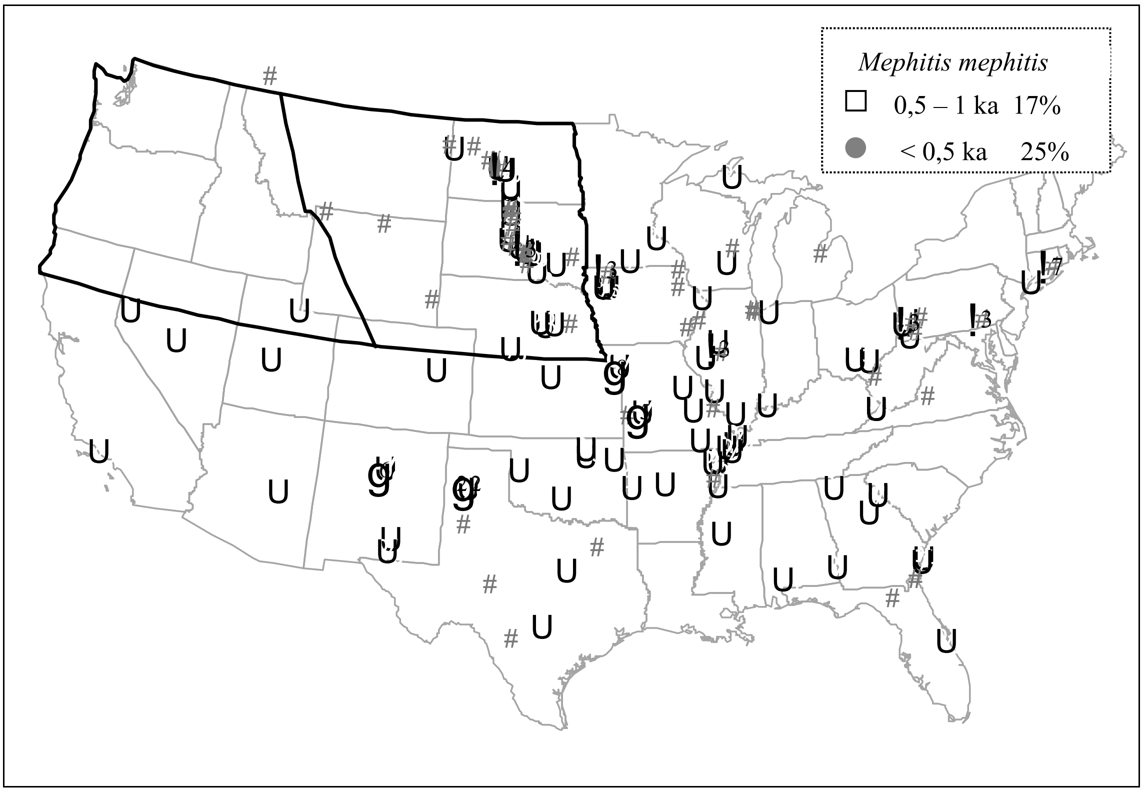


Fig. 110 The evolution of Arealsystem of *Mephitis mephitis* (the last 1 ka)

and agricultural clearings. They are usually never found further than two miles from a water source (Dig. Ref.).

Striped Skunk distributed in the Florida, Appalachia, Mexico and California Refugium before 15 ka. From 15 to 8 ka, the hot spots were not obvious. But during 8 and 3 ka it had reached Wisconsin and New York. About 1% of the records contained more than 50% of the total MNIs, and the hot spots were located in southern Illinois and Tennessee (Fig. 108). From 3 to 1 ka the ISVAs are more than 25%. Records with the highest MNIs were found in Missouri and New Jersey (Fig. 109). During 1 and 0,5 ka it entered the upper Missouri River basin. In the last 500 years, about 25% of the records contained more than 50% of the total MNIs. And the hot spots first appeared on the west side of the Rockies (Fig. 110).

Carnivora

Mustelidae

4. 2. 13 *Mustela vision* **Mink**

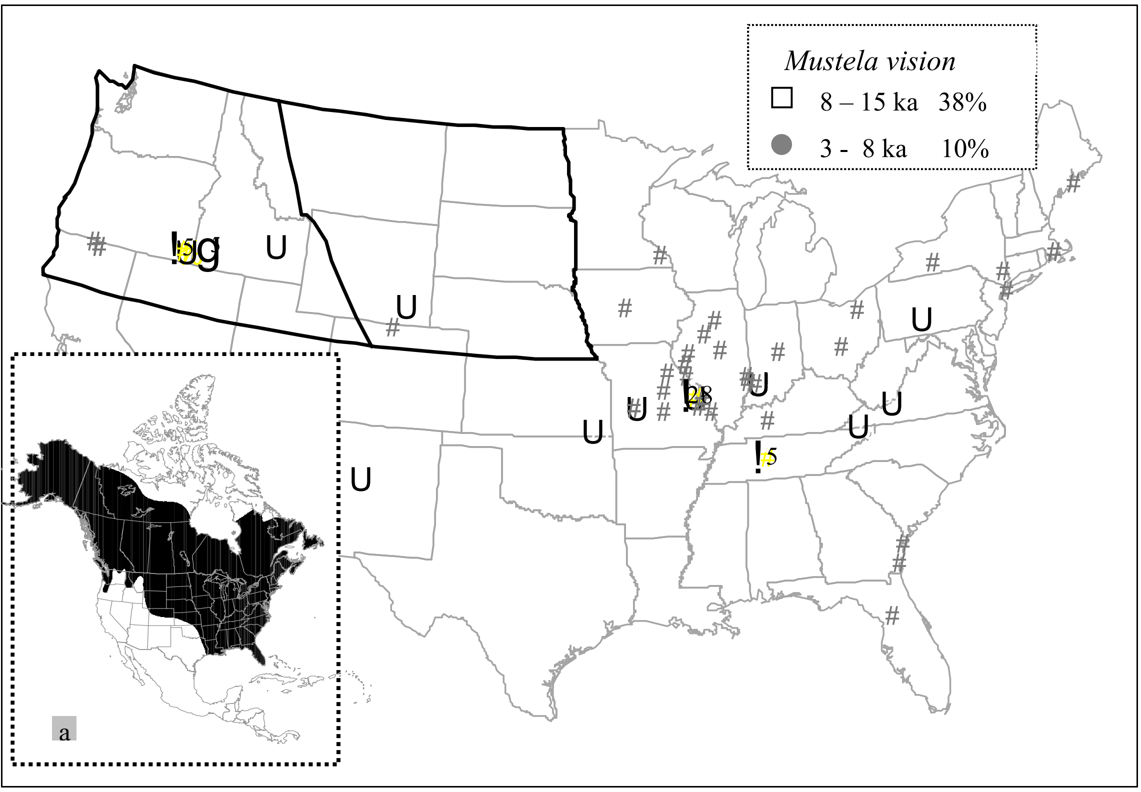


Fig. 111 The evolution of Arealsystem of *Mustela vision* (15 – 3 ka)

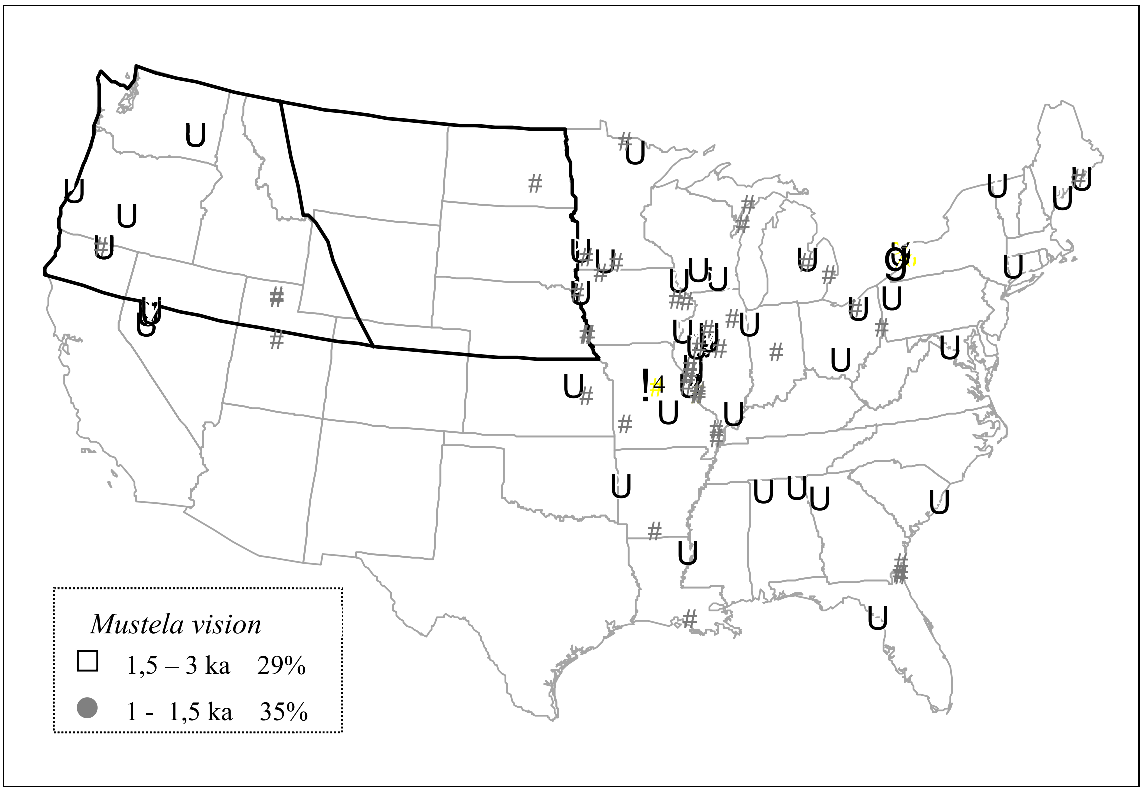


Fig. 112 The evolution of Arealsystem of *Mustela vision* (3 - 1 ka)

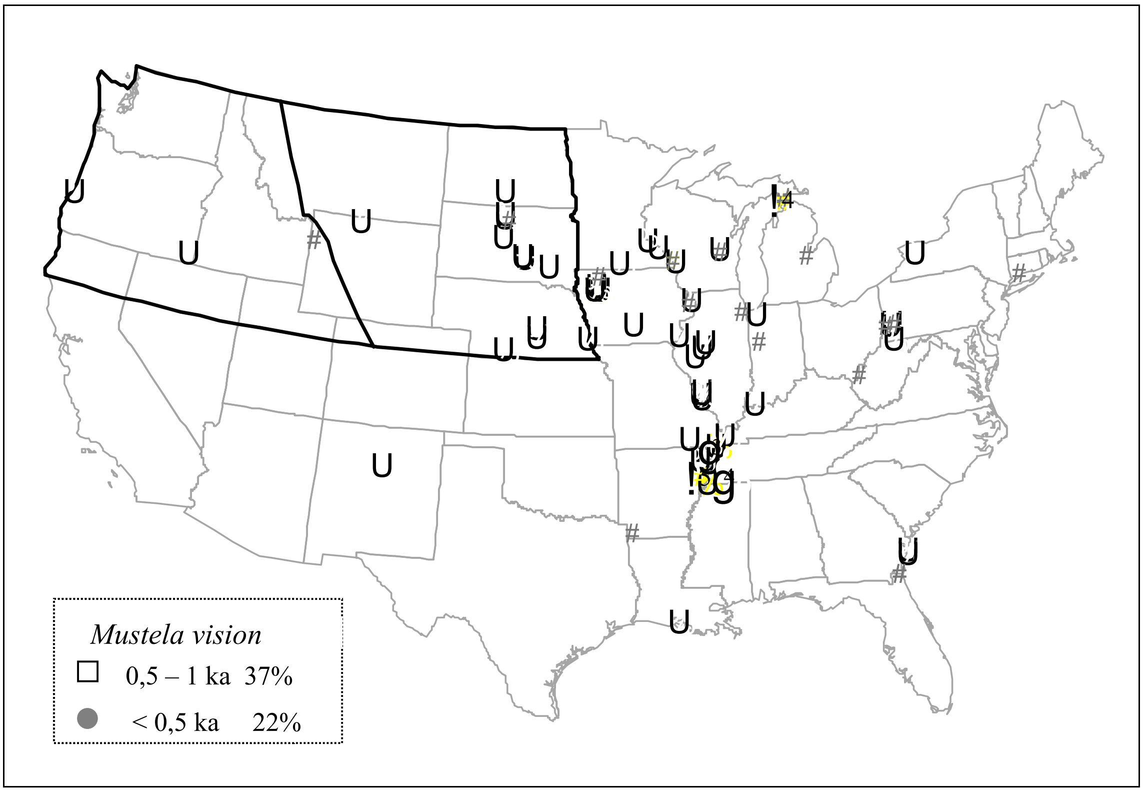


Fig. 113 The evolution of Arealsystem of *Mustela vision* (1 – 0.5 ka)

Mink are found throughout the United States, appearing in parts of every state except Arizona. They are also present in most of Canada, including an introduced population on Newfoundland. Only along the arctic coast and some offshore islands are they absent (Fig 111a). Although the mink is found throughout North America, it tends to be frequent in forested areas that are in close proximity to water. Streams, ponds, and lakes, with some sort of brushy or rocky cover nearby are considered optimal territory (Digital Ref.).

Mink distributed in the Appalachia and Rocky Mountaun Refugium before 15 ka. From 15 to 8 ka the hotspots were not obvious. But during 8 and 3 ka, about 10% of the records contained more than 50% of the total MNIs, and the hot spots were located in southern Illinois, southern Idaho and Oregon (Fig.111). During 3 to 1.5 ka, about 29% of the records contained more than 50% of the total MNIs. The records with the highest MNIs were found in Missouri and also in New York. From 1.5 to 0.5 ka, the hot spots were also not obvoius. During 1 and 0.5 ka, the mink first appeared in South Dakota and Nebraska. In the last 500 years, the ISVA equals 22%, the hot spots were in Tennessee (Fig. 112, 113). Just like the North American river otter, there are no fossil records found in the southern and southwestern United States. So the appearance in these states may be very recent.

Carnivora

Ursidae

4. 2. 14 *Ursus americanus* **American Bear**

Black bears can be found from northern Alaska east across Canada to Labrador and Newfoundland, and south through much of Alaska, virtually all of Canada, and most of the U.S. into central Mexico (Fig. 28a). Throughout its range, prime black bear habitat is characterized by relatively inaccessible terrain, thick understory vegetation, and abundant sources of food in the form of shrub or tree-borne soft or hard mast (Dig. Ref.).

American bear was a polycentric species, which distributed mainly in the Appalachia and Florida Refugium before 15 ka. From 15 to 8 ka, its hot spots were not apparent. During 8 to 3 ka, about 28% of the records contained more than 50% of the total MNIs, and the records with the highest MNIs were found in Missouri and Washington. During 3 and 1 ka, the hot spots were also not apparent. The records with the highest MNIs were found in New York and Indiana.

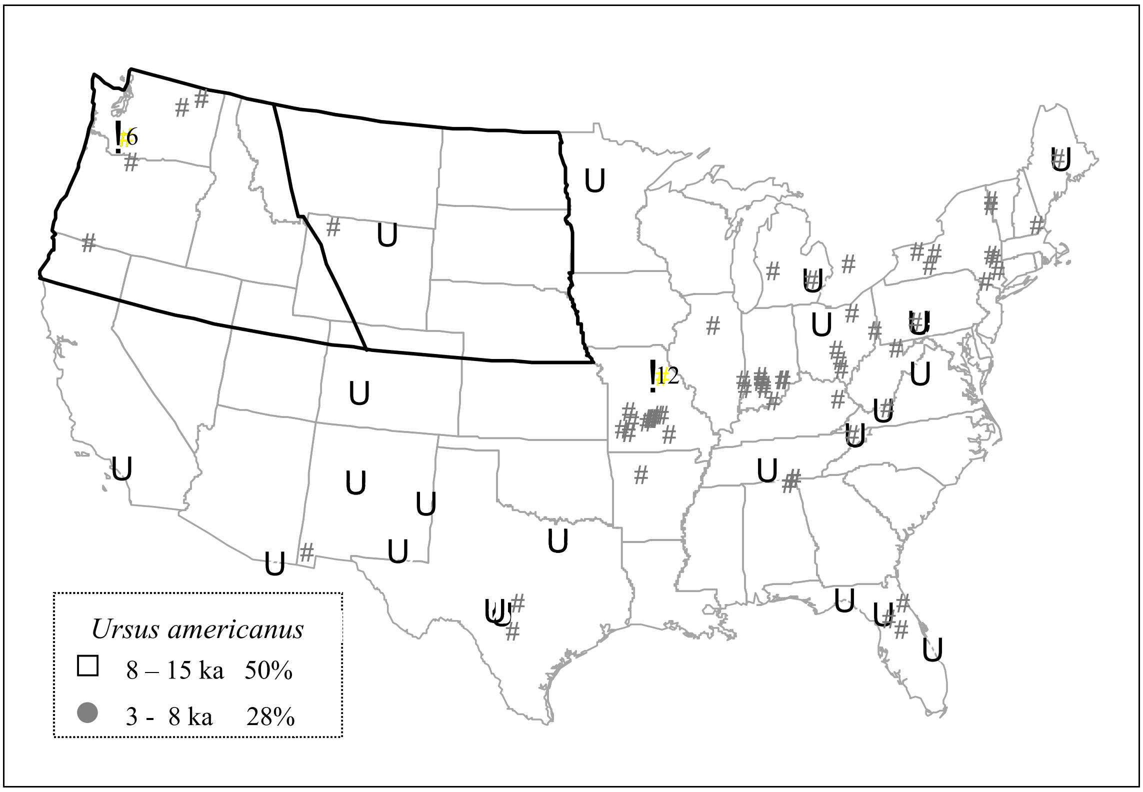


Fig. 114 The evolution of Arealsystem of *Ursus americanus*(15 – 8 ka)

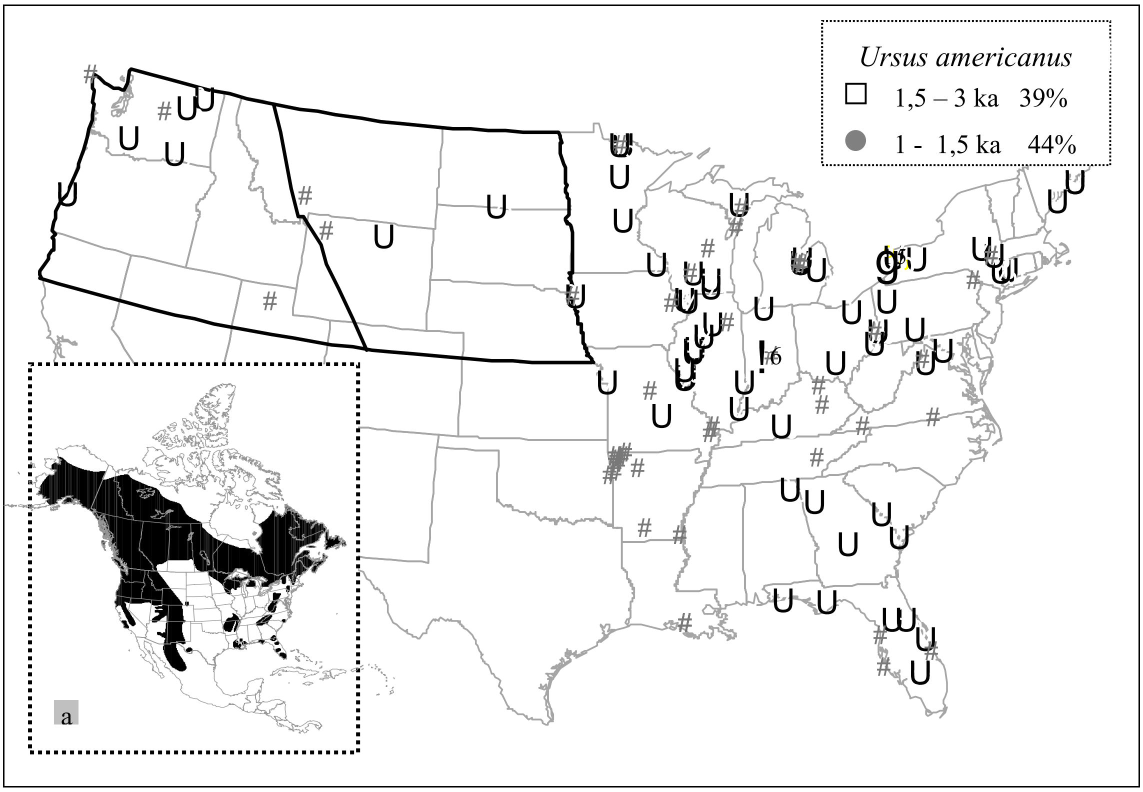


Fig. 115 The evolution of Arealsystem of *Ursus americanus* (3 - 1 ka)

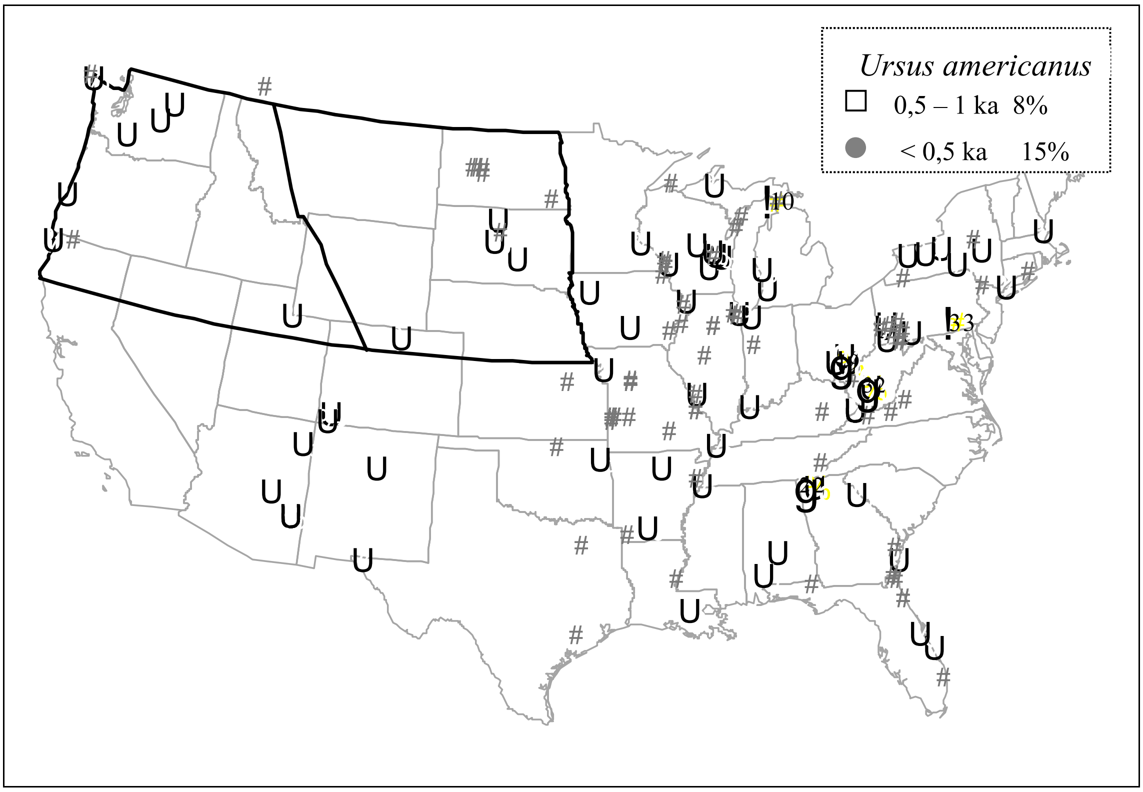


Fig. 116 The evolution of Arealsystem of *Ursus americanus* (the last 1 ka)

From 1 to 0.5 ka, it had entered the upper Missouri River basin. About 8% of the records contained more than 50% of the total MNIs, and in the last 500 years, about 15% of the records comprised more than 50% of the total MNIs. The hot spots were mainly located in the Appalachia area (Fig. 28, 29).

4. 3 THE LEWIS AND CLARK'S PUZZLE

Meriwether Lewis and William Clark found during their expedition in 1805-1806 that big game then abundant on the east side were rare on the west side of the Rocky Mountains. This is further verified in recent by the analysis of the historical data in the Journals of Lewis and Clark (Martin, 1999, Lyman, 2002). But why this could happen has puzzled modern ecologist and biogeographer for 200 years (Moore, 2002). Many theories have been proposed to explain this phenomenon, but there exist still many disputes. We call their finding the Lewis and Clark's pattern. It will be argued that the two large movements of hot spots of mammals described above might be the historical process, which had caused the pattern.

4. 3. 1 A brief summary

The large movements of hot spots of mammals described above could be briefly summarized here. There are 16 species of mammals whose hot spots had moved from the west side to the east side of the Rockies (Tab. 13). From Tab. 13 it can be clearly seen that the hot spots of most mammals disappeared on the west side of the Rockies around 1500 and 1000 years ago and reappeared on the east side of the Rockies during 1000 and 500 years. However, there are some exceptions. *Onychomys leucogaster* and *Peromyscus maniculatus* had aready lost their hot spots on the west side of the Rockies between 3000 and 1500 years ago, while *Thomomys talpoides* and *Bison bison* lost their hot spots only after 500 years ago. *Cervus canadensis* might never lose its hot spots on the west side. The hot spots of *Bison bison* appeared in the upper Missouri River basin around 15, 000 years ago, and had stayed in these areas till it was destroyed by the White American. This is an exception, because the hot spots of other mammals appeared much later in these areas. *Peromyscus maniculatus* regained its hot spots on the east side of the Rockies during 3000 and 1500 years ago, the same time as it lost its hot spots on the west side of the Rockies. Some carnivores enter the upper Missouri basin during 1000 and 500 years ago, and some gained their hot spots there only in the last 500 years. This means that the movement of the hot spots had started around 3000 years ago but happened mainly around 1500-1000 years ago.

Tab. 13 Mammals whose hot spots had moved from the west side to the east side

Species	Disappearing from the west side of the Rockies (ka)	Appearing in the east side of the Rockies (ka)
Antilocapra americana	1.5 – 1	1 – 0.5
Lepus townsendii	1.5 – 1	1 – 0.5
Dipodomys ordii	1.5 – 1	1 – 0.5
Vulpes velox	1.5 – 1	1 – 0.5
Onychomys leucogaster	3 – 1.5	1 – 0.5
Thomomys talpoides	after 0.5	1 – 0.5
Cervus canadensis		1 – 0.5
Vulpes vulpes	1.5 – 1	1 – 0.5*
Mustela frenata	1.5 – 1	1 – 0.5*
Lynx rufus	1.5 – 1**	1 – 0.5*
Erethizon dorsatum	1.5 – 1(?)	1 – 0.5*
Taxidae taxus	1.5 – 1**	1.5 – 1*
Bison bison	after 0.5	Since 15
Peromyscus maniculatus	3 – 1.5	3 – 1.5
Canis latrans	1.5 – 1	after 0.5
Canis lupus	1.5 – 1	after 0.5

* appearing of fossil records (not hot spots) ** disappearing of records with the highest MNIs (not the hot spots)

Fig. 117 shows the main hot spot areas on both sides of the Rockies, the number of species and the periods in which the hot spots of these species appeared in the hot spot area. The hot spot area is a region where the hot spots of many species are located. It can be seen that before 1500 years ago the hot spots of the 16 mammals mainly appeared on the west side, but after 1000 years ago, most of the hot spots had disappeared from their hot spot areas on the west side of Rockies, but reappeared on the east side of the Rockies.

The shift of hot spots from the east of USA to the east side of the Rockies is not as strong as the former one. Unlike the turnover of hot spots from the west side to the east side of the Rockies, many mammals first entered the upper Missouri River basin during 1000 and 500 years ago, but their hot spots did not disappeared in the eastern USA. Only *Clethrionomys gapperi*, *Microtus pennsylvanicus* and *Microtus orchrogaster* lost their hot spots in the east of USA, and their hot spots had already reappeared in the upper Missouri River area around 3000 and 1500 years ago (Tab.14, Fig.118).

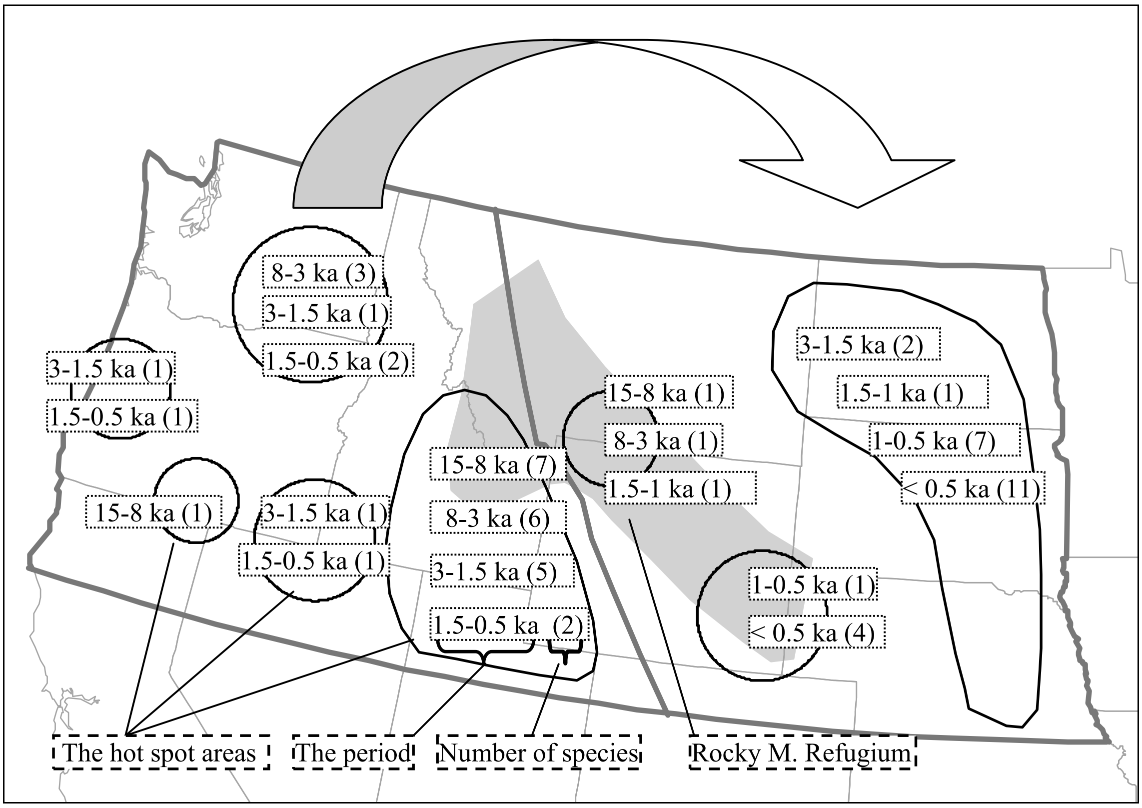


Fig. 117 The spatial turnover of hot spots of the 16 mammals between both sides of the Rockies

Tab. 14 Mammals whose hot spots might have moved from the East of USA

Species	Disappearing from the East (ka)	Appearing in the east side of the Rockies (ka)
Mephitis mephitis		after 0.5
Canis familiaris		1 - 0.5
Spermophilus tridecemlin		1 - 0.5
Sylvilagus floridanus		1 - 0.5*
Urocyon cinereoargenteus		1 - 0.5*
Ursus americanus		1 - 0.5*
Lutra canadensis		1 - 0.5*
Odocoileus virginianus		1 - 0.5*
Mustela vision		1 - 0.5*
Ondatra zibethicus		1.5 - 1*
Castor canadensis		3 - 1.5*
Clethrionomys gapperi	3 - 1.5	3 - 1.5
Microtus pennsylvanicus	3 - 1.5	3 - 1.5
Microtus orchrogaster	1 - 0.5	3 - 1.5

* the appearance of fossil records (not the hot spots)

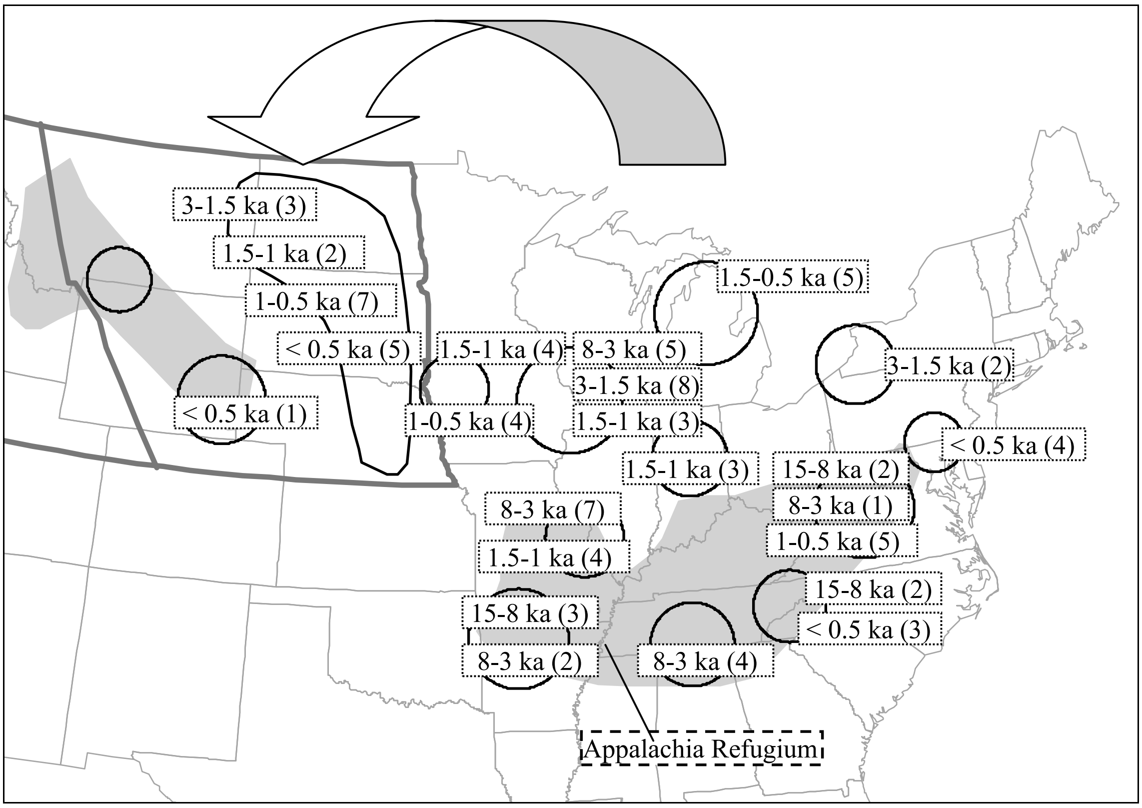


Fig. 118 The spatial shift of hot spots of the 14 mammals from the East to the west side of the Rockies

4. 3. 2 Lewis and Clark met the hot spots of many mammals in the Upper Missouri River basin

Due to the two large movements above, the upper Missouri River basin was not only rich in wildlife, but also became the hot spot area of many mammals around 1000 years ago. The Upper Missouri in the days of Lewis and Clark is commonly regarded by historians, biologists and TV producers alike as the very essence of "wild" America (Martin, 1999). And the hot spots of many mammals have been observed by Lewis and Clark during their expedition from 1805 to 1806. Around the mouth of the Yellow River, "Buffalloe, Elk and Goats or Antelopes feeding in every direction, we kill whatever we wish…" And near the Great Fall, Lewis estimated 10,000 bison in one sighting, blanketing the Plains. When they're snorting, it reverberates. They couldn't believe the numbers of the prairie dogs that they were seeing. Between 25 April and 13 June 1805, in 50 days of travel along the upper Missouri between present-day Williston, North Dakota, and Great Falls, Montana, the expedition killed 79 deer, 50 elk, and 44 adult bison, 7 bison calves, and 12 grizzly bears. In addition, they killed 9 mountain sheep, 8 pronghorn, 3 wolves (Tab.15). It was a marker that they saw the bountiful wildlife on the Great Plains. If we go to the Great Plains today, the things that Lewis and Clark remarked the most on are absent.

Tab. 15 Samples of Lewis and Clark's game kill during their traval 1805-1806[a] (Martin, 1999)

Travel Game	Upper Missouri River (*25 Apr.-13 Jul. 1805*)	Columbia River (*18 Sep.- 6 Nov. 1805*)	Camp Clatsop (*1 Jan.- 19 Feb. 1806*)	Columbia River (*23 Mar.- 11 May 1806*)	Yellowstone and Upper Missouri River *30 Jun.- 18 Aug. 1806*
Deer	79	28	8	38	191
Elk	50	0	51	22	51
Bison	44	0	0	0	55
Pronghorn	8	0	0	0	9
Bear	12	0	0	1	12
Dog	0	101	5	83	0

4. 3. 3 Lewis and Clark met cool spots of big game on the west side of the Rockies

As showed above, the hot spots of many mammals had disappeared from the west side of the Rockies and turned to be cool spots in this area around 1500 and 1000 years ago. So it is not surprising that the Corps of Discovery found game was scarce in the Columbia drainage. During the 50 days from the Clearwater, the Snake and the Columbia rivers to the Cascade Mountains, roughly equivalent to their distance of travel on the Upper Missouri, They killed only 28 deer(Tab. 15). They had to turn for survival to the domestic animals of the local people such as dogs and horses. But if they had been there 1000 years earlier, what they would have seen would be another matter.

CHAPTER 5 TEMPORAL VARIATION IN ABUNDANCE IN SW USA: THE BAYHAM'S PATTERN

In this chapter we will discuss the movement of hot spots from the west side of the Rockies to the Southwest of the USA and the test of this movement by the zooarchaeological study.

5. 1 THE MOVEMENT FROM THE WEST SIDE OF THE ROCKIES TO THE SOUTHWEST

Artiodactyla

Cervidae

5. 1. 1 *Odocoileus hemionus* **Black-tailed deer**

Odocoileus hemionus occurs over most of North America west of the 100th meridian from 23 degrees to 60 degrees N. The eastern edge of the usual range extends from southwestern Saskatchewan through central North and South Dakota, Nebraska, Kansas, and western Texas Isolated occurrences have been reported from Minnesota, Iowa, and Missouri. Major gaps in geographic distribution can be found in southern Nevada, southeastern California, southwestern Arizona, and the Great Salt Lake desert region (Fig. 119a). *Odocoileus hemionus* is remarkably adaptable. These habitat provinces include the California woodland chaparral, the Mojave Sonoran desert, the Interior semidesert shrub woodland, the Great Plains, the Colorado Plateau shrubland and forest, the Great Basin, the Sagebrush steppe, the Northern mountain, and the Canadian boreal forest (Dig. Ref.).

Black-tailed deer distributed in the California, Mexico, Great Basin and Rocky Mountain Refugium in the glacial time. Its distribution around about 3 ka might have already been similar to its current range. During 15 and 8 ka about 28% of the records contained more than 50% of the total MNIs. Records of highest MNIs were found in Utah. From 3 – 8 ka, about 13% of the records contained more than 50% of the total MNIs. The hot spots were still located in Utah, and also in Oregon (Fig. 119). During 3 – 1.5 ka, about 38% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were found in southern Idaho, but

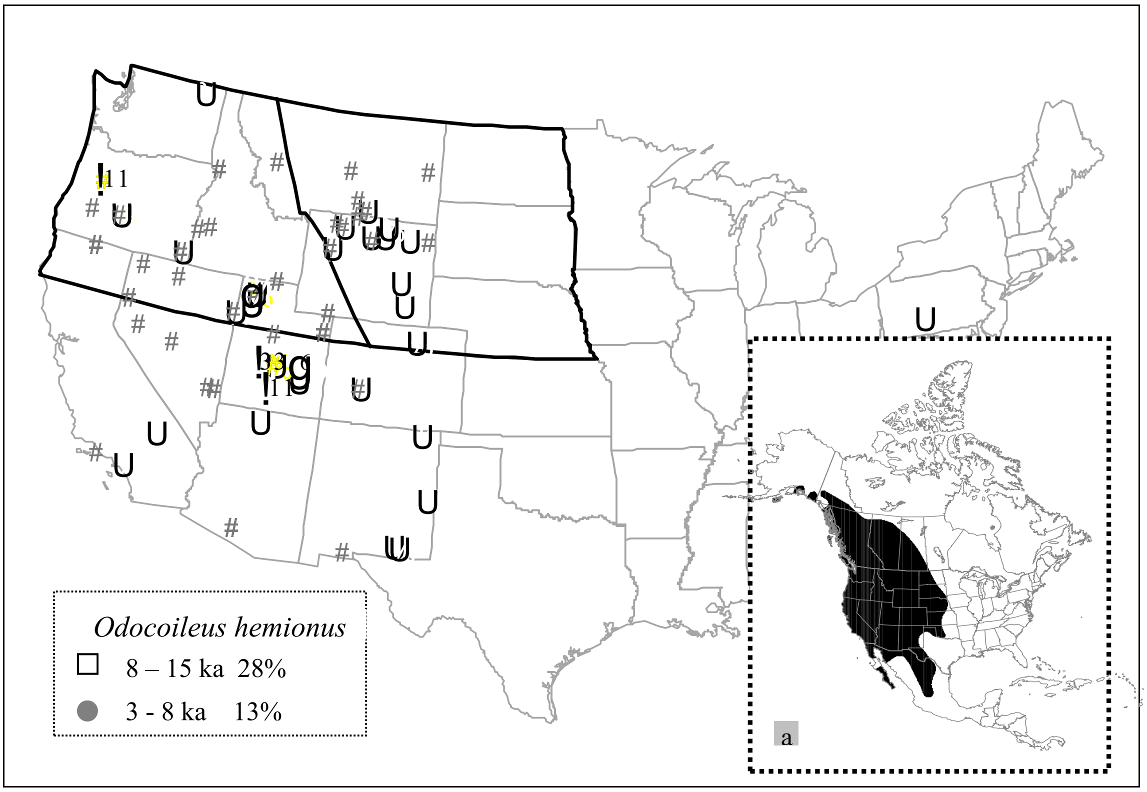


Fig. 119. The evolution of Arealsystem of *Odocoileus hemionus* (15-3 ka)

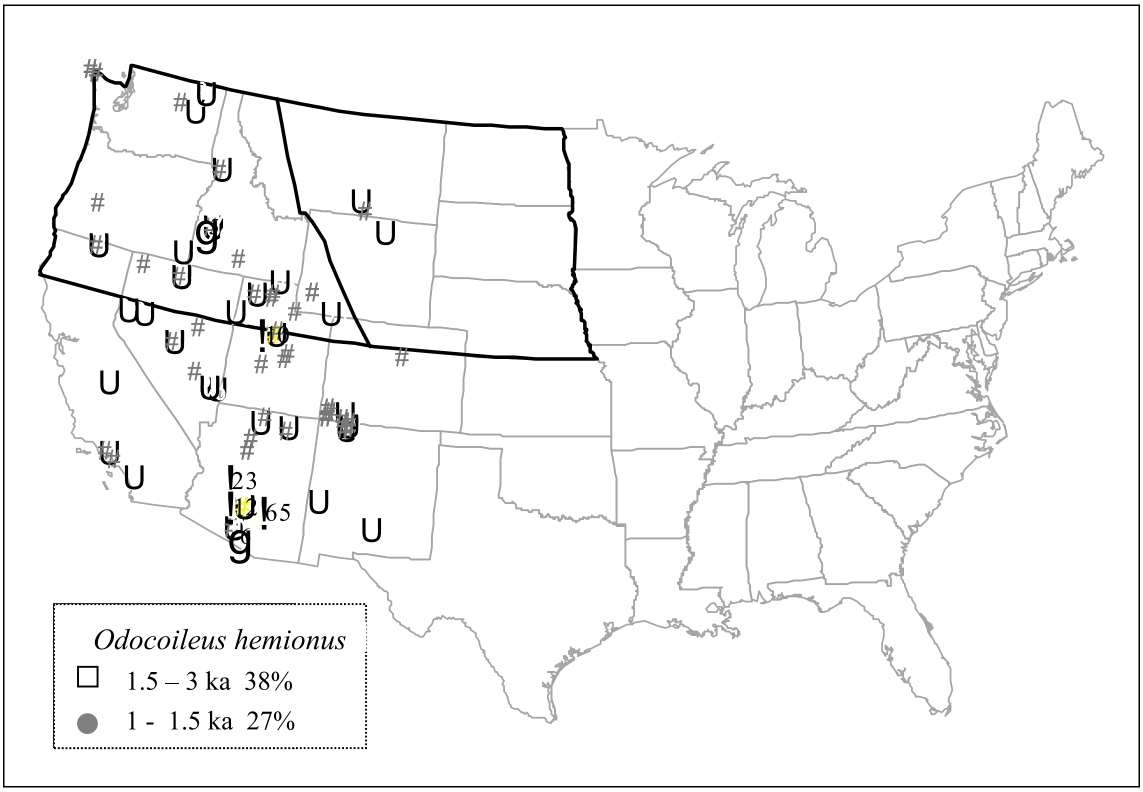


Fig. 120 The evolution of Arealsystem of *Odocoileus hemionus* (3 - 1 ka)

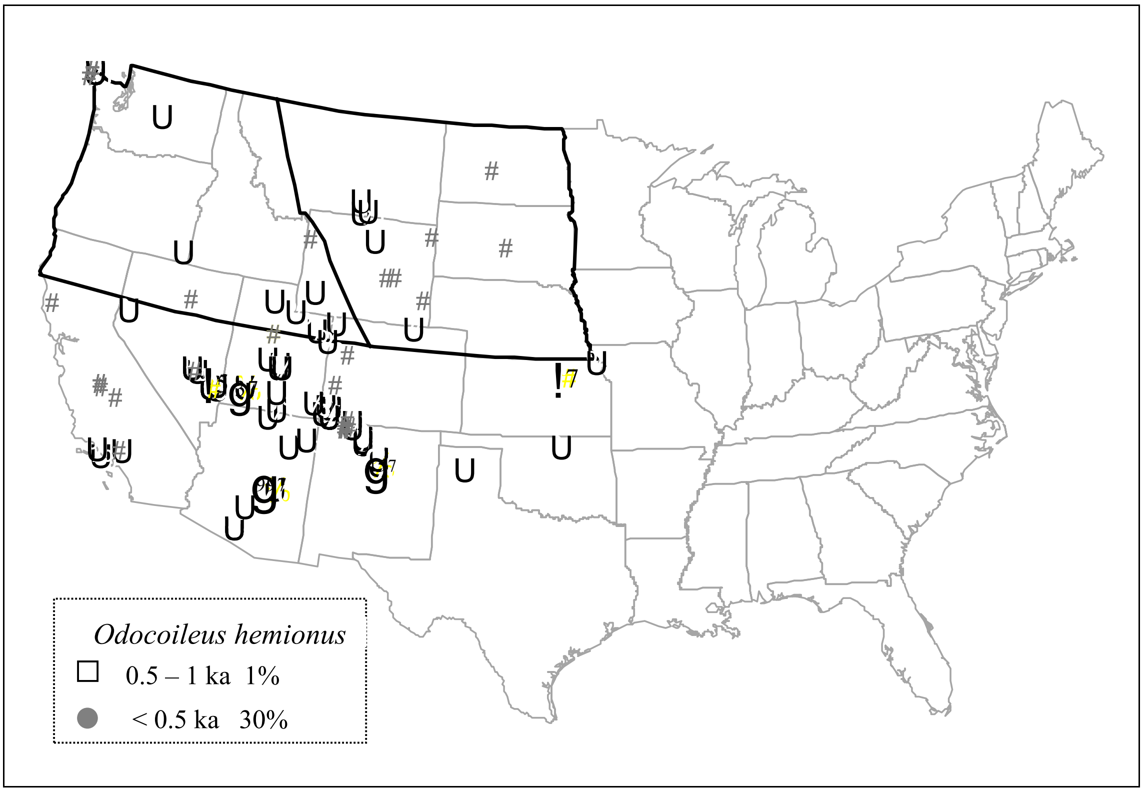


Fig. 121 The evolution of Arealsystem of *Odocoileus hemionus* (the last 1 ka)

also in southern Arizona. From 1.5 – 1 ka, about 27% of the records contained more than 50% of the total MNIs. Records of the highest MNIs were found in Utah, but mainly in southern Arizona (Fig. 120). After about 1 ka, the hotspots seemed to have disappeared on the west side of the Rockies. From 1 – 0.5 ka, only 1% of the records contained already more than 50% of the total MNIs. The hot spots were mainly located in southeastern Utah, Arizona and northern Mexico. No fossil records were found in Minnesota, Iowa, and Missouri and in the major gaps among the southern Nevada, southeastern California, southwestern Arizona, and the Great Salt Lake desert region (Fig. 121).

Artiodactyla

Bovidae

5. 1. 2 *Ovis canadensis* **Bighorn Sheep**

Ovis canadensis is found in the Rocky Mountains from southern Canada to Colorado, and as a desert subspecies (*Ovis canadensis* nelsoni) from Nevada and California to west Texas and south into Mexico. *Ovis canadensis* canadensis inhabits alpine meadows, grassy mountain

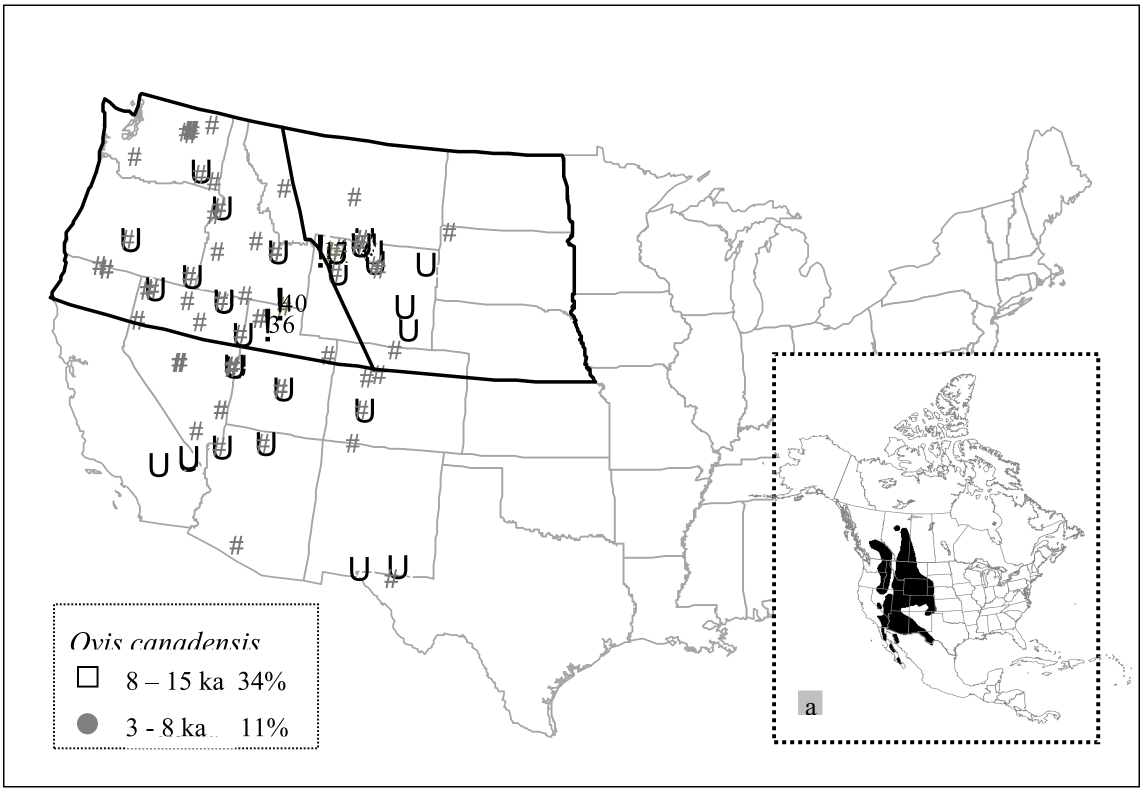


Fig. 122 The evolution of Arealsystem of *Ovis canadensis* (15-8 ka)

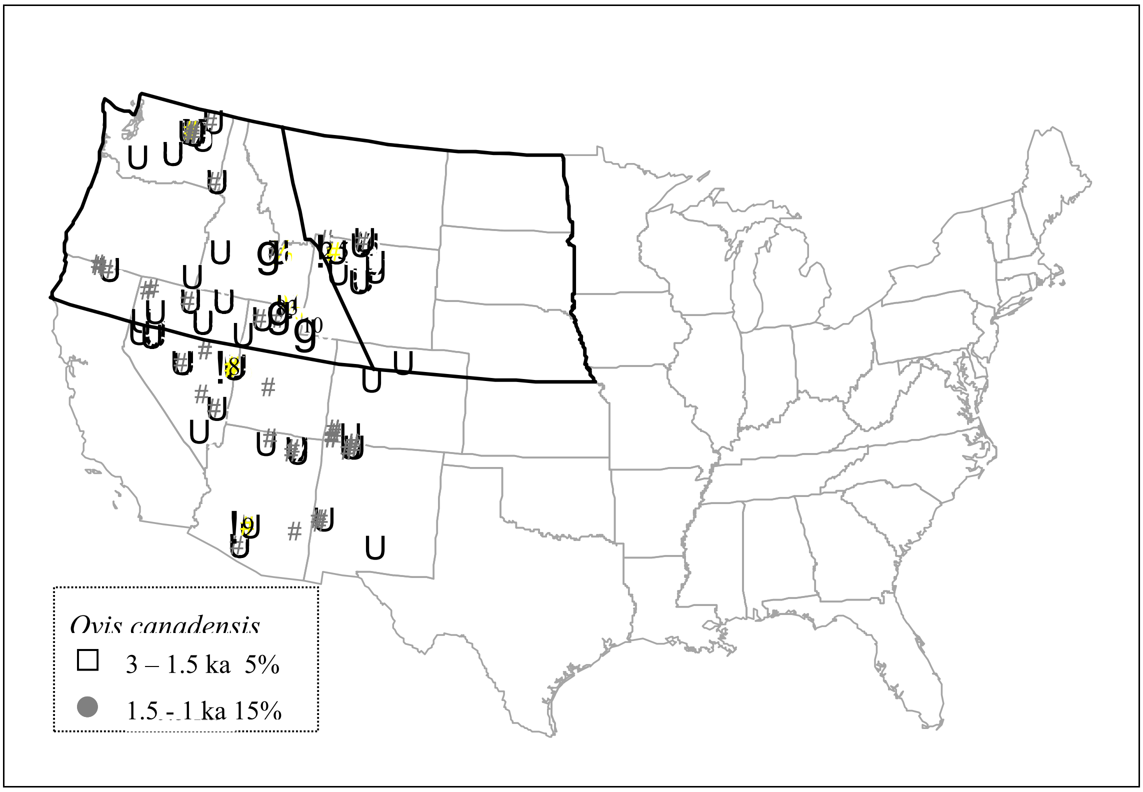


Fig. 123 The evolution of Arealsystem of *Ovis canadensis* (3-1 ka)

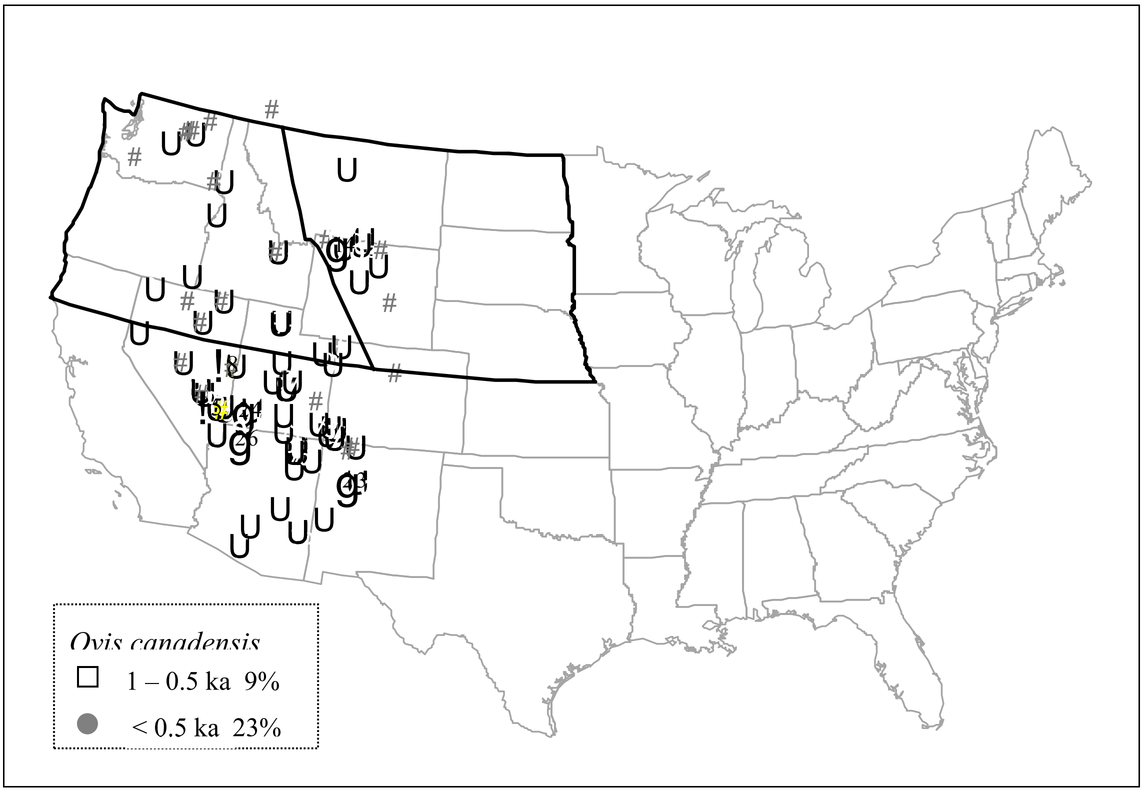


Fig. 124 The evolution of Arealsystem of *Ovis canadensis* (the last 1 ka)

slopes and foothill country in proximity to rugged, rocky cliffs and bluffs (Fig. 122a). The availability of escape territory in the form of rocky cliffs is important to bighorn sheep survival (Dig. Ref.).

Before 15 ka it distributed mainly in the Great Basin and Rocky Mountain Refugium. During 8 and 3 ka its fossil records were found widely in Oregon, Washington and Idaho. The ISVA equals 11%, and the hot spots were in northern Utah and northeastern Wyoming (Fig. 122). Since 3 ka much less fossil records were found in Oregon but more were found in Arizona, western New Mexico and southwestern Colorado. The ISVA from 3 to 1.5 equals 5%, and the position of the hot spots was the same as before. The ISVA from 1.5 and 1 equals 15%, and the hot spots first appeared in eastern Nevada and southern Arizona (Fig. 123). After 1 ka the hot spots could mainly be found in southern Utah, northern Arizona and New Mexico (Fig. 124).

Lagomorpha

Leporidae

5. 1. 3 *Lepus californicus* **Black-tailed Jackrabbit**

Lepus californicus ranges over all of the southwestern United States into Mexico, east to Missouri and north into Washington, Idaho, Colorado and Nebraska, west to California and Baja California (Fig. 125a). Black-tailed jackrabbits inhabit desert scrubland, prairies, farmlands and dunes and moors. They favor arid regions and areas of short grass rangeland from sea level to about 3,800 m (Dig. Ref.).

In the Last Ice Age, it distributed mainly in the California and Mexico Refugium. From 15 to 8 ka it migrated northward. The ISVA equals 2%, and the hot spots were in northern Utah (Fig. 125). From 8 to 1.5 ka the position of hot spots had not changed. But from 1.5 to 1 ka, the ISVA equals 6%, and the hot spots first appeared in southern Nevada and Arizona (Fig. 126). After 1 ka the hot spots were mainly located in these areas (Fig. 127). Its current range is larger

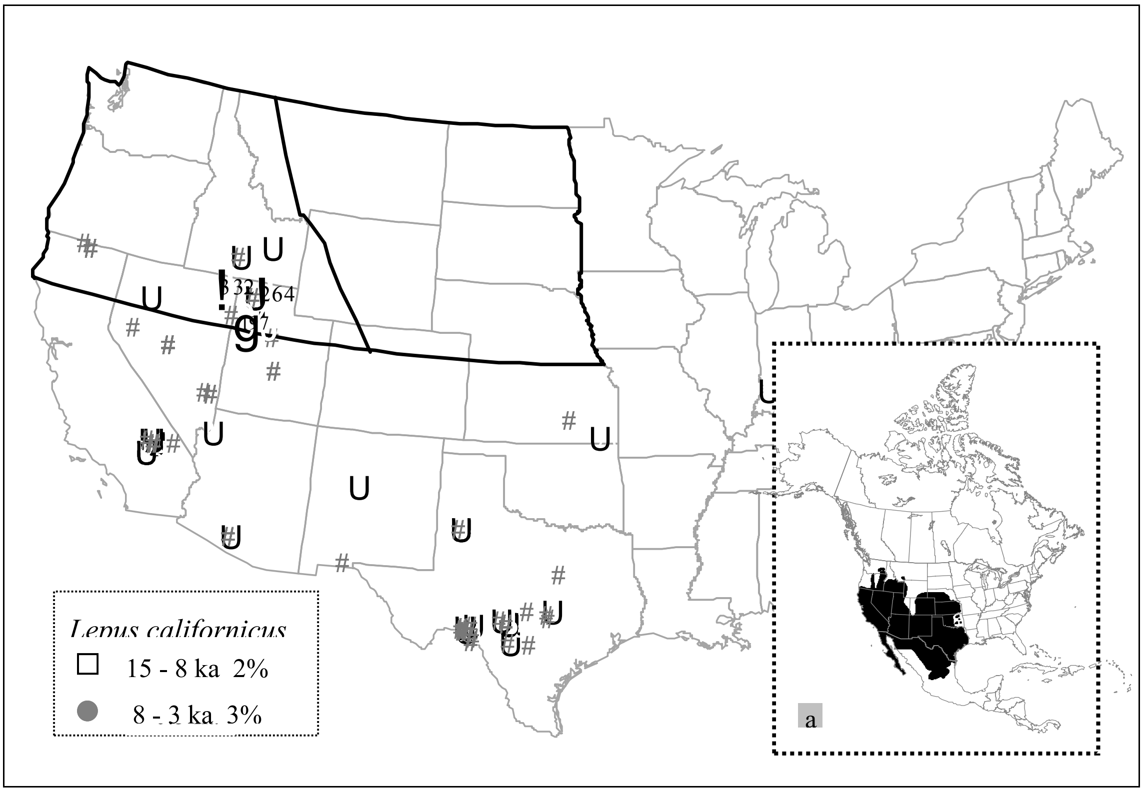


Fig. 125 The evolution of Arealsystem of *Lepus californicus* (15-8 ka)

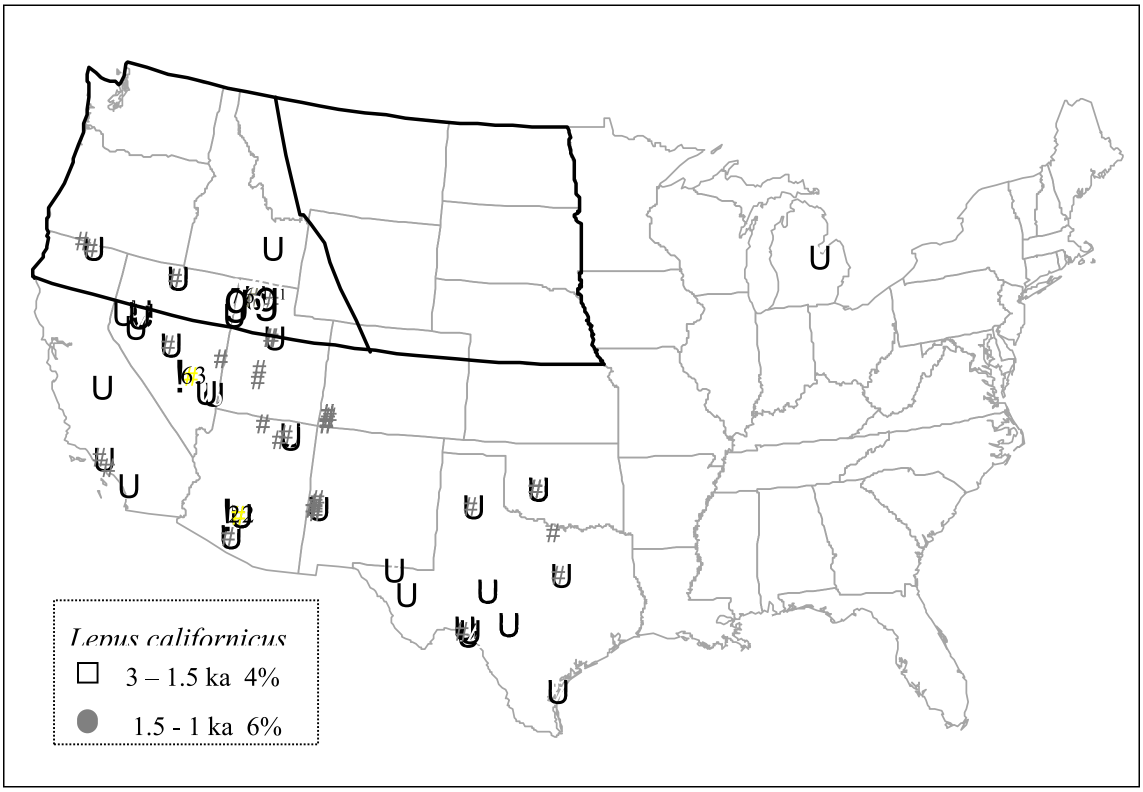


Fig. 126 The evolution of Arealsystem of *Lepus californicus* (3-1 ka)

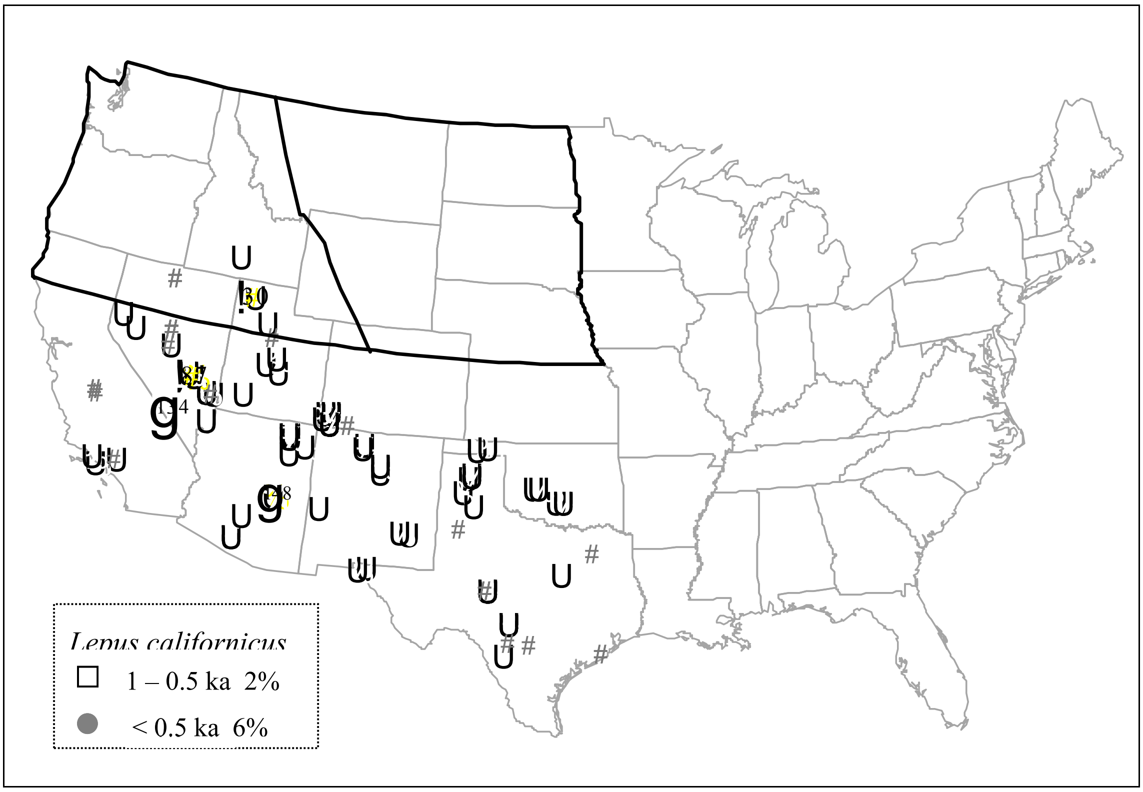


Fig. 127 The evolution of Arealsystem of *Lepus californicus* (the last 1 ka)

than its historical distribution, indicating its range is extending. But its expansion might have happened after the European arrived in North America about 500 years ago. This resulted from the expansion of cultivated fields, which produce much more alfalfa, the favorite food of this Jackrabbit, than any other natural habitats such as Barren areas, prairies and meadows.

Lagomorpha

Leporidae

5. 1. 4 *Brachylagus idahoensis* **Pygmy Rabbit**

The pygmy rabbit is found in southern Idaho, eastern Oregon, northeastern California, and Nevada (Fig. 128a). It has only recently been found in Wyoming. Pygmy rabbits prefer dense sagebrush habitat. Their movements are confined to a 30-meter radius of the burrow (Dig. Ref).

Before 15 ka it distributed mainly in the Rocky Mountain Refugium. And from 15 to 1.5 ka, the hot spots had stayed in southern Idaho and northern Utah (Fig. 128, 129). After about 1.5 ka, much less fossil records were found than before (Fig. 130). This is not the normal temporal

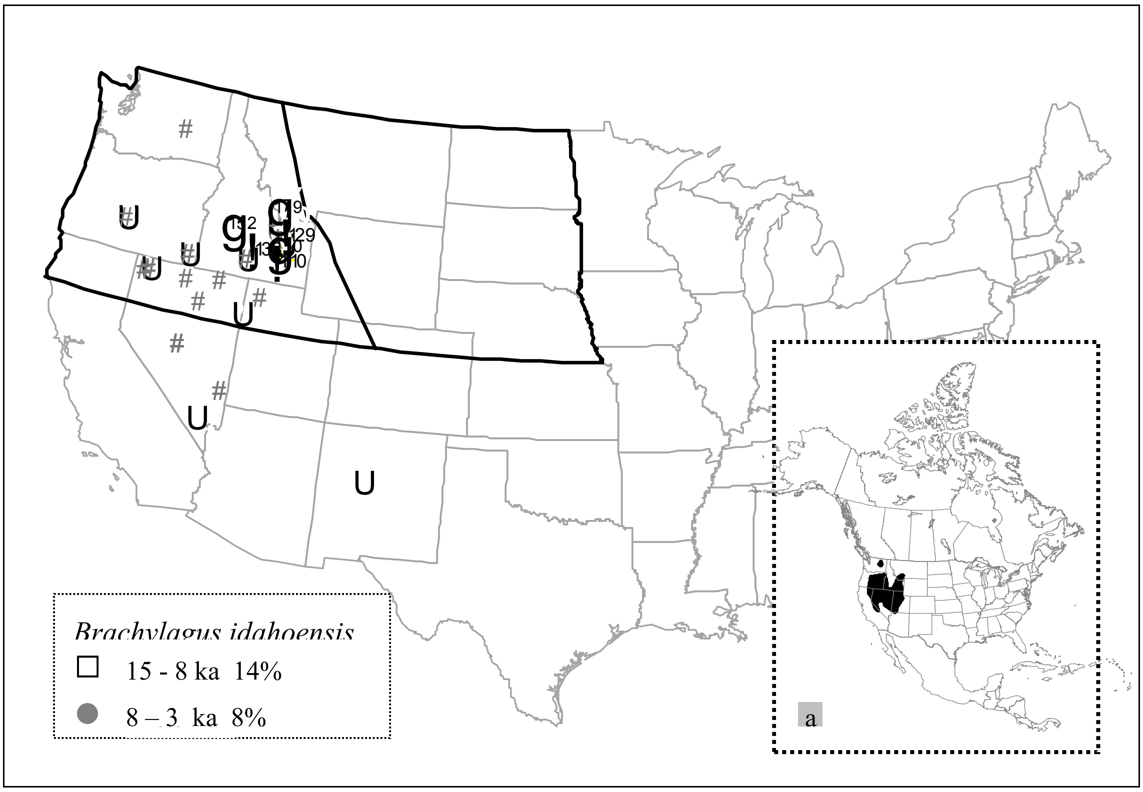


Fig. 128 The evolution of Arealsystem of *Brachylagus idahoensis* (15-8 ka)

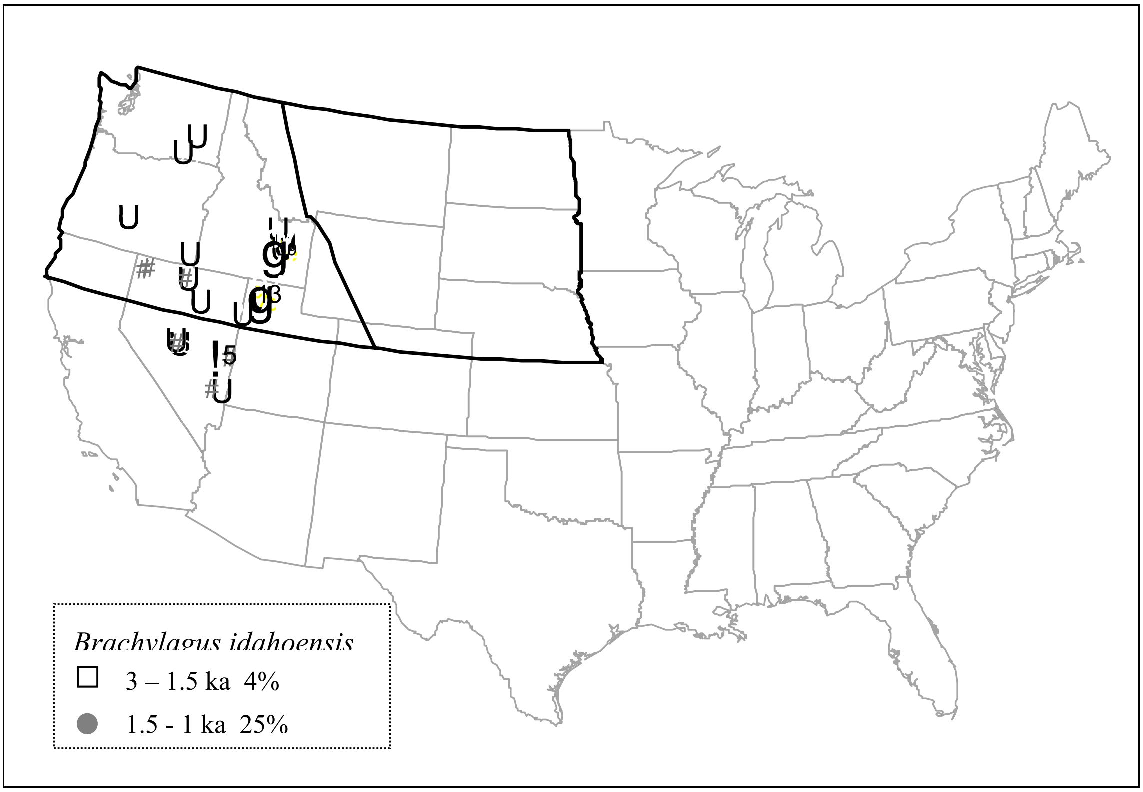


Fig. 129 The evolution of Arealsystem of *Brachylagus idahoensis* (3-1 ka)

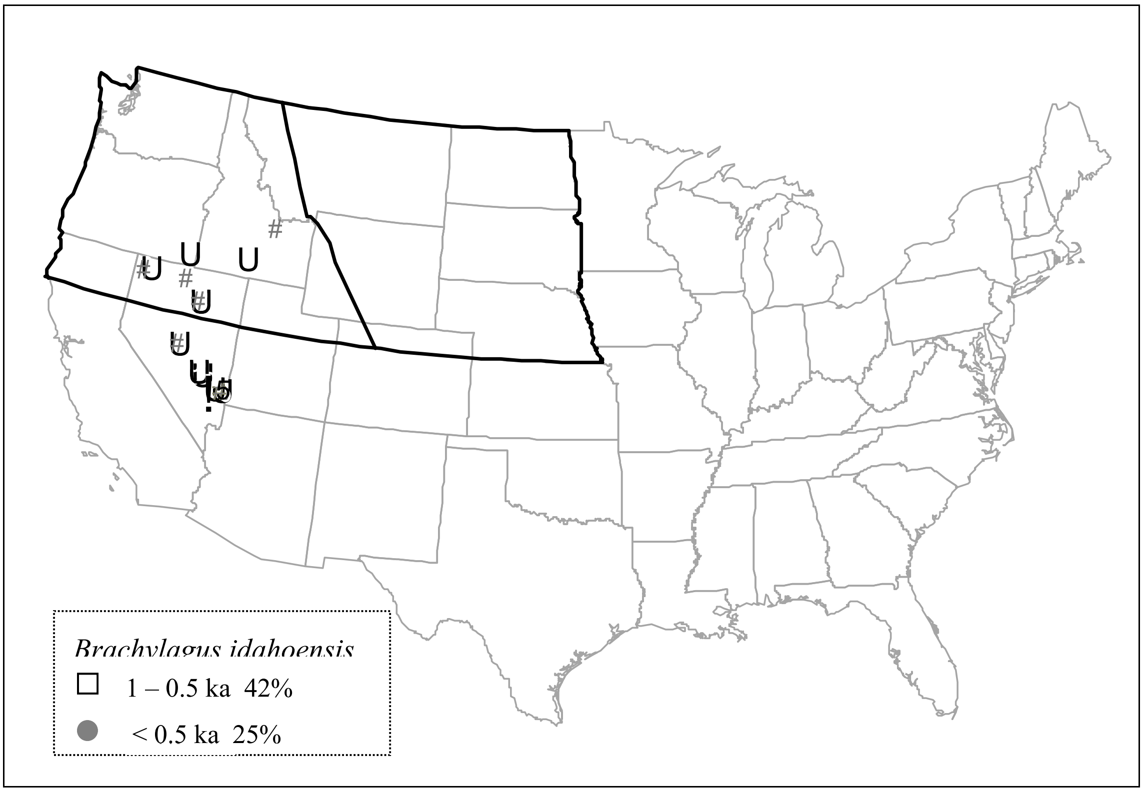


Fig. 130 The evolution of Arealsystem of *Brachylagus idahoensis* (the last 1 ka)

distribution pattern (the more the recent, the higher the number of fossil records found), which indicates that the population size of pygmy rabbit was decreasing. From 1.5 to 1 ka, the ISVA equals 25%, and the hot spots first appeared in eastern Nevada.

Lagomorpha

Leporidae

5. 1. 5 *Sylvilagus auduboni* **Desert Cottontail**

The desert cottontail can be found throughout much of southwestern North America, from northern Montana down to central Mexico, and as far west as the Pacific coast (Fig. 131a). This species is mainly found in arid regions, giving it the common name desert cottontail. It can also inhabit woodlands and grasslands, and it ranges in elevation from sea level up to about 6,000 feet (Dig. Ref.).

Before 15 ka it distributed mainly in the California and Mexico Refugium. From 15 to 3 ka its fossil records were found on the west side, but not on the east side of the Rockies. The hot spots were located in the northern Utah (Fig. 131). But during 3 and 1.5 ka the hot spots can

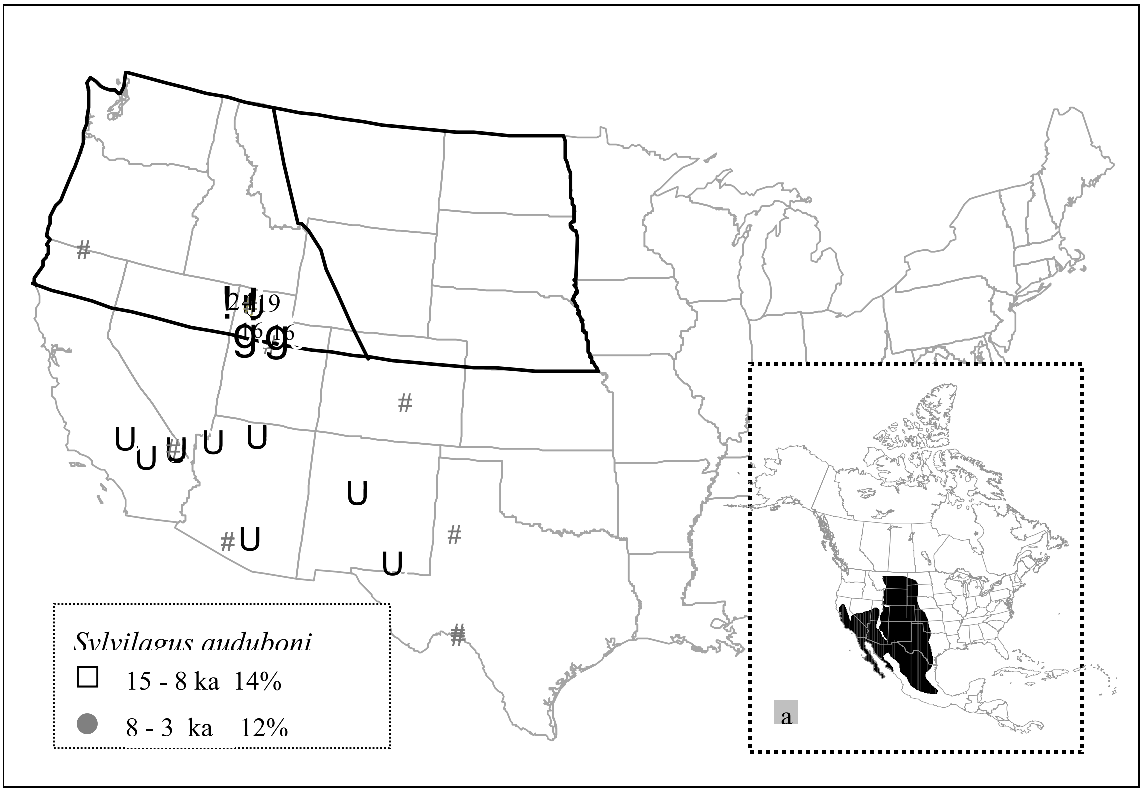


Fig. 131 The evolution of Arealsystem of *Sylvilagus auduboni* (15-3 ka)

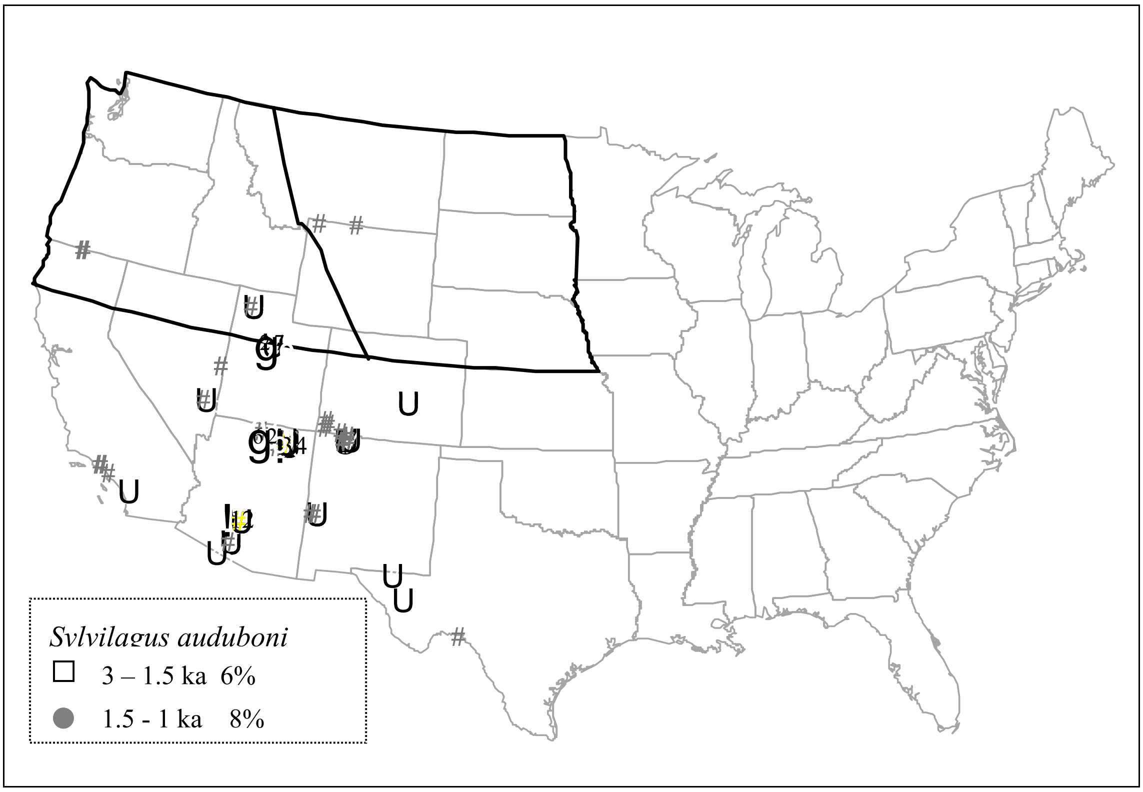


Fig. 132 The evolution of Arealsystem of *Sylvilagus auduboni* (3-1 ka)

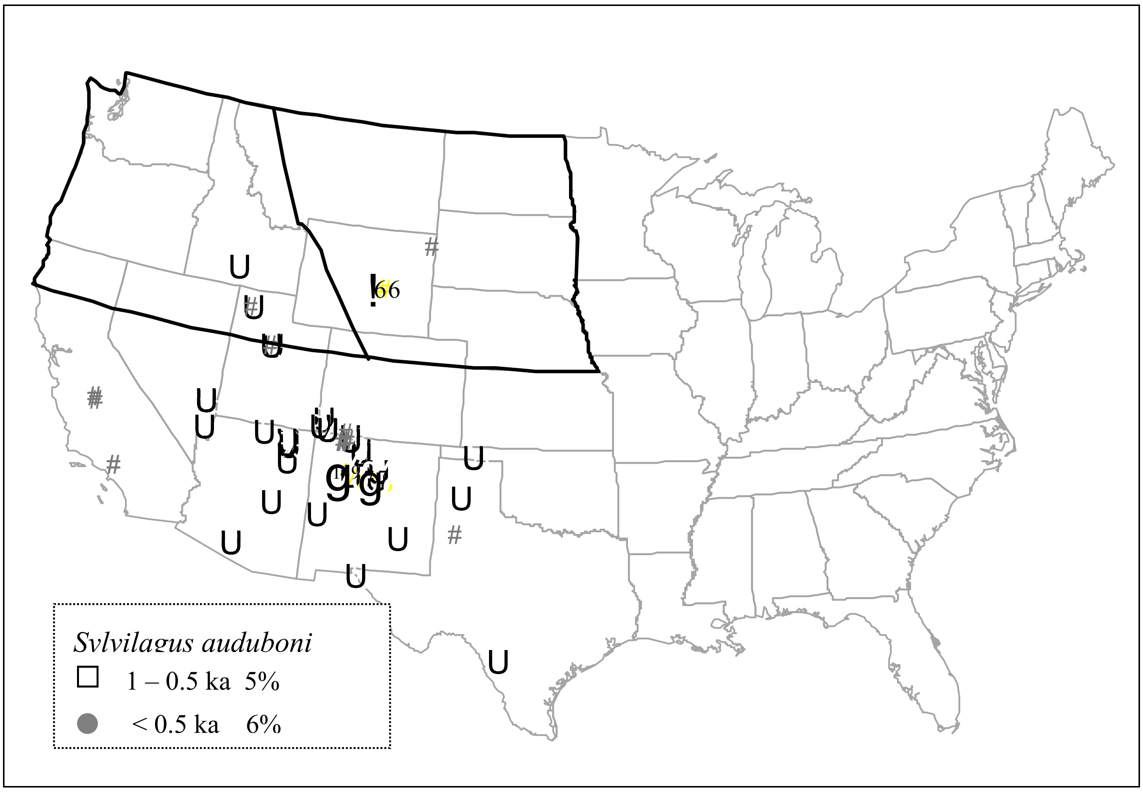


Fig. 133 The evolution of Arealsystem of *Sylvilagus auduboni* (the last 1 ka)

still be found in this area, but also first appeared in Arizona. From 1.5 to 1 ka the hot spots disappeared in northern Utah, and were mainly found in Arizona. At this time the desert cottontail was first found in Wyoming (Fig. 132). From 1 to 0.5 ka, the ISVA equals 5%, the hot spots were in northern New Mexico. In the last 500 years, the ISVA equals 6%, and the hot spots first appeared in Wyoming (Fig. 133).

Lagomorpha

Leporidae

5. 1. 6 *Sylvilagus nuttallii* **Mountain Cottontail**

The mountain cottontail lives mostly in the western part of the United States. Its range is bordered in the east by Montana's eastern border, in the west by the Sierra Nevada Mountains, in the south by the middle of New Mexico and Arizona, and in the north by the US/Canadian border; however a small area of Canada right above Montana and Washington is also included (Fig. 134a). The cottontail inhabits brushy or wooded areas on slopes or riverbanks that are often covered with grasses, willows, and most importantly, sagebrush. If vegetation is sparse, as on a rocky mountainside, these rabbits can hide in burrows or rock crevices (Dig. Ref.).

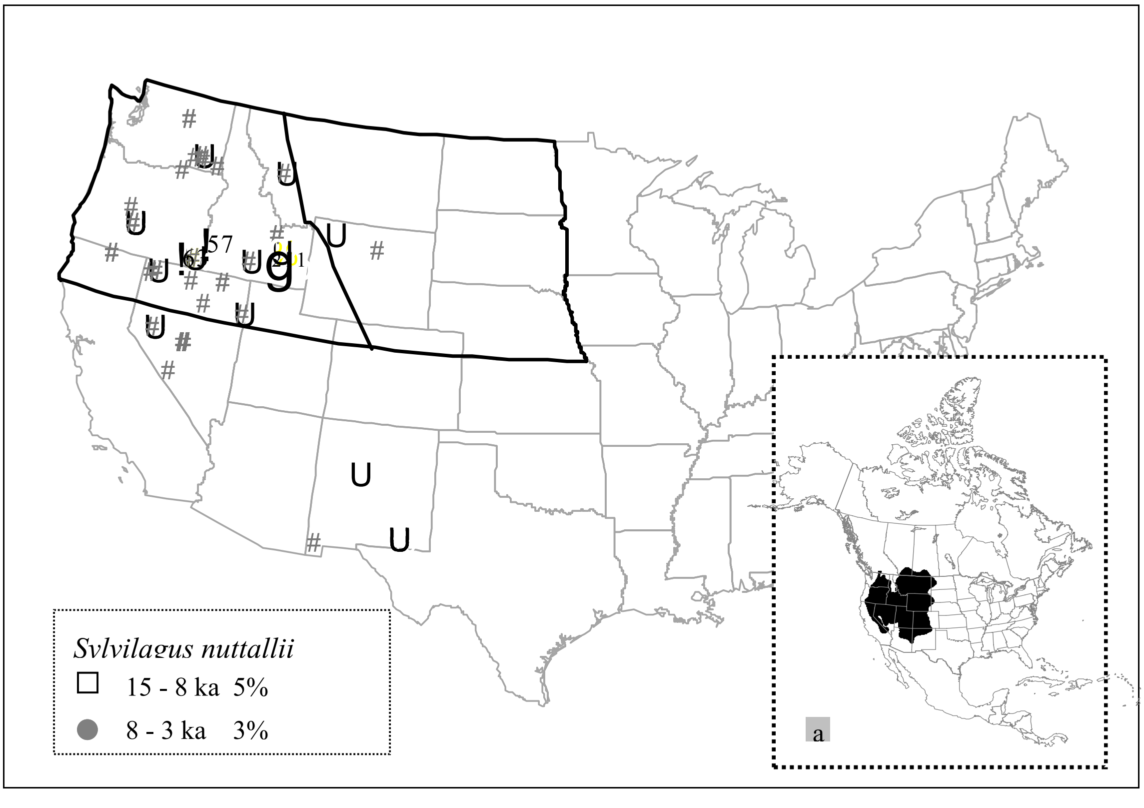


Fig. 134 The evolution of Arealsystem of *Sylvilagus nuttallii* (15-8 ka)

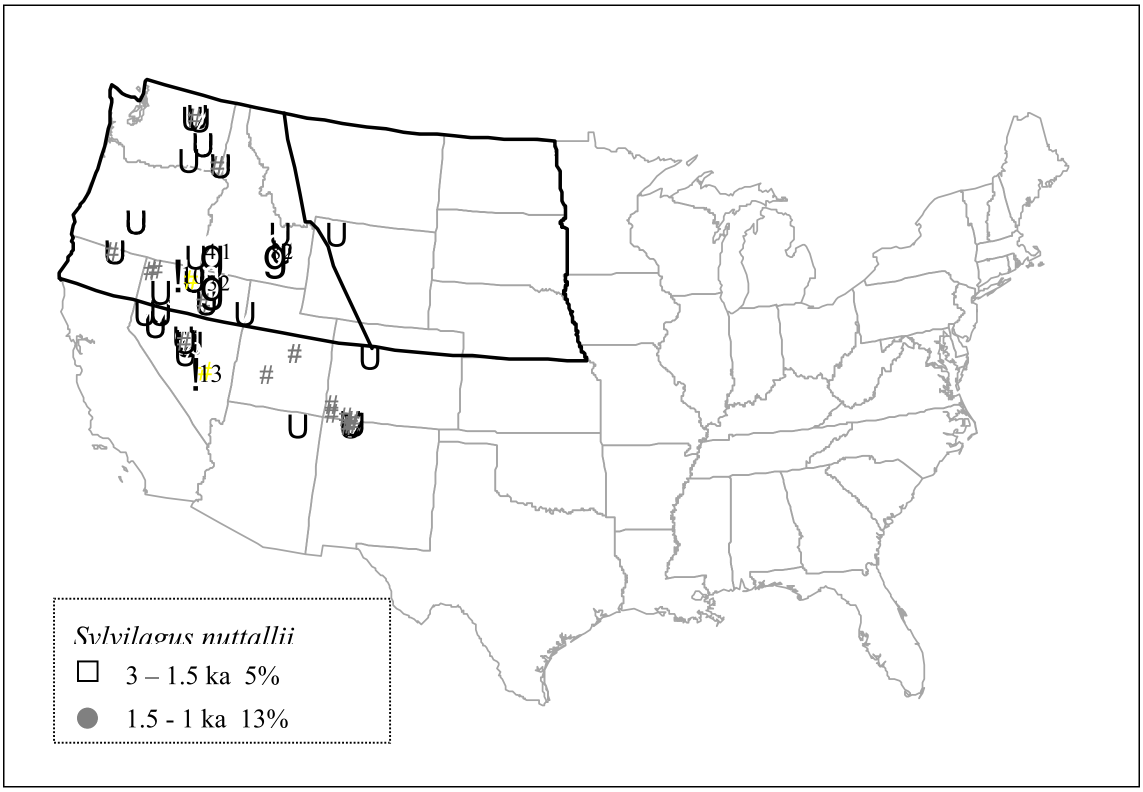


Fig. 135 The evolution of Arealsystem of *Sylvilagus nuttallii* (3-1 ka)

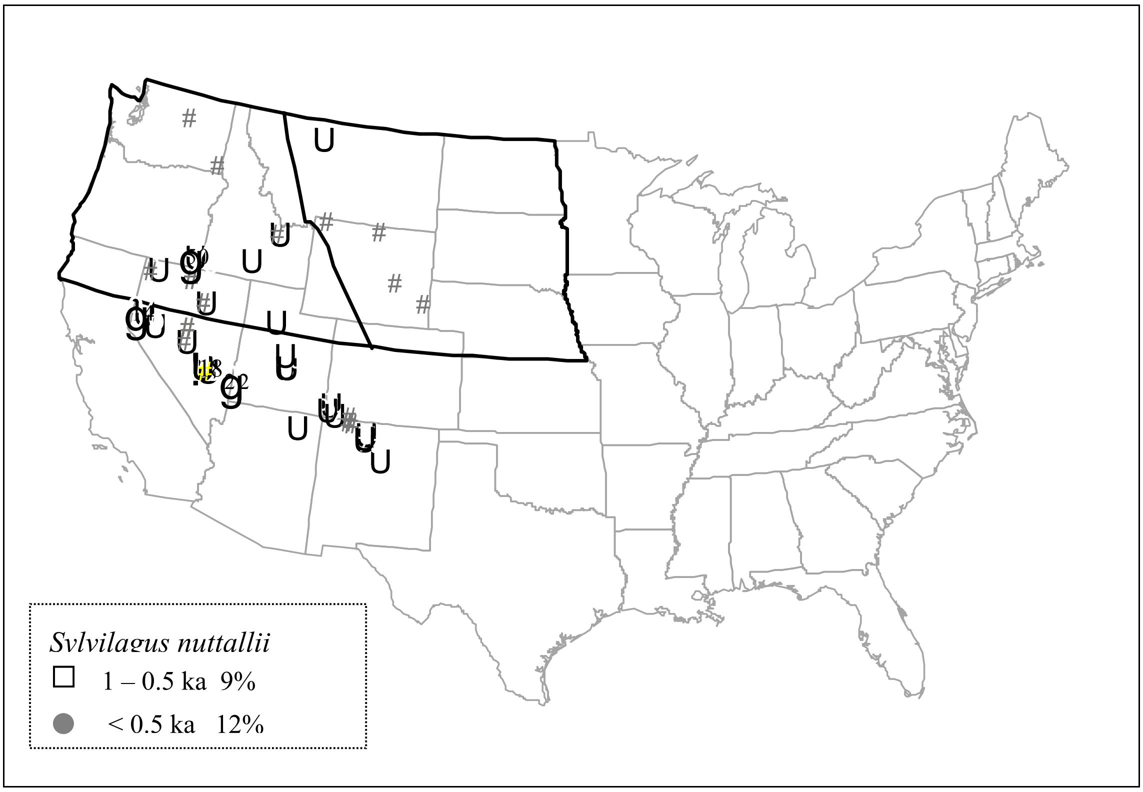


Fig. 136 The evolution of Arealsystem of *Sylvilagus nuttallii* (the last 1 ka)

Before 15 ka it distributed mainly in the Great Basin and Mexico Refugium. From 15 to 3 ka it still lived in the Mexico Refugium, but after this time it disappeared from this area. The ISVAs from 15 to 8 ka and from 8 to 3 ka are 5% and 3% respectively. The hot spots were in southern Idaho. From 1.5 to 1 ka the ISVA equals 13%, and the hot spots first appeared in southern Nevada. After 1 ka the ISVAs are 9% and 12%, and the hot spots were mainly in southern Nevada. Fossil records were found since 0.5 ka widely in Wyoming.

Rodentia

Muridae

5. 1. 7 *Neotoma lepida* **Desert Woodrat**

The desert woodrat ranges from SE Oregon and SW Idaho, south through Nevada and S California, USA, to S Baja California, Mexico (Fig. 137a). Common to abundant in Joshua tree, pinyon-juniper, mixed and chamise-redshank chaparral, sagebrush, and most desert habitats. Also found in a variety of other habitats. Most abundant in rocky areas with Joshua trees (Dig. Ref.).

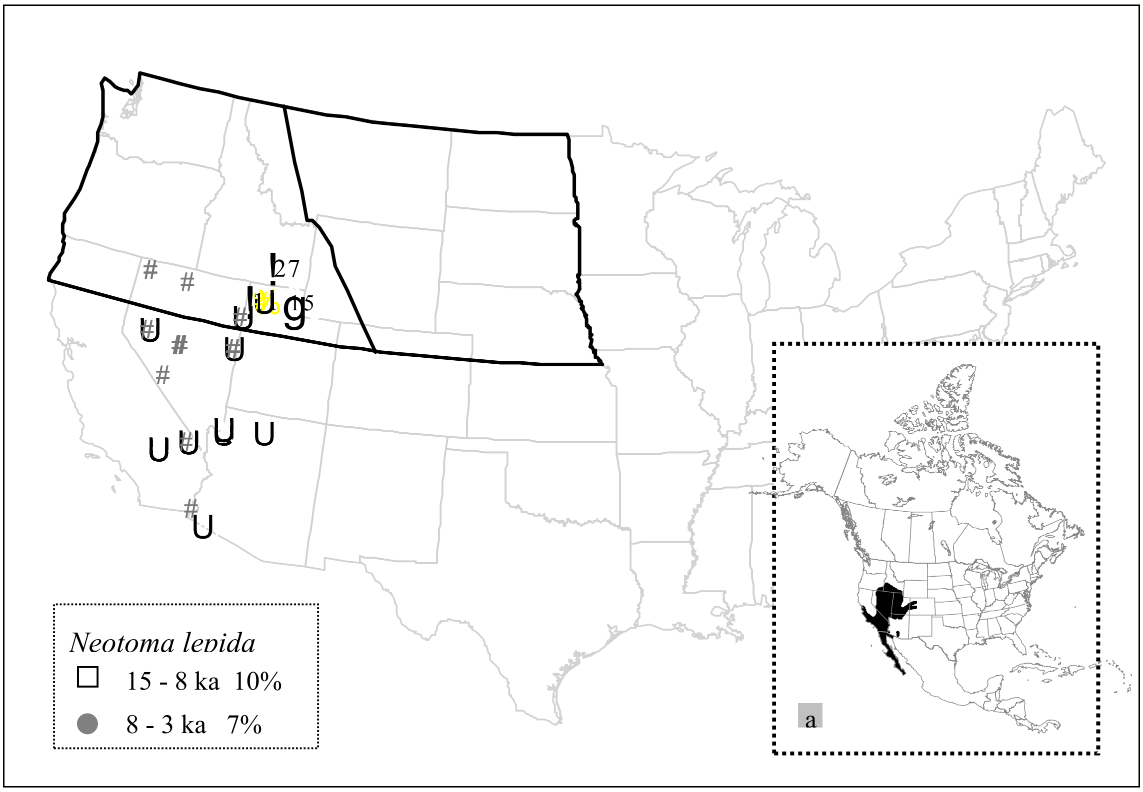


Fig. 137 The evolution of Arealsystem of *Neotoma lepida* (15-3 ka)

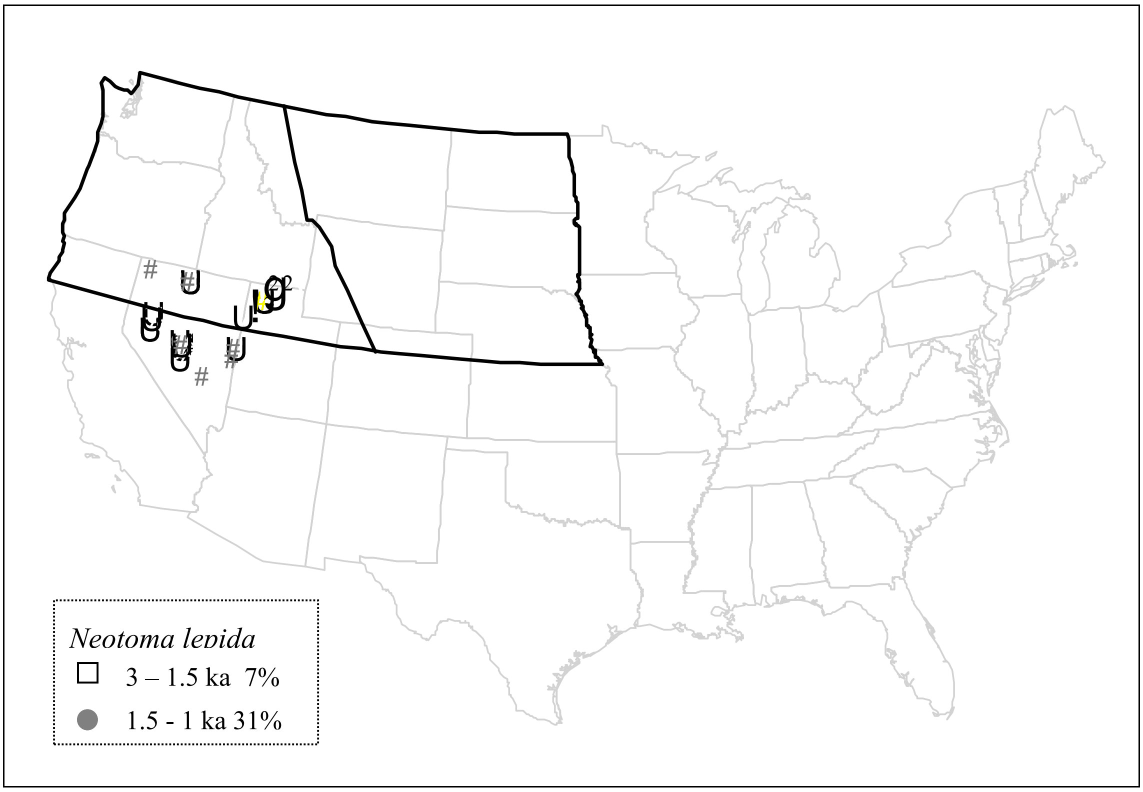


Fig. 138 The evolution of Arealsystem of *Neotoma lepida* (3-1 ka)

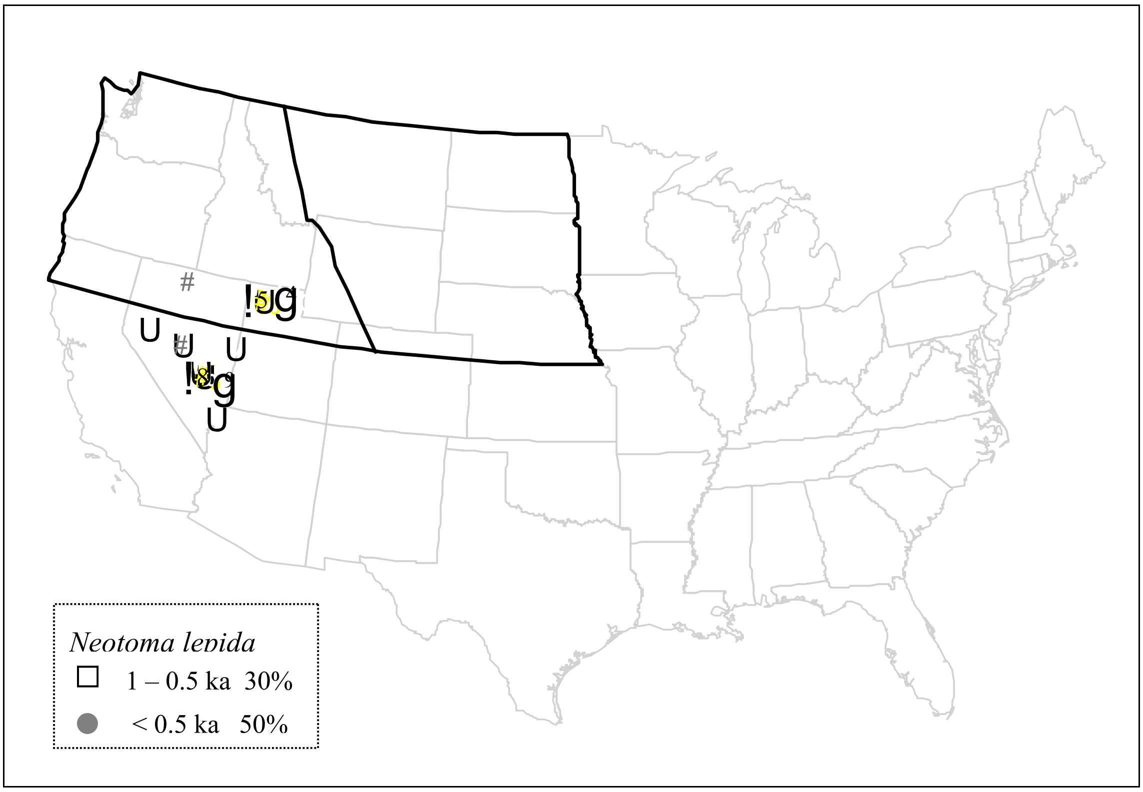


Fig. 139 The evolution of Arealsystem of *Neotoma lepida* (the last 1 ka)

Before 15 ka it distributed mainly in the California and Great Basin Refugium. From 15 to 1.5 ka it migrated northward, and the hot spots were located in northern Utah (Fig. 137, 138). During 1.5 to 1 ka the hot spots were not obvious, but after 1 ka the hot spots appeared in southern Nevada (Fig. 139).

5. 2 NATIVE AMERICAN HUNTED IN THE HOT SPOTS OF LARGE GAME

There are 15 species of mammals involved in this shift, eight of which were also involved in the turnover from the west side to the east side of the Rockies (Tab. 16). This means that those species had experienced two directions of movements. Unlike the appearing of the hot spots on the east side of the Rockies, which mainly happened around 1-0.5 ka, the appearing of the hot spots in the Southwest occurred in three periods: 3-1.5 ka, 1.5-1 ka, 1-0.5 ka. This can be also seen in Fig. 140.

Of the 15 species of mammals, there are *Bison bison*, *Antilocapra americana*, *Ovis canadensis*, and *Odocoileus hemionus*, which were the favorite game in western American. Larger prey items, such as artiodactyls, provide more energy per individual and are likely to be taken in preference to small game when they are available (Pyke, 1977, Stephens, 1986). So the shift of the hot spots of these game would influence the foraging efficiency. As the appearing of hot

Tab. 16 Mammals whose hot spots had moved from the west side of Rockies to the Southwest

Species	Disappearing from the west side of the Rockies (ka)	Appearing in the Southeast (ka)
Neotoma lepida	1 – 0.5	1 – 0.5
Antilocapra americana *	1.5 – 1	1 – 0.5
Lepus townsendii *	1.5 – 1	1 – 0.5
Canis lupus *	1.5 – 1**	1 – 0.5
Canis latrans *	3 – 1.5	1 – 0.5
Ovis canadensis	1 – 0.5	1.5 – 1
Brachylagus idahoensis	1.5 – 1	1.5 – 1
Lepus californicus	1.5 – 1	1.5 – 1
Sylvilagus nuttallii	after 0.5	1.5 – 1
Lynx rufus *	1.5 – 1**	1.5 – 1**
Sylvilagus auduboni	1.5 – 1	3 – 1.5
Dipodomys ordii *	1.5 – 1	3 – 1.5
Odocoileus hemionus	1.5 – 1	3 – 1.5
Bison bison *	after 0.5	3 – 1.5
Taxidae taxus *	1.5 – 1**	3 – 1.5**

* Species involved in two directions of movements ** Records with the highest MNIs (not the hot spots)

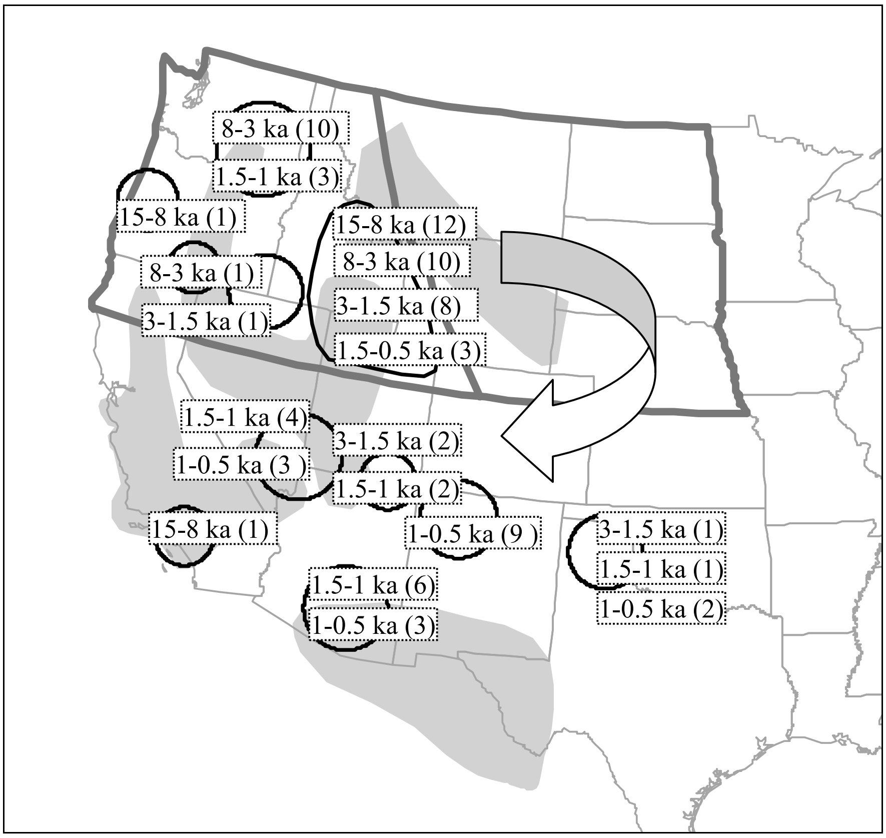


Fig. 140 The spatial turnover of hot spots of the 15 species of mammals from the west side of the Rockies to the Southwest

spots of the big game in Southwest, the foraging efficiency of the hunter-gatherers would increase after 3 ka. This prediction can be tested by the pattern in faunal exploitation described by Bayham (1982), Speth and Scott (1989), and Szuter and Bayham (1989) for essentially the same period. They maintain that archaeofaunas in Arizona and New Mexico contain increasing numbers of large game relative to small game through time. But the Bayham's pattern has confused zooarchaeologists for a long time. Firstly, it does not support the conventional view that gathering activities increased in importance from the early Archaic through the later Archaic Periods culminating in horticulture, and that hunting decreased to a level of lesser importance (Szuter, 1989). Secondly, Using faunal data collected from sites in California and Nevada, Broughton (1994) and Broughton and Grayson (1993) have described a contrasting pattern in animal use. They maintained that hunter-gatherers shifted emphasis from large, high-ranked game to smaller, lower-ranked animals, reflected in faunal assemblages decreasing numbers of large game relative to small game through time. This pattern of faunal exploitation has also been noted in Utah (Janetski, 1997) (Fig. 141).

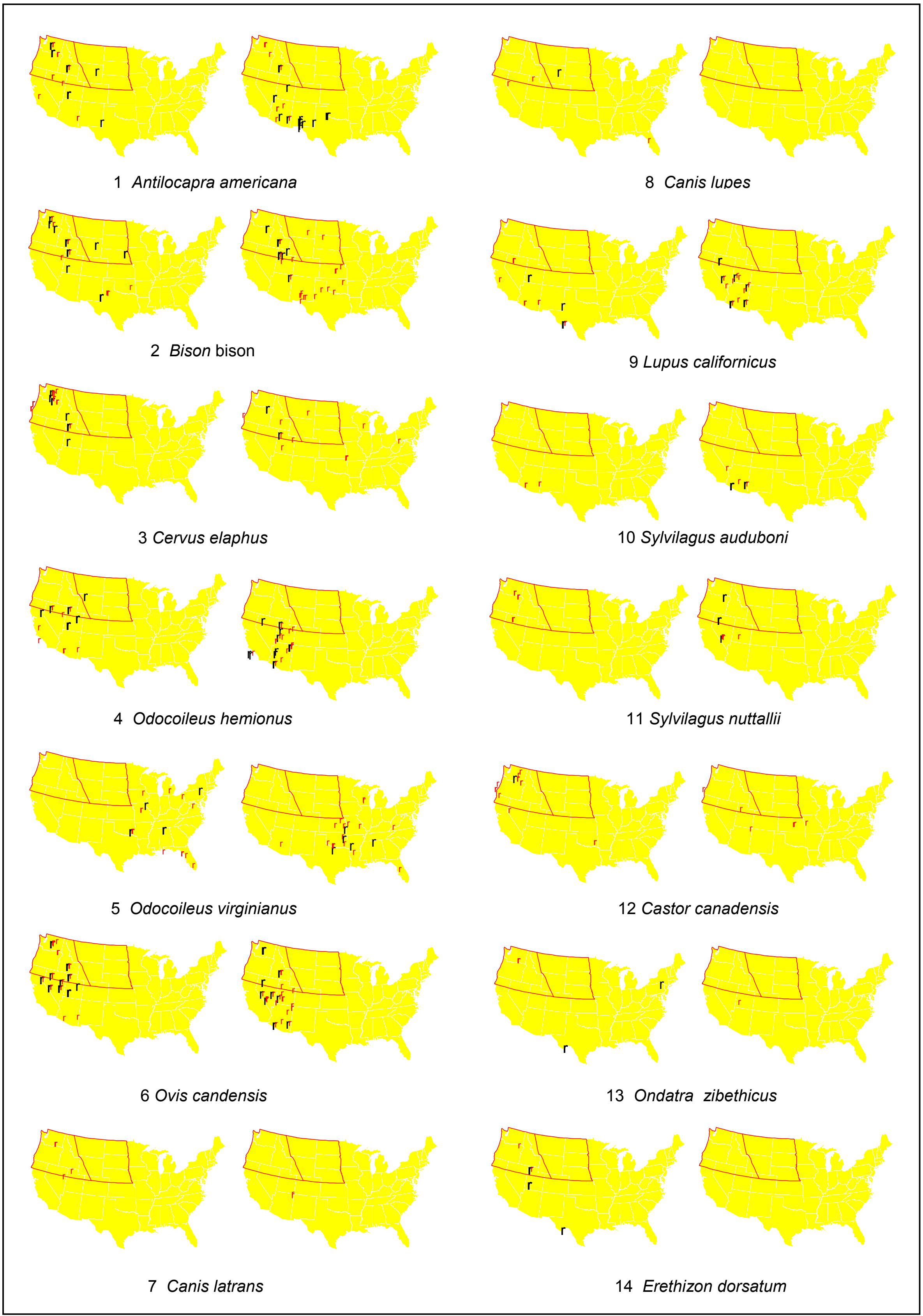
Broughton's research (1994a, b, 1995) on hunter-gatherers in California attributes the drop in larger animals to resource depression due to central place foraging and human population growth. Resource depression describes the process of game depletion in the vicinity of villages (central places) as a consequence of local ecology modification due to gardening or as a result of hunting. Ethnographical studies have documented how hunters reduce the populations of large game animals near villages, forcing a choice between taking lower-ranked prey close at hand or moving farther afield in pursuit of larger animals (Hames and Vickers, 1982). Transport and travel costs increase with distance and play an important role in prey selection decisions (see Metcalfe and Barlow, 1992 for discussion of transport costs). Prey choice should be reflected in faunal assemblages in the relative abundance of large and small animals (Broughton, 1995). The Bayham's pattern has been explained with reference to changes in the environment. Packrat midden studies document a trend in effective moisture that is declining over time: from a woodland in early Holocene, to a wet summer desert scrub, to the drier arid regime of today (Van Devender, 1977; Van Devender and Spaulding, 1979). Speth and Scott reject climate, technology and absolute population growth as potential explanations for the increase in artiodactyls through time. Rather, they suggest that the Bayham's pattern is a by-product of the "socioeconic responses, which accompany the aggregation of populations into more residentially stable and more horticulturally based communities" (Speth, 1989). Szuter and Bayham (1989) also consider this pattern as socioeconomic consequences of increased

Fig. 141 Two contrasting pattern in animal use in the Southwestern USA

sedentism and farming commitments, although they acknowledge that this pattern could be accounted for, if environmental changes increased the abundance of artiodactyls over time.

However, increased sedentism will cause resource depression and high transport and travel costs, which in turn will affect prey choice of taking small animals at hand, rather than moving father afield in pursuit of larger mammals. So increased sedentism will cause the Broughton's pattern. The shift of hot spots of large game from the west side of the Rockies to Arizona, New Mexico provides a strong evidence suggesting the relative or absolute availability of mule, bighorn sheep, pronghorn antelope and bison increased through time, which might be caused directly by the environmental change from a wet woodland to the drier arid regime.

At least 104 species on which bones existed burn or butcher markings or whose bones were modified for decorate, bone tools were indicated to be hunted. The 7 most frequently modified (hunted) mammals are: *Ovis canadensis* (139 times found), *Bison bison* (91), *Odocoileus hemionus* (86), *Antilocapra Americana* (69), *Lepus californicus* (60), *Odocoileus virginianus* (59), *Cervus elaphus* (58). Kill sites are the sites where at least one specimen of a sample of species had hunted markings such as burn or butchering marks, or used as bone tools or decoration. Fig. 142 shows the spatial movement of kill sites. Kill sites in the West are much more frequent than in the East. *Odocoileus virginianus* was the main game in the East. It can be seen that before 1.5 ka, the kill sites of many game were mainly on the Pacific Northwest, but after 1.5 ka, the kill sites of these game had moved to the Southwest, which coincided with the movement of hot spots of these game. This indicates that Native American hunted in the hot spot area of their favourite game.



1 *Antilocapra americana*

8 *Canis lupes*

2 *Bison* bison

9 *Lupus californicus*

3 *Cervus elaphus*

10 *Sylvilagus auduboni*

4 *Odocoileus hemionus*

11 *Sylvilagus nuttallii*

5 *Odocoileus virginianus*

12 *Castor canadensis*

6 *Ovis candensis*

13 *Ondatra zibethicus*

7 *Canis latrans*

14 *Erethizon dorsatum*

Fig. 142 The spatial movement of kill sites. **Left**, **before 1.5 ka**: Black, from 8 to 3 ka, Red, from 1.5 to 0.5 ka; **Right**, **after 1.5 ka ago**: Black, from 1.5 to 1.0 ka ago. Red, from 0.5 to 0.1 ka. Red Quadrangle, the west and east side of the Rockies.

CHAPTER 6 DISCUSSIONS AND IMPLICATIONS

In chapter one we have discussed how to use historical data to study the evolution (the origin, development, formation and dynamics) of Arealsystems and the requirements of the historical data for this kind of analytical utility. In chapter two we have considered how to use the fossil data in the Faunmap to study the Refugium Stage (the first stage) of the evolution of Arealsystems. Chapter three concerns how to explore the internal structure of Arealsystems by analyzing the fossil data with Brown's hot spots model. From then on, we have considered the hot spots within a species range inferred from MNIs, the shift of the hot spots and the test of the hot spots and their movements. But we have not discussed the causes of the shift of the hot spots. In this chapter we will first explore the possible causes of the shift of hot spots, and then we will summarize the implications and suggestions of this work to ecologists and biogeographers, to palaeontologists and zooarchaeologists, and for wildlife management and effective conservation.

6. 1 AN ENVIRONMENTAL CHANGE MODEL

The Brown's model has already pointed out that local abundance is determined primarily by the extent to which different resources and conditions of local environment meet the requirements of a given species. This implies that the shift of hot spots may result from the environmental changes. In chapter three we have discussed that the temporal differences in the number of species that had hot spots were coincident with the varied environmental conditions. In chapter five we have demonstrated that the shift of hot spots of large game to the Southwest caused the Bayham's pattern. Here we will present our environmental change model showing the relationship between the shift of hot spots and the environmental changes.

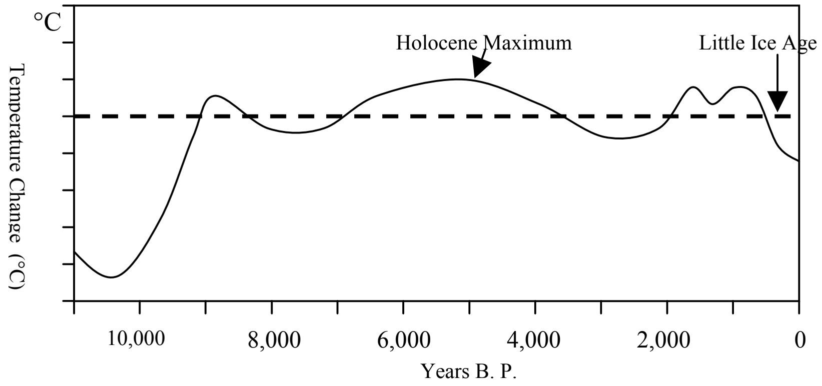


Fig. 143 A graphical representation of the mean global air temperature (Houghton, 1990)

The Holocene was categorized as an unstable period of long-term climatic change (Fig. 142). The Early Holocene Amelioration is recorded through pollen data as a stage of abrupt temperature increase starting 10,000 years BP (Bell, 1953). Further analysis suggested a 3 to 4 degree increase every 500 years. The Holocene Maximum or Altithermal lasted from 9 ka to 4 ka. Data from various U.S. sites indicate a thermal maximum from 10ka to 5ka through pollen analysis. A general cooling trend called the Late Holocene Deterioration followed this warm period. The Medieval Warm Period occurred from 900 AD to 1380 AD (Houghton, 1990). After this warm period, approximately 500 years ago, another cold interval called the Little Ice Age (1580 – 1850 AD) took place. This is the general trend of global climatic change during the Holocene, but there are regional differences in the western USA (Fig. 144).

During the Last Ice Age, the southwestern United States was much wetter and cooler than it is today. In the Great Basin deep fresh-water lakes covered many of the now arid valleys and the current southwestern deserts supported plants and animals that are now restricted to higher elevations and more northerly latitudes. Subalpine trees such as spruce were present in the Great Basin, Grand Canyon, and central Arizona during the Last Glacial Maximum (18,000 yr B.P.). Wetter-than-modern conditions continued into the early Holocene. Climatic conditions in the southwestern deserts became warmer but still wetter by the middle Holocene. The subalpine forest expanded at least 100 m lower in elevation in response to greater available soil moisture. The upper limits of the subalpine forest also expanded during this period. Many of the modern desert species became established within their modern ranges since 6000 yr B.P. After 3500 yr B. P. as it became much drier, and covered mainly by scrub and sagebrush (Thompson, 1993)

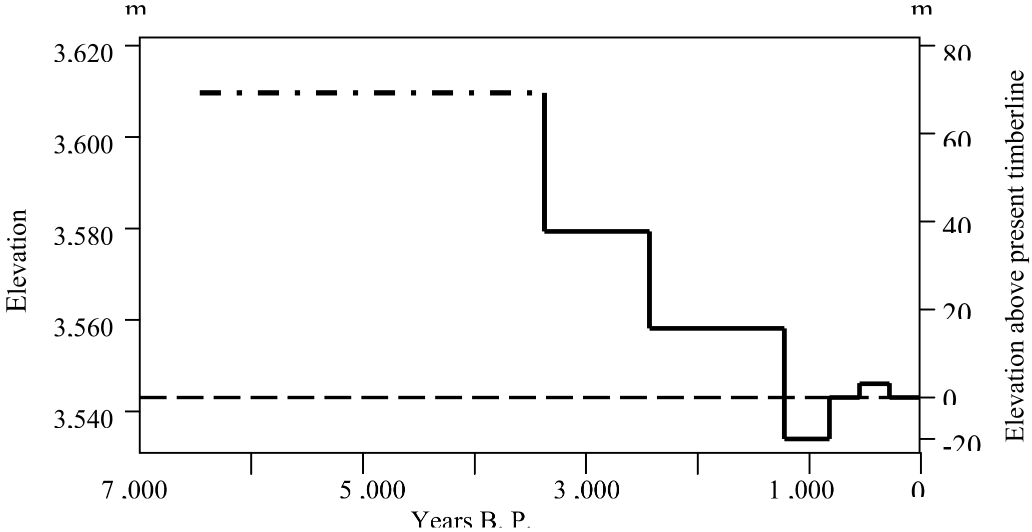


Fig. 144 Subalpine trees in the Sierra Nevada remained as much as 65 m above modern timberline until 3500 yr B.P. (Scuderi, 1987).

In the Midwestern USA, the pollen and plant macrofossils show that these areas were largely forested from 14 to 6 ka. The forest changed gradually from a boreal-like vegetation dominated by *Picea* and *Larix* from 14 to 10 ka to mesic deciduous forest shortly before 10 ka. A dramatic change occurred very rapidly about 6 ka, when prairie rapidly replaced forest in the central midwestern USA (Baker, 1996). A resurgence of *Quercus* pollen was largely responsible for the return of arboreal pollen to over 35%, and the concurrent presence of pollen and plant macrofossils of both tree and prairie taxa indicates that a savanna vegetation was present from about 3 ka to pre-settlement times. The regional *Ambrosia* peak signals the beginning of cultivation about 150 years ago (Baker, 2001).

However, the vegetational and climatic change in the Pacific Northwest showed a contrary trend. Palynological data and mammalian faunal data indicate it was warmer and drier in eastern Washington during the early and middle Holocene (Barnosky, 1987, Lyman, 1983, 1986) Sagebrush-dominated steppe habitats expanded throughout eastern Washington until about 5,500 years ago, stabilized for about 1,000 years, and then retreated toward the arid center of the Columbia Basin as effective moisture increased (Lyman, 1991, Mehringer, 1985). The modern conifer forest became established by about 3800 year ago in the Pacific Northwest (Pellatt, 2001). How could these regional differences in the climatic and vegetaional changes

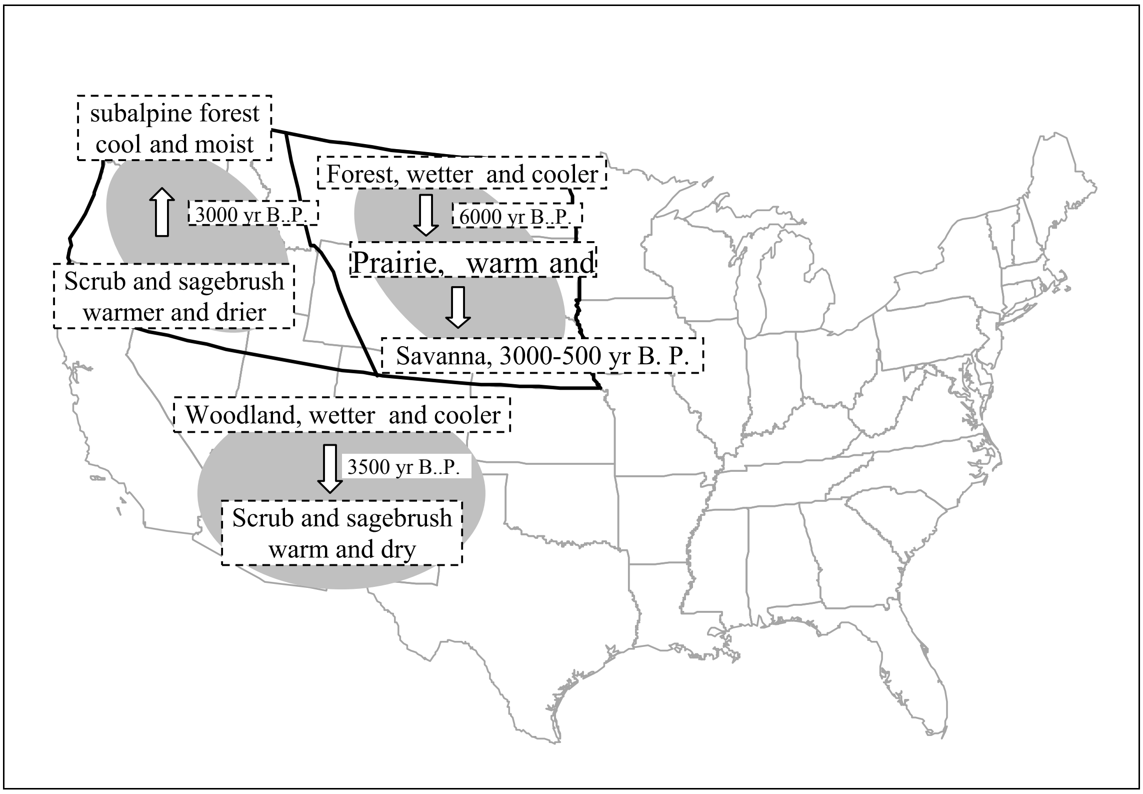


Fig. 145 Regional differences in the Holocene climatic and vegetational changes in western USA

result in the shift of hot spots of many mammals? Or how would warm and drier conditions affect artiodactyls populations? It was commonly considered that wetter and warmer climates should favour artiodactyls (Durrant, 1952, Szuter and Bayham, 1989). But recent studies show that more plant-available moisture reduces the nutrient content of plants but increase productivity. Because larger herbivore species tolerate lower plant nutrient content but require greater plant abundance, the highest potential herbivore diversity should occur in locations where are dry enough to yield high quality plants and support smaller herbivores, but productive enough to support larger herbivores (Olff, 2002). So it is easy to understand that the Pacific Northwest (Idaho, Washington and Oregon) was the hot spot area of many herbivores during the early and middle Holocene, because it was dry and warm with a widespread sagebrush-dominated steppe. But as it became wetter and cooler in the late Holocene (after about 3000 year ago), the sagebrush decreased markedly in abundance, while the modern conifer forest became established, this area could not support as many hot spots of herbivores as before. So the hot spots of many mammals that prefer arid grassland moved to the Southwest and the Midwestern, where it had become warm and dry, and sagebrush-dominated steppe or savannah had replaced their forests existed before.

6. 2 IMPLICATIONS FOR WILDLIFE MANAGEMENT AND CONSERVATION

Lyman (1996) described several instances of the significance of zooarchaeological and palaeontological data for helping resolve particular kinds of modern problems faced by those concerned with wildlife management. Many nations have one or more forms of national park and game preserve. Wildlife managing sometimes involves attempting to enhance or modify the biotas of these parks or preserves so that they reflect what are variously referred to as pristine ecosystems, wildness or native (pre-industrial) or natural biotas, and sometimes involves supplementing resident populations with individual organisms transplanted from elsewhere or attempting to re-establish species in areas where native populations have become extirpated. Lyman (1996) has argued that zooarchaeological research can be applied to identify which forms or taxa should be reintroduced to which areas to recreate natural biotas, to identify which forms or taxa are exotic and should be removed from an area to create a natural biota, to help to define the boundaries of biological preserves in order to preserve biota in perpetuity.

The knowledge gained from the unique perspective of the evolution of the Arealsystem reconstructed from paleobiological data can help us understand our current environmental problems further and protect the natural resources more efficiently. The evolution or history of

Arealsystem of a species can tell us where it survived during the ice time, when it had reached its maximum distribution in size, where its most suitable area within the range reflected by the hot spots is, and how greatly the human activities had changed its natural distributions. This information will undoubtedly help us take more wise protection strategies and develop more effective protection measures. In the USA there are 44 species of mammals on the IUCN Red List, 18 (41%) of which were monocentric species of the glacial refugia. The evolution of their Arealsystems shows that most of them did not disperse or dispersed only a little from their refugia in the late Quaternary (Tab. 17). This indicates that these animals have specific requirements for some environmental factors in their refugia. Ensuring that their habitations are not artificially destroyed in the future would seem be the only way to guarantee their survival.

Tab. 17 The monocentric species of refugia on the IUCN Red List

Scientific Name	Common Name	Refugium	Conservation Status
*Dipodomys heermani**	Heermann's kangaroo rat	California	C
*Dipodomys ingens**	Giant kangaroo rat	California	C
*Neotoma fuscipes**	Dusky-footed woodrat	California	C
Canis rufus	Red wolf	Florida	C
*Peromyscus polionotus**	Oldfield mouse	Florida	C
*Perognathus longimembris**	Little pocket mouse	Great Basin	C
*Tamias umbrinus**	Uinta chipmunk	Great Basin	C
*Enhydra lutris**	Sea otter	California	En
*Ammospermophilus nelsoni**	Nelson's antelope squirrel	California	En
Felis pardalis	Ocelot	Florida	En
*Sylvilagus palustris**	Marsh rabbit	Florida	En
*Myotis grisecens**	Gray myotis	Appalachia	En
*Myotis sodalis**	Indiana bat	Appalachia	En
Zapus hudsonius	Meadow jumping mouse	Appalachia	En
Ovis canadensis	Bighorn sheep	Rocky Mountain	En
*Peromyscus pectoralis**	White-ankled mouse	Mexico	Ex
*Geomys pinetis**	Southeastern pocket gopher	Florida	Ex
Peromyscus gossypinus	Cotton mouse	Florida	Ex

* did not dispersed or dispersed only a little from their refugium; C: Critically Endangered;
En: Endangered; Ex: Extinct in the wild

Identifying the glacial refugia and the hot spot areas is crucial to effective conservation. It is commonly known that the glacial refugia are characterized by their richness in species and endemic species. Our research shows that the hot spots of many species tended to be located in a region, which is called the hot spot area. The Appalachia refugium has many hot spot areas in the East. The Rocky Mountain refugium was also a large hot spot area before 1,000 years ago (Fig. 145). As the movement of hot spots happened around 1,500 years ago, some new hot spot areas such as the hot spot areas in the upper Missouri River basin, in northern Texas and northwestern New Mexico developed out of the refugia. The highest priority of conservation should be given to the protection of the refugium and the hot spots areas. The disappearance of the hot spots of a species is the prelude to its extinction. The hot spot area, usually determined by climate and vegetation, did not seem to have been changed by Native American hunting. The hot spot area in southern Idaho and northern Utah had existed for over 5000 years. High intensive native human hunting in this area had not destroyed this hot spot area. The main threat to the hot spot area comes probably from alteration of habitat. The hot spots of many mammals met by Lewis and Clark have already disappeared from the upper Missouri River basin.

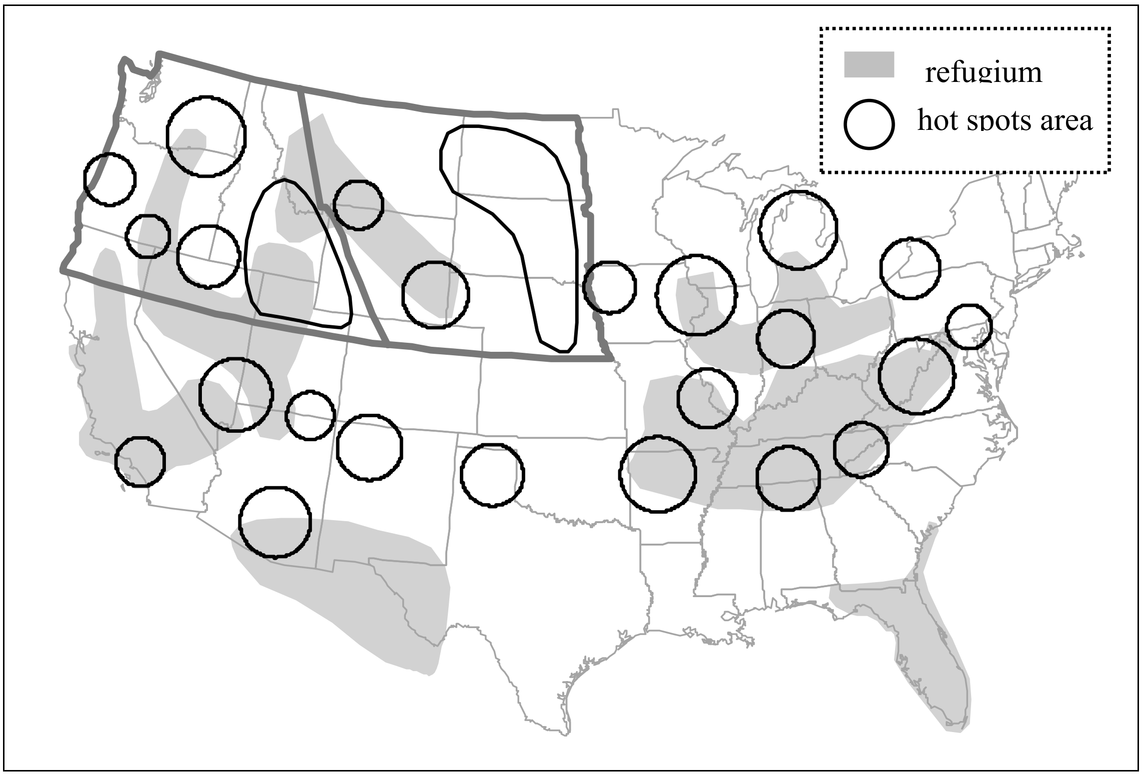


Figure 145. The glacial refugia and the hot spot areas in the USA

6. 3 SUGGESTIONS FOR ECOLOGISTS AND BIOGEOGRAPHERS

It may be very difficult for ecologists and biogeographers to believe in the valuable information, which can be provided by fossil data. Our researches show that the fossil data can provide reasonably accurate and valuable information for the study of current ecological and biogeographical problems, though possible evolutionary changes and biases in preservation might exist. It is argued that large amounts of historical data of high quality could be used to document the evolutionary processes of Arealsystems, identifying refugium, showing when the current shape and size of Areals come into being; to assist biogeographers to find the "hot spots" of the Arealsystem of a species; to reveal biogeographical patterns and historical processes. Some results can be tested by ecologists and biogeographers through the use of their own data. Seven Refugia in North America have been identified, five of which coincide with De Lattin's dispersal centers recognized by biogeographical methods using data on modern distributions. The hot spots inferred from MNIs and their movements can be verified by the marker made by Lewis and Clark during their expedition, and the historical process could also explain the ecologists and biogeographers' puzzle "Why were big game then abundant on the east side rare on the west side of the Rocky Mountains?" (Moore, 2002). Because the study of spatial variation in abundance with a range is still in the beginning, the hot spots inferred from MNIs of each species need to be further examined with its modern population data. This could be the object of future studies.

6. 4 SUGGESTIONS FOR PALEONTOLOGIST AND ZOOARCHAEOLOGIST

It is very valuable that Faunmap have collected the absolute chronological data, the quantitative information of MNI and NISP, the coordination data of each species, which are crucial to its ecological and biogeographical utility. However, many records have still no quantitative data on the field of MNI and NISP. This may be result from two reasons: Firstly, the builders of the Faunmap did not take enough time and energy to gather the information from the original literatures. Secondly, the research was reported in detail insufficient to know the MNI and NISP information. So enough attention should be paid to collect such quantitative information in the future building of database. In the Faunmap there are still no information about the area ($m^{2)}$ and volume ($m^{3)}$ excavated at each site, which were used to determine when rare zooarchaeological phenomena are truly absent (Lyman, 1995). This kind of information will also help compare the MNIs and NISPs among sites, determining the relative abundance within a range.

The NISP, the number of identified specimens is commonly used in the zooarchaeological study. Not all animals have the same quantity of bones. Therefore differences in NISP from different taxa may be a result of skeletal variation. Fragments of bones are interdependent and may be from the same animal. Excavation techniques, along with differential breakage or preservation rates, or butchering methods, will affect the number of fragments per taxon differently (Szuter, 1989). But the MNI, the minimum number of individuals, attempts to derive more realistic estimate of number of animals represented, contains therefore more ecological and population information than the NISP. For these reasons, we have opted to use MNIs rather than NISPs in their ecological and biogeographical utility. The relationship between MNIs and NISPs in the records having hunted bones in California has been tested. The correlation between MNIs and NISPs was significant, r(8) = .988, $p < .01$. Records with high MNIs also tended to have high NISPs. Records with low MNI tended to have low NISP. In the future the relationship between MNIs and NISPs from palaeontological and archaeological sites should be further studied.

Summary

This dissertation develops a rationale of how to use fossil data in solving biogeographical and ecological problems. It is argued that large amounts of fossil data of high quality can be used to document the evolutionary processes (the origin, development, formation and dynamics) of Arealsystems, which can be divided into six stages in North America: the Refugium Stage (before 15,000 years ago: > 15 ka), the Dispersal Stage (from 8,000 to 15,000 year ago: 8.0 – 15 ka), the Developing Stage (from 3,000 to 8,000 years ago: 3.0 – 8.0 ka), the Transitional Stage (from 1,000 to 3,000 years ago: 1 – 3 ka), the Primitive Stage (from 5,00 to 1,000 years ago: 0.5 – 1 ka) and the Human Disturbing Stage (during the last 500 years: < 0.5 ka). The division into these six stages is based on geostatistical analysis of the FAUNMAP database that contains 43,851 fossil records collected from 1860 to 1994 in North America.

Fossil data are one of the best materials to test the glacial refugia theory. Glacial refugia represent areas where flora and fauna were preserved during the glacial period, characterized by richness in species and endemic species at present. This means that these (endemic) species should have distributed purely or primarily in these areas during the glacial period. The refugia can therefore be identified by fossil records of that period. If it is not the case, the richness in (endemic) species may not be the result of the glacial refugia. By exploring where mammals lived during the Refugium Stage (> 15 ka), seven refugia in North America can be identified: the California Refugium, the Mexico Refugium, the Florida Refugium, the Appalachia Refugium, the Great Basin Refugium, the Rocky Mountain Refugium and the Great Lake Refugium. The first five refugia coincide well with De Lattin's dispersal centers recognized by biogeographical methods using data on modern distributions.

The individuals of a species are not evenly distributed over its Arealsystem. Brown's Hot Spots Model shows that in most cases there is an enormous variation in abundance within an areal of a species: In a census, zero or only a very few individuals occur at most sample locations, but tens or hundreds are found at a few sample sites. Locations where only a few individuals can be sampled in a survey are called "cool spots", and sites where tens or hundreds of individuals can be observed in a survey are called "hot spots". Many areas within the areal are uninhabited, which are called "holes". This model has direct implications for analyzing fossil data: Hot spots have a much higher local population density than cool spots. The chances to discover fossil individuals of a species are much higher in sediments located in a "hot spot" area than in a "cool spot" area. Therefore much higher MNIs (Minimum Number of Individuals) of the

species should be found in fossil localities located in the hot spot than in the cool spot area. There are only a few hot spots but many cool spots within an areal of a single hypothetical species, consequently only a few fossil sites can provide with much high MNIs, whereas most other sites can only provide with very low MNIs. This prediction has been proved to be true by analysis of 70 species in FAUMAP containing over 100 fossil records. The temporal and spatial variation in abundance can be reconstructed from the temporospatial distribution of the MNIs of a species over its Arealsystem. Areas with no fossil records from the last thousands of years may be holes, and sites with much higher MNIs may be hot spots, while locations with low MNIs may be cool spots.

Although the hot spots of many species can remain unchanged in an area over thousands of years, our study shows that a large shift of hot spots occurred mainly around 1,500-1,000 years ago. There are three directions of movement: from the west side to the east side of the Rockies, from the East of the USA to the east side of the Rockies and from the west side of the Rockies to the Southwest of the USA. The first two directions of shift are called Lewis and Clark's pattern, which can be verified with the observations mad by Lewis and Clark during their expedition in 1805-1806. The historical process of this pattern may well explain the 200-year-old puzzle why big game then abundant on the east side were rare on the west side of the Rocky Mountains noted by modern ecologists and biogeographers. The third direction of shift is called Bayham's pattern. This pattern can be tested by the model of Late Holocene resource intensification first described by Frank E. Bayham. The historical process creating the Bayham pattern will challenge the classic explanation of the Late Holocene resource intensification.

An environmental change model has been proposed to account for the shift of hot spots. Implications of glacial refugia and hot spots areas for wildlife management and effective conservation are discussed. Suggestions for paleontologists and zooarchaeologists regarding how to provide more valuable information in their future excavation and research for other disciplines are given.

ZUSAMMENFASSUNG

Die vorliegende Dissertation entwickelt ein Prinzip, in wie weit Daten von Fossilen zur Lösung biogeograpahischer und ökologischer Fragestellungen Verwendung finden können. Es wird bestätigt, dass eine große Anzahl fossiler Daten hoher Qualität zur Dokumentation evolutiver Prozesse (dem Ursprung, der Entwicklung der Formation und Dynamik) von Arealsystemen dienen können. Die evolutiven Prozesse können in Nordamerika in sechs Abschnitte gegliedert werden: die Refugialphase (vor 15000 Jahren: >15 ka), die Verbreitungsphase (vor 8000 bis 15000 Jahren: 8-15 ka), die Entwicklungsphase (vor 3000 bis 8000 Jahren: 3-8 ka), die Übergangsphase (vor 1000 bis 3000 Jahren: 1-3 ka), die Primitive Phase (vor 500 bis 1000 Jahren: 0,5-1 ka) und die anthropogene Störungsphase (die letzten 500 Jahren: <0.5 ka). Diese zeitliche Gliederung ergibt sich aus geostatistischen Analysen von FAUNMAP Daten. FAUNMAP ist eine Datenbank, in der 43,851 fossile Datensätze eingetragen sind, die zwischen 1860 bis 1994 in Nordamerika gesammelt wurden.

Zur Überprüfung eiszeitlicher Refugialgebiete eignen sich Daten fossiler Funde sehr gut. Eiszeitliche Refugien repräsentieren Gebiete, in die sich die Flora und Fauna während der letzten Eiszeit zurückgezogen hatte und die sich heute durch ihren Artenreichtum und ihre Anzahl endemischer Arten auszeichnen. Das bedeutet, dass diese (endemischen) Arten während der Eiszeit ausschließlich oder hauptsächlich in diesen Gebieten ihre Vorkommen hatten. Diese Gebiete können also durch ihre fossilen Dokumente aus dieser Zeit identifiziert werden. Die Entwicklung der Artenvielfalt in solchen Gebieten würde ansonsten nicht durch Eiszeitliche Refugien verursacht. Während der Refugialphase (>15 ka) besieldelten die verschiedenen Säuger vorzugsweise sieben Refugialgebiete in Nordamerika: das Kalifornia Refugium, das Mexikanische Refugium, das Florida Refugium, das Appalachia Refugium, das Great Basin Refugium, das Rocky Mountain Refugium und das Great Lake Refugium. Die ersten fünf stimmen gut mit den Verbreitungszentren überein, die von De Lattin definiert wurden. Er nahm die biogeographische Methode der Chrologie zu Hilfe.

Die Verbreitung von Individuen einer Art ist nicht gleichmäßig über ihr Arealsystem verteilt. Das Hot Spot Modell von Brown zeigt, dass es große Schwankungen der Bestandsdichten innerhalb des Verbreitungsgebietes einer Art gibt. Bei einer Untersuchung beobachtet man in den meisten Standorten keine oder nur einige Individuen, während man an einigen anderen Stellen über 10 –100 findet. Gebiete mit geringer Individuenzahl werden als „cool spots“ bezeichnet, solche mit einer großen Zahl an Individuen als „hot spots“. Einige Gebiete, die innerhalb des Areal einer Art nicht besiedelt sind, werden „holes“ genannt. Dieses Modell

wirkt sich unmittelbar auf die Analyse fossiler Daten aus. Im Vergleich zu „cool spots“ weisen „hot spots“ eine wesentlich höhere lokale Populationsdichte auf. Deshalb ist die Wahrscheinlichkeit, Individuen im Sediment sogenannter „hot spots“ zu finden, deutlich höher, als im Sediment von „cool spots“. Die Minimale Anzahl von Individuen (MNI) einer Arten sollte in fossilen Funden von hot spot-Gebieten also deutlich höher sein als von cool spot-Gebieten. Es gibt jedoch nur wenige hot spots, dafür aber viele cool spots innerhalb eines Arealsystems einer einzigen hypotetischen Art. In den meisten Fossilorten werden daher meist geringe MNIs und nur selten hohe MNIs festgestellt. Dieses Vorhersage wurde anhand von 70 Arten aus FAUNMAP mit mehr als 100 fossilen Nachweisen überprüft und analysiert. Damit wurde die Verbreitung von Arten in Abhängigkeit von zeitlicher und räumlicher Variation mit Hilfe der räumlichen Verbreitung der MNIs dieser Arten innerhalb deren Arealsysteme rekonstruiert. Gebiete ohne fossile Funde der letzten Jahrtausende wurden als „holes“ interpretiert. Gebiete mit hohen MNIs werden als hot spots, Gebiete mit nur geringen MNIs als cool spots definiert.

Obwohl das Vorkommen vieler Arten in hot spots über Tausende von Jahren konstant sein kann, zeigt die vorliegende Untersuchung, dass innerhalb des Zeitraums 1.5-1 ka große Verlagungen stattfanden. Die Verlagerungen erfolgten in drei Richtungen: vom Westen zum Osten der Rocky Mountains, vom Osten der USA zum Osten der Rocky Mountains und vom Westen der Rocky Mountains zum Südwesten der USA. Die ersten beiden werden Lewis und Clarks Muster genannt. Lewis und Clark konnten diese Verlagerung durch Beobachtungen während ihrer Expedition 1805-1806 belegen. Das 200 Jahre alte, von modernen Ökologen und Biogeographen beschriebene Rätsel „warum waren Säuger auf der Ostseite häufig, während sie auf der Westseite der Rocky Mountains selten waren“ wird durch den historischen Prozess erklärt. Die dritte Verlagung wird Bayhams Muster genannt. Dieses Muster kann mit Hilfe eines Modells der Intensivierung spätholocener Ressourcen überprüft werden, das Frank E Bayham als erster beschrieb. Der historische Prozess von dem Bayham Muster wird die klassische Erklärung der Intensivierung spätholozäner Resourcen herausfordern.

Zuletzt wird versucht, unter Berücksichtigung von Umweltveränderungen die Verlagerungen von hot spots zu erklären. In diesem Zusammenhang werden die Auswirkungen der eiszeitlichen Refugien und der hot spot-Gebiete für einer wirksamen Schutz und ein wildlife management diskutiert. Es werden Vorschläge für Paläontologen und Zooarchäologen unterbreitet, um in Zukunft die wertvollen Informationen für weitere Grabungen und die weitere Forschung auch in anderen Disziplinen zu nutzen.

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The Canada Biodiversity Web Site: http://www.canadianbiodiversity.mcgill.ca/english/index.htm

CURRICULUM VITAE

PERSONAL INFORMATION

Name: Li Chuanling
Date of Birth: 5, Dec., 1966
Citizenship: Chinese
Family Status: Married

EDUCATION

Since 2000. 1	Ph. D candidate in Institute of Biogeography, the University of Trier. Dissertattion: “ Dynamics of Late Quaternary Mammal Population Inferred from Geostatistical Study of the Faunmap Database and Its Implications for Conservation ”
1997. 9 -1998. 7	Beijing Language and Culture University, Beijing: Intensive German training
1988. 9 -1991. 7	Department of Geology, Northwest University (NWU): Master degree of Palaeontology. Dissertation: “The Xishuidong Quaternary Mammalian Fauna and Its Taphonomy”
1984. 9 -1988. 7	Department of Biology, Lanzhou University: Bachlor degree of Zoology

RESEARCH EXPERIENCE

1998. 10 -1999. 10	Institute of Biogeography, University of Saarlandes, Germany, Visiting Scholar
2000. 1 – 2003. 12	Assisstant in department of Biogeography and „Umweltprobenbank des Bundes“
1996 -1997	Taking part in the GEF(Global Environment Fund)-China Nature Reserve Management Program as an interpreter of the program director, the Database expert, the ecotourist expert, the socioeconomics expert and the program training specialist.
1994 -1997	Taking part in a program supported by Shaanxi Scientific Fund and Shaanxi Educational Funds.
1993 -1996	In charge of programs supported by NWU Scientific Fund and by Shaanxi Special Education Fund For Youth"

TEACHING EXPERIENCE

1993 -1997	An assistant professor of Deparment of Geology, Northwest University
1996, 1994, 1993	As a chief teacher of geological field practice for the second year students
1995, 1994	As a tutor of the geological field practice for the third year students and their graduation theses