Pleistocene and Holocene Records of *Antilocapra Americana*: A Review of the FAUNMAP Data

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ABSTRACT

FAUNMAP is an electronic database documenting the late Quaternary (Pleistocene and Holocene) distribution of mammal species in the United States, developed at the Illinois State Museum with support from the National Science Foundation. The primary purpose of the database is to investigate evolution of mammalian communities, although individual species distributions are readily examined. With 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. As of 1994, it included data from 2919 sites in the contiguous 48 states covering the last 40,000 years. The database is highly incomplete and does not represent the entire locality distribution of species, primarily because only a select few cultural resource management reports were included. The FAUNMAP database was queried for Antilocapra americana, *the sole living representative of a once-extensive family of pecoran artiodactyls. GIS maps were generated showing the distribution of* Antilocapra americana *from the Wisconsinan through the Holocene and the modern extant range. These maps reveal* Antilocapra americana *has been consistently present throughout what early twentieth century mammalogists consider the species' historic range, with only an occasional locality outside those boundaries. These latter localities can be correlated with short-term shifts in the distribution of the short-grass prairie eastern border or slight changes in the western limits of the species range.*

Keywords: pronghorn; Antilocapra; FAUNMAP; Holocene distribution; Wyoming; paleontology.

Pronghorn have been recorded from paleontological or prehistoric archaeological sites from almost every county in Wyoming, normally considered the heart of the species' range (Figure 1). Most of these localities are centered in western Wyoming, throughout the Green River and Great Divide basins. One must question whether this apparent distribution is real or an artifact of where cultural resource management and other archaeological projects have been conducted. Looking strictly at paleontological or major archaeological localities (those with a large pronghorn MNI; see Walker 1987a), a state-wide prehistoric distribution still is apparent (Figure 2), similar to the modern distribution in Wyoming (Long 1965; Sundstrom et al. 1973).

However, we must go beyond just looking at such a distribution map encompassing all time periods. What was the Pleistocene and Holocene distribution of the American pronghorn across North America; how can we look at that distribution; and what does it tell us about the modern distribution of the species? The present study does this by using FAUNMAP (FAUNMAP Working Group 1994), a compiled database of Pleistocene and Holocene mammalian distributions. The database is often used to investigate evolution of mammalian communities, although individual species distributions are also readily examined. With a Geographic Information System (GIS), changes in the distributions of individual species, (in this case *Antilocapra americana*, the American pronghorn) and the ef-

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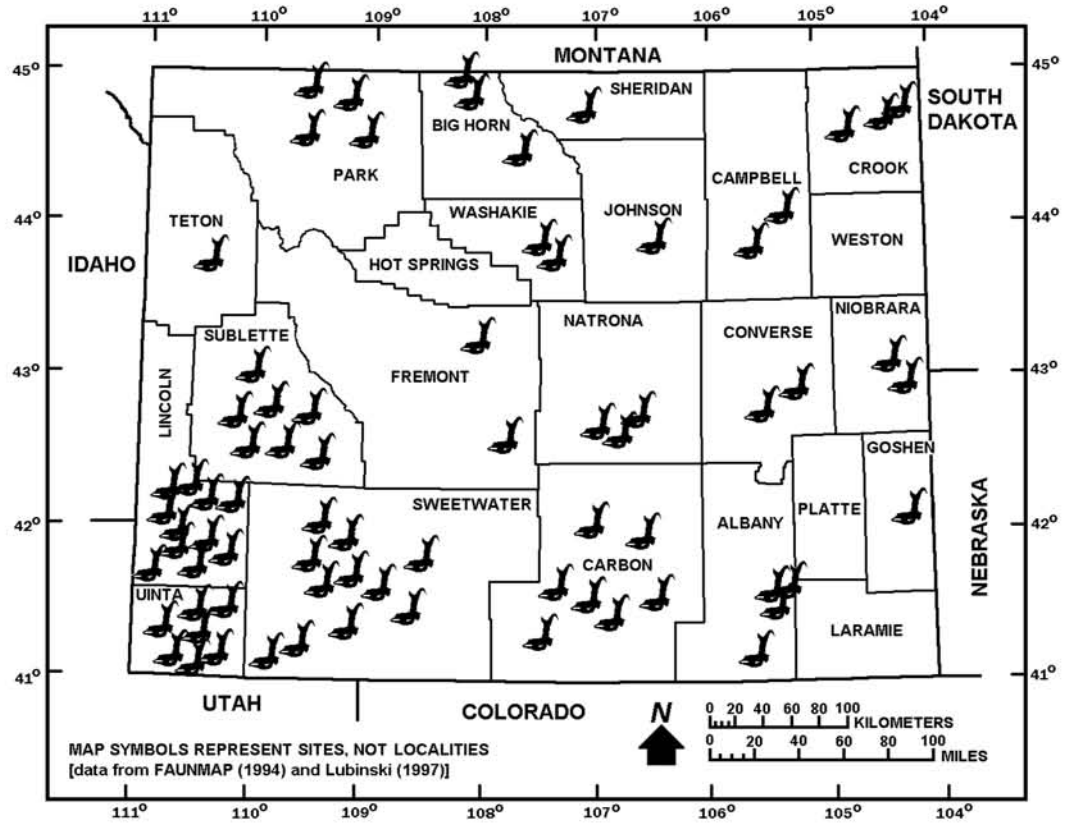

Figure 1. Distribution of pronghorn sites in Wyoming. Not all sites are included and placement of symbols does not reflect specific geographic location of sites (data from FAUNMAP Working Group 1994 and Lubinski 1997).

fects of those changes upon mammal community compositions can be documented for the late Quaternary and Holocene.

THE PLEISTOCENE FOSSIL RECORD

First, we must look at the fossil record to see where *Antilocapra americana* was derived. The fossil record of North American antilocaprids goes back to the Miocene, when the Merycodontinae first appeared (Webb 1973; O'Gara 1978; Kurtén and Anderson 1980). This now-extinct group of antilocaprids was characterized by forked horns that at first glance appear more cervid than antilocaprid. However, the horn was permanent and not shed like cervid antlers. We do not know whether the Merycodontinae had deciduous horn sheaths. By the end of the early Pleistocene, the Antilocaprinae had evolved from the Merycodontinae, including many with what we today would call bizarre horn core shapes: *Ilingoceros* had a twisted horn core; while both *Hexameryx* and *Hexobelomeryx* had a trifurcate shape to the core (Frick 1937; Furlong 1941; Webb 1973).

By the Upper Pliocene, these forms had all died out. The evolutionary line from those forms to the modern pronghorn is uncertain, primarily because few specimens date to the intervening time between the Upper Pliocene and the appearance of the fully modern *Antilocapra americana*. This is probably due to the species' preferred habitat being the open plains where the chances of preservation are lower (Webb 1973). It is also probable these taxa were never present in large numbers during the Pleistocene (Graham and Lundelius 1984).

Researchers have proposed various evolutionary sequences for pronghorns (see Merriam 1911; Barbour and Schultz 1934; Matthews 1934; Heese 1935; Frick 1937; Colbert and Chaffee 1939; Furlong 1941; Skinner 1942). A later theory is that of

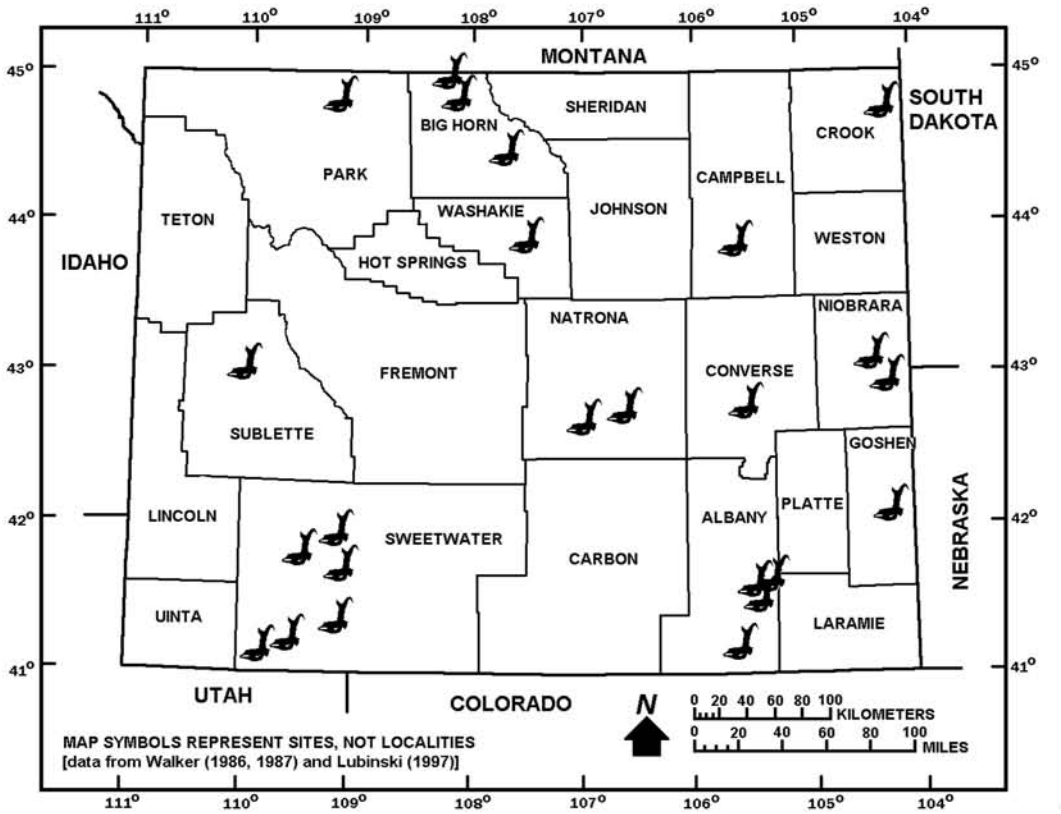

Figure 2. Distribution of Pleistocene and major Holocene pronghorn sites in Wyoming. Placement of symbols does not reflect specific geographic location of sites (data from Walker 1986, 1987; Lubinski 1997).

Webb (1973) who proposed this line began with *Sphenophalos* in the Late to Middle Pliocene. This taxon had a short horn core apparently similar to the base of the modern pronghorn (Webb 1973). This form apparently developed into what we now know as *Antilocapra americana* during the Pleistocene, probably through the intermediate species, *Antilocapra (Subantilocapra) garciae* (Webb 1973). Richards and McCrossin (1991) described a Middle Pleistocene (Irvingtonian) species, *Antilocapra pacifica,* from California. It was described as a form ancestral to, but larger than, the extant *Antilocapra americana.* It also differs from the extant form in its horn core, orbit and temporal-fossa morphology. The validity of this taxon is in dispute (Saysette 2000).

Contrary to many of the other large North American Pleistocene mammalian taxa such as *Bison* (Wilson 1975; McDonald 1981; Walker 1986), there is no evidence of a diminution in body size of *Antilocapra americana* in the past 10,000 years (Chorn et al. 1988; Saysette 1999):

> Standard measurements . . . on metatarsals, metacarpals, tibiae, femora, and humeri did not consistently discriminate between fossil and Recent elements . . . This lack of discriminatory power, in addition to the similar morphology, is consistent with the hypothesis that the fossil and Recent pronghorns are conspecific and differ in no significant detail despite a lapse of nearly 20,000 years between our samples (Chorn et al. 1988).

During this same time, three other Pleistocene antilocaprid genera are recognized: *Capromeryx*, *Tetrameryx*, and *Stockoceros*. These latter forms all died off before or at the end of the Pleistocene. No evidence exists for human cultural associations between *Capromeryx* and *Tetrameryx* (Kurtén and Anderson 1980; Anderson 1984). A possible cultural association may be present with *Stockoceros* at Burnet Cave in New Mexico dated at 11,500

RCYBP (Kurtén and Anderson 1980). Again, these antilocaprids had horn cores drastically different from the modern pronghorn in that each had a bifurcated core. Although most researchers believe these forms probably had a deciduous horn sheath, absolute data have not been recovered. The Merycodontidae did not have deciduous horn sheaths (Webb 1973; O'Gara and Matson 1975; Solounias 1988; Byers 1997). The structure of the horn core itself of these Pleistocene forms more closely resembles that of the modern pronghorn than the earlier antilocaprines or merycodontines.

All three of these forms were smaller than *Antilocapra americana.* This may have been one reason, along with habitat loss, for their extinction by the end of the Pleistocene. Guthrie (1984:282) proposes a change in vegetation patterns at the end of the Pleistocene, with less of a mosaic of vegetative communities.

> The large bovids, *Bison* and *Bos*, came to dominate the now "grazophilic" prairies, parklands and plains. Many of the small selective feeding ruminants of the grasslands died out. Pronghorn (*Antilocapra americana*) came to dominate the plains with bison. They appear complementary to bison, thriving on the browse and forbs exposed when bison intensively graze the shortgrass prairie. All the other antilocaprids and even camels were squeezed out in this new environment (Guthrie 1984:282).

If this concept is correct, these smaller antilocaprids were unable to adapt to the changing vegetation pattern and went extinct, while *Antilocapra americana* did adapt and may have actually expanded its population size.

Graham and Lundelius (1984) also addressed why *Antilocapra* was able to survive the Pleistocene, in a manner related to that of Guthrie:

> *Rangifer tarandus*, *Ovibos moschatus* and *Antilocapra americana* (pronghorn) are gregarious herd herbivores which survived the Late Pleistocene extinction. These species are known from late Pleistocene faunas, but at low frequencies. This may reflect their actual paucity in the biocoenosis or may result from taphonomic or sampling factors independent of their actual relative abundance in the fauna. However, the high relative frequencies in late Pleistocene faunas of other presumably gregarious taxa such as *Camelops*, *Equus*, *Hemiauchenia* (llamalike camel), *Mammuthus*, and *Platygonus* suggest that taphonomy cannot be the complete explanation. Instead, it is possible that *Rangifer*, *Ovibos*, and *Antilocapra* existed in low numbers in the highly diverse megafaunas of the late Pleistocene. With the extinction of numerous herd herbivores, other preadapted species such as *Rangifer*, *Ovibos*, and *Antilocapra* were able to invade the newly formed communities and expand their population sizes in response to lower diversity. Thus the late Pleistocene environmental changes not only influenced the evolution of new communities, and the extinction of a diverse fauna, but may also have directed the sociobiological evolution of some surviving species (Graham and Lundelius 1984:242).

We may never know why *Antilocapra americana* survived the Pleistocene basically unchanged to its present form, but the two arguments above are good food for thought. Regardless, it appears this taxon was a highly successful group throughout the Holocene, at least until the twentieth century, when uncontrolled hunting and loss of habitat by Euroamerican expansion and destructive activities resulted in a drastic decline in population across western North America (Nelson 1925; Nowak 1991).

MODERN DISTRIBUTIONS

Before turning to the Pleistocene and Holocene distribution of *Antilocapra americana*, a review of thought on its historic and modern ranges is in order. The earliest discussion of the historic range and a comparison to the range at the time was presented by Nelson in 1925 (Figure 3); however, Nelson does not state how he determined this historic range. Unfortunately, all later zoologists who mapped the modern pronghorn distributions with comparisons to historic ranges apparently used Nelson's historic range map, again with no discussion on how that map was derived (Yoakum 1978; Hall 1981). Regardless, Nelson (1925), Sundstrom et al. (1973) Yoakum (1978) and O'Gara (1978) also show the modern distributions during those time periods and how the range has decreased from the historic range presented by Nelson. These various studies differ in how the maps were presented. Some are all encompassing, while others show only known areas where pronghorn existed. Generally, the same historic and modern ranges were consistently displayed, with the only differences being the interpretation of the actual modern range. Most important is the apparent basic consistency in the historic and modern range of pronghorn.

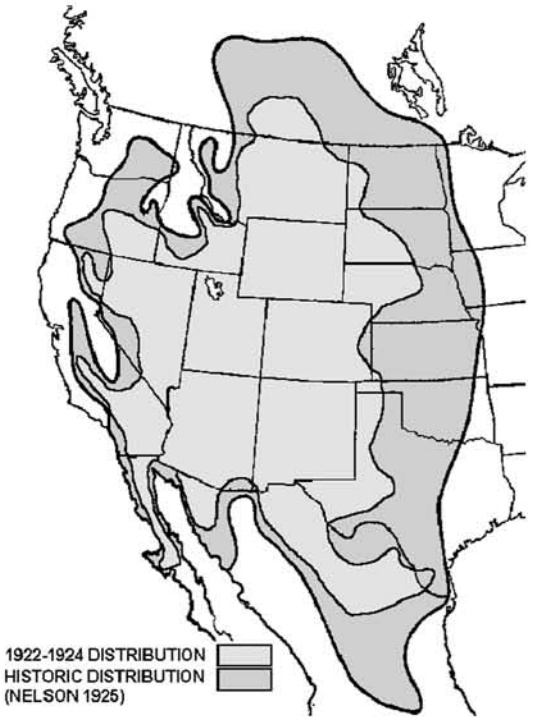

Figure 3. Historic and modern (1925) distribution of *Antilocapra americana* (adapted from Nelson 1925).

FAUNMAP

How can we look at the Pleistocene and Holocene distributions of *Antilocapra americana*? In 1994, Illinois State Museum published FAUNMAP, an electronic database documenting the late Quaternary distribution of mammal species in the United States (Faunmap Working Group 1994). This is a two-volume publication, along with an electronic copy of the databases comprising FAUNMAP. Those databases can be incorporated into searchable database programs available for most personal computers. From there, the data can be read into GIS systems, with any number of available overlays, depending on the local system. The database is also available on-line through the World Wide Web home page of the Illinois State Museum.

After incorporation into a GIS system and specific queries on a taxon completed, the selected time frame distribution is returned with an overlay of the "modern" range, along with a scatter plot of all localities present in the database for that taxon. The time periods available with FAUNMAP are not inclusive (Table 1). That is, each time period must be queried to get a complete return of all the distribution. A query for Wisconsinan (covering 10,000 to 110,000 RCYBP) will only return localities encoded as Wisconsinan based on data available to the encoders. More detailed breakdowns would result from querying for Glacial, Full Glacial, or Late Glacial, covering the same period. The encoders placed site localities within the smallest period available, but if they could not determine an exact age for the site based on published reports, it was placed within an encompassing period.

In 1994, there were encoded data in FAUNMAP from 2919 sites in the contiguous 48 states covering the last 40,000 years. A major problem with the database is that the data are highly incomplete and do not represent the entire locality distribution of species. This is because only a select few cultural resource management reports were included. Additions are being made to the main database as reports are presented to the Illinois State Museum, but are not yet available electronically or on-line. Similarly, Canadian sites are also now being incorporated into FAUNMAP (Graham 1999).

The FAUNMAP database was queried for *Antilocapra americana*, the sole living representative of this once widespread family of pecoran artiodactyls. GIS maps were generated showing the distribution of pronghorn from the Wisconsinan through the Holocene and the modern range. Interestingly, these maps show that the historic range of the American pronghorn depicted by Nelson (1925:Figure 3) is probably a true reflection of where pronghorn lived in North America throughout its evolutionary history (Figure 4B).

Maps were generated for all time periods (Figure 4B), the Wisconsinan (covering 10,000 to 110,000 years) (Figure 4C), Late Wisconsinan (covering 20,000 to 40,000 years) (Figure 4D), Full Glacial (14,500 to 20,500 years) (Figure 5A), Glacial (9500 to 20,500 years) (Figure 5B), Late Glacial (9500 to 15,500 years), (Figure 5C), Early Holocene (7500-10,500 years) (Figure 5D), Middle Holocene (3500 to 8500 years) (Figure 6A), Late Holocene (450 to 4500 years) (Figure 6B), and Post-Columbian (450 to the present) (Figure 6C).

DISCUSSION

As discussed earlier, these maps are instructive in examining how the extant pronghorn range

Table 1. FAUNMAP age definitions (from FAUNMAP Working Group 1994).

FAUNMAP PERIOD NAME	DATE(S) Yrs BP	NUMBER OF LOCALITIES
Post-Columbian	0-550	50
Late Holocene	450-4500	173
Post-Columbian/Late Holocene	0-4500	73
Middle Holocene	3500-8500	29
Late Holocene/Middle Holocene	0-8500	16
Early Holocene	7500-10,500	13
Early Holocene/Middle Holocene	3500-10,500	11
Late Glacial	9500-15,500	13
Early Holocene/Late Glacial	7500-15,500	3
Full Glacial	14,500-20,500	1
Glacial	9500-20,500	2
Holocene	0-10,000	16
Holocene/Pleistocene	0-110,000	16
Late Wisconsin	20,000-40,000	11
Wisconsin	10,000-110,000	2
TOTAL NUMBER		429

Table 2. Extralimital pronghorn sites in North America, arranged by FAUNMAP time period.

SITE NAME	STATE	COUNTY	FAUNMAP REFERENCE
Wisconsinan (10,000-110,000 Yrs B.P.)			
Galena Lead Region	IL	Jo Daviess	Anderson 1905; Allen 1876
Late Wisconsinan (20,000-40,000 Yrs B.P.)			
Maricopa	CA	Kern	Jefferson 1991; Kurten and Anderson 1980
McKittrick	CA	Kern	Jefferson 1991; Kurten and Anderson 1980
Rancho La Brea	CA	Los Angeles	Marcus and Berger 1984; Woodard and Marcus 1973; Marcus 1960
Early Holocene (7500-10,500 Yrs B.P.)			
Albertson	AR	Benton	Dickson 1991
Middle Holocene (3500-8500 Yrs B.P.)			
Glen Annie Canyon	CA	Santa Barbara	Owen, Curtis and Miller 1964
Rodgers Shelter	MO	Benton	Purdue 1982; Parmalee, McMillan and King 1976
Late Holocene (450-4500 Yrs B.P.)			
Arthur	IA	Dickenson	Tiffany 1982; Semken and Falk 1987
CA-Ven-294	CA	Ventura	Rosen 1979
Pohly	OK	Mayes	Ray 1965; Davis 1987
Rodgers Shelter	MO	Benton	Purdue 1982; Parmalee, McMillan and King 1976
Roth	KS	Bourbon	Johnson 1987
Williamson	KS	Coffey	Schmits 1987

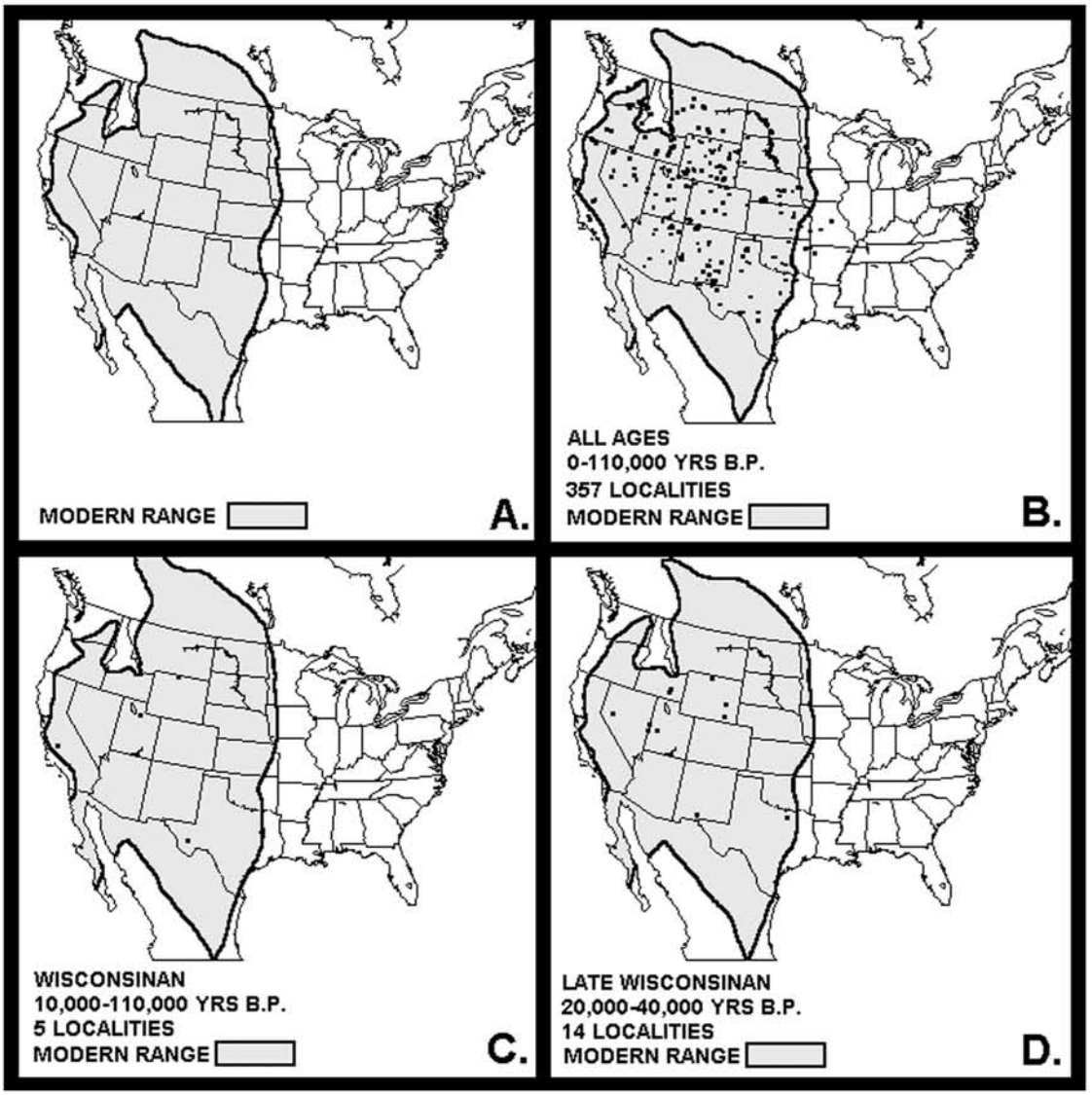

Figure 4. FAUNMAP generated GIS maps of *Antilocapra americana* distribution, by time period. A: Modern Range; B: All ages; C: Wisconsinan; D: Late Wisconsinan.

compares to the distribution of *Antilocapra americana* through time. Thirteen FAUNMAP localities were recorded as being outside the historic range of *Antilocapra americana*, apparently the same historic range presented by Nelson (1925) (Table 2). One locality in Illinois was identified as Wisconsinan (10,000-110,000 RCYBP) while three California localities were identified as Late Wisconsinan (20,000-40,000 RCYBP). However, it must be remembered these two age periods overlap and cover over 100,000 years. Dating of the individual specimens from these specific localities is needed to refine these distributions. One Early Holocene site (7500-10,500 RCYBP) was recorded from Arkansas, while two Middle Holocene sites were recorded from Missouri and California (3500-8500 RCYBP). Six Late Holocene localities were recorded from Iowa, Kansas, Missouri, Oklahoma,

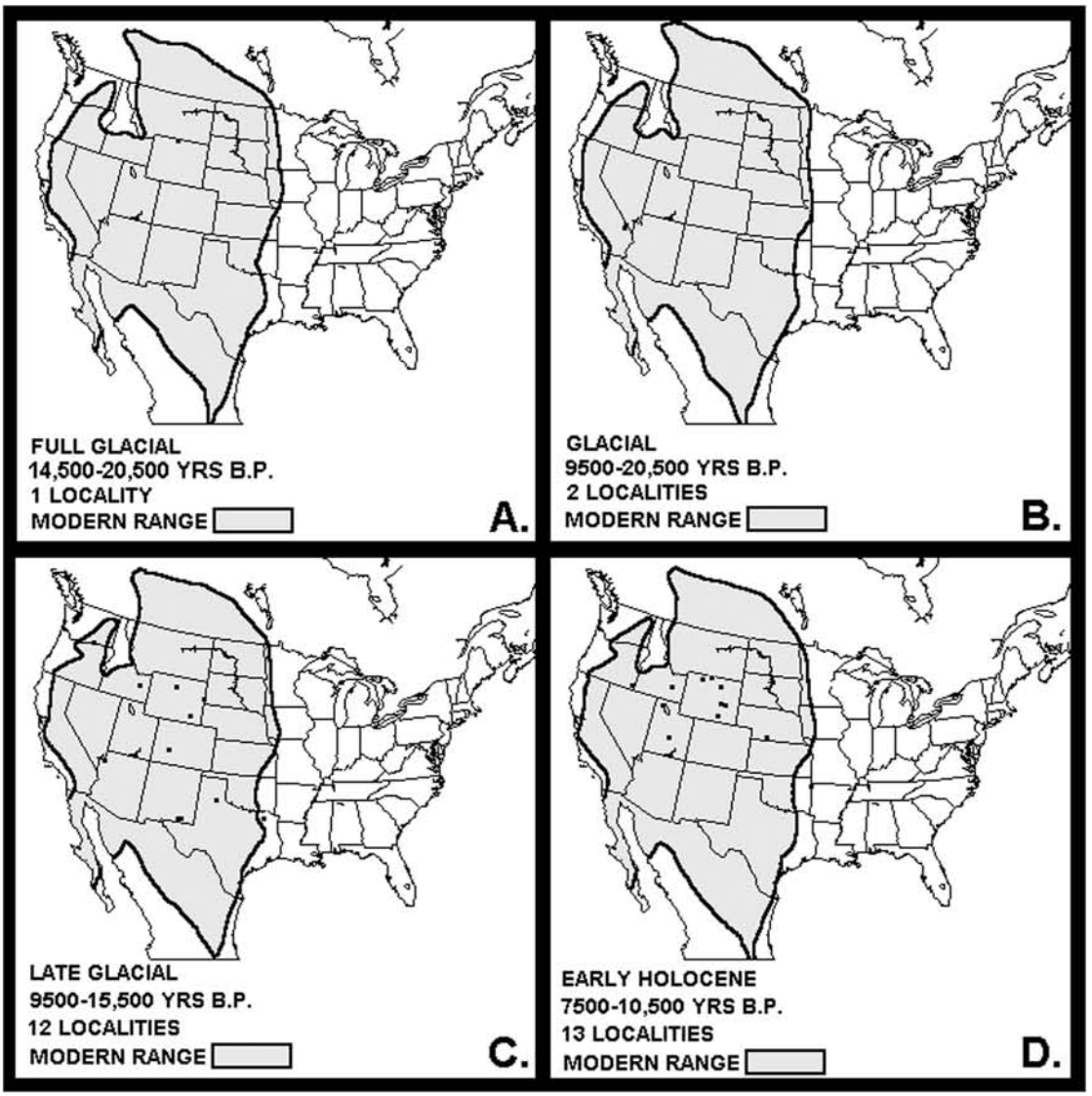

Figure 5. FAUNMAP generated GIS maps of *Antilocapra americana* distribution, by time period. A: Full Glacial; B: Glacial; C: Late Glacial; D: Early Holocene.

and California (450-4500 RCYBP) (Table 2). These more time-specific Holocene localities illustrate best how FAUNMAP distributions can be used to examine prehistoric distributions.

The reports for these nine localities were not specifically examined for paleoenvironmental data for this project, nor were they examined to see what specific elements of pronghorn were present and upon what the investigators based the identification. Generally, based on the periods involved, an expansion of pronghorn habitat, primarily eastward, can be postulated during selective parts of the Holocene, beginning around 10,000 years ago. During this period, *Antilocapra americana* is recorded from only one locality to the west of the present range.

The eastern boundary of the Plains shifted depending on climatic variability during this period. This climatic change and the associated vegetation change would have allowed pronghorn to move

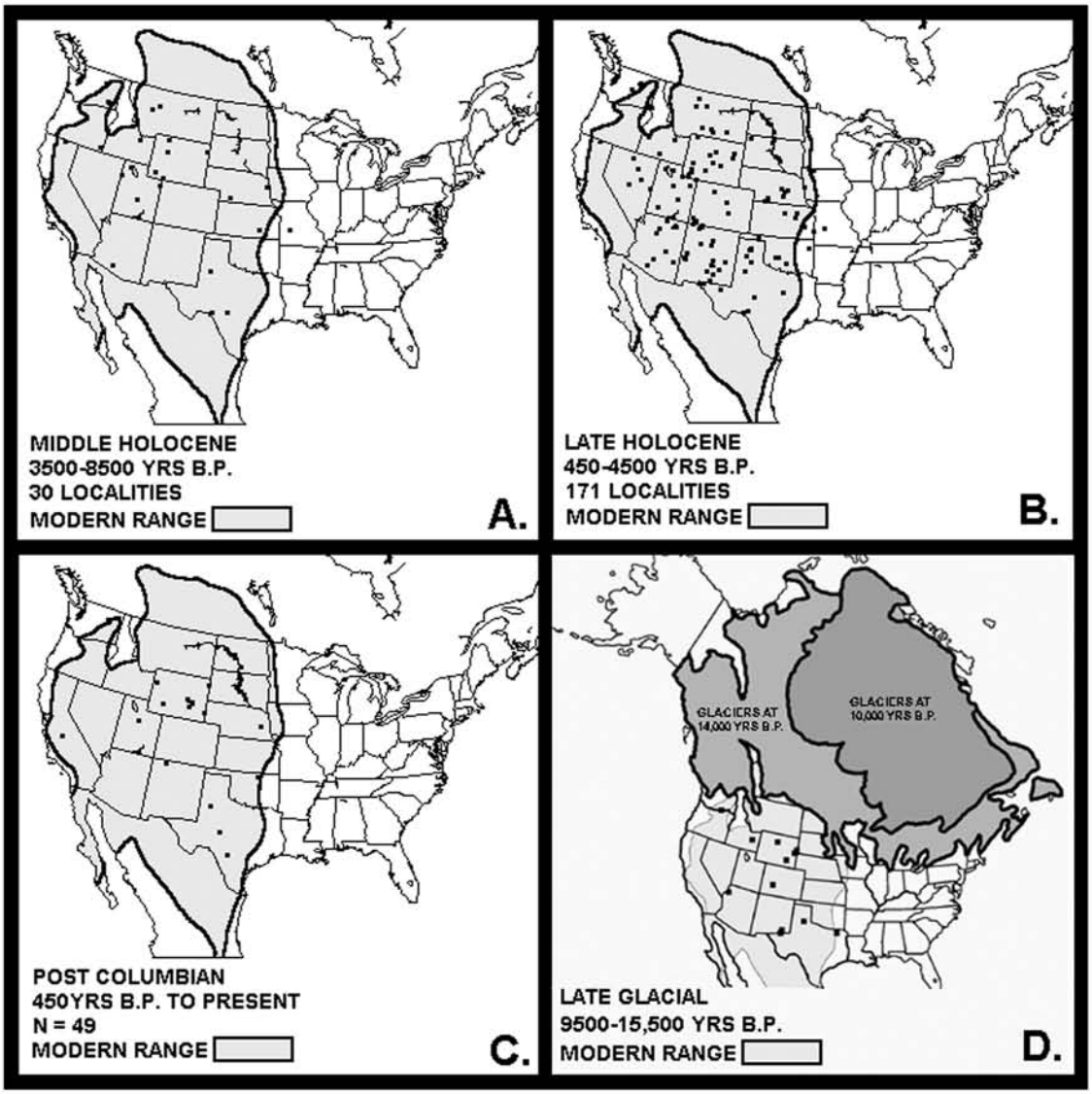

Figure 6. FAUNMAP generated GIS maps of *Antilocapra americana* distribution, by time period. A: Middle Holocene; B: Late Holocene; C: Post Columbian; D: Late Glacial (with glacial distribution overlain). Figure 6D is reproduced with permission of the Illinois State Museum.

east for limited times, and then retreat back west to the home range when the climate changed back again to what we see today. This indicates that pronghorn are truly adapted to the habitat and environment in which they occur today: the short grass prairie and sagebrush steppe biome.

This can be further illustrated by looking at another GIS map generated by FAUNMAP. This map shows the modern range and the maximum distribution of continental glaciers during the Pleistocene (Figure 6D). The northern portion of the modern range was under the ice during the latest part of the Pleistocene, during the final evolutionary period of this taxon (Byers 1997). While habitat destruction by Euroamericans remains a major cause, glaciation of the area also may help explain the reduction in the historic Canadian pronghorn range presented by Banfield (1974). The habitat

found in southern Canada where pronghorn were recorded historically was perhaps never the preferred habitat (such as that seen farther south in the intermountain basins). It was perhaps similar to that found in the eastern plains during the Holocene expansion of the pronghorn range. We saw a reduction in that eastern range following the end of the Holocene, and perhaps the same contraction of the range was going on in Canada during the last third of the twentieth century.

The distribution of pronghorn sites in Wyoming can also be broken down by FAUNMAP periods (Appendix 1). These data suggest that, during the late Holocene, more pronghorn were present in Wyoming than earlier, as predicted by Guthrie (1984) and Graham and Lundelius (1984) who feel pronghorn were never present in the Pleistocene in large numbers. Perhaps the vast extent of pronghorn herds seen by Euro-Americans during the early nineteenth century in western North America was the culmination of the post-Pleistocene expansion of this taxon into its primary habitat. The final development of this sagebrush-steppe habitat was also seen during this time.

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Appendix 1. Selected Wyoming Holocene pronghorn localities, by FAUNMAP time periods.

SITE NAME	COUNTY	FAUNMAP REFERENCE
Late Wisconsinan (20,000-40,000 Yrs B.P.)		
Horned Owl Cave	Albany	Guilday, Hamilton and Adam 1967
Little Box Elder Cave	Converse	Anderson 1968; Indeck 1987
Prospects Shelter	Big Horn	Chomko and Gilbert 1987
Full Glacial (14,500-20,500 Yrs B.P.)		
Natural Trap Cave	Big Horn	Chomko and Gilbert 1987; Chorn et al. 1988
Late Glacial (9500-15,500 Yrs B.P.)		
Agate Basin	Niobrara	Walker 1982; Hill et al. 1999
Colby	Washakie	Walker and Frison 1980; 1986
Sheaman	Niobrara	Walker 1982; Frison and Stanford 1982
Holocene (0-10,000 Yrs B.P.)		
48LN74	Lincoln	Brown 1980
48SW2356	Sweetwater	Wyoming Cultural Records Office Files
48SW2302	Sweetwater	Wyoming Cultural Records Office Files
48UT194	Uinta	Wyoming Cultural Records Office Files
48UT199	Uinta	Schroedl 1985
Early Holocene (7500-10,500 Yrs B.P.)		
Casper	Natrona	Wilson 1974
Eagle Shelter	Big Horn	Chomko 1982
Horner	Park	Walker 1987a
Little Box Elder Cave	Converse	Anderson 1968; Indeck 1987
Sister's Hill	Johnson	Agogino and Galloway 1965
Rattlesnake Pass	Carbon	Smith and McNees 1990
Middle Holocene (3500-8500 Yrs B.P.)		
McKean	Crook	Frison 1991; Kornfeld et al. 1995
Hawken	Crook	Frison, Wilson and Wilson 1976
Dead Indian Creek	Park	Frison and Walker 1984
Maxon Ranch Site	Sweetwater	Harrell and McKern 1986
Trapper's Point	Sublette	Miller, Sanders and Francis 1999
48UT370	Uinta	Schroedl 1985
48UT199	Uinta	Schroedl 1985
Late Holocene (450-4500 Yrs B.P.)		
48CA403	Campbell	McKibbin, Metcalf and Black 1987
48CA1391	Campbell	McKibbin, Metcalf and Black 1987
48UT199	Uinta	Schroedl 1985
48UT390	Uinta	Reiss and Walker 1982
48UT779	Uinta	Schroedl 1985
Austin Wash	Uinta	Schroedl 1985
Bentzen Kaufman Cave	Sheridan	Grey 1962
Bessie Bottom Site	Uinta	McKern 1988
Birdshead Cave	Fremont	Bliss 1950
Buffalo Hump Site	Sweetwater	Harrell 1989
Butler-Rissler	Natrona	Miller, Waitkus and Eckles 1987
Castle Gardens Access Road	Fremont	Walker and Todd 1984
Daughtery Cave	Washakie	Frison 1968
John Gale	Carbon	Miller 1981
Lamar	Park	Hadley 1990
Maxon Ranch Site	Sweetwater	Harrell and McKern 1986

Appendix 1. (continued)

SITE NAME	COUNTY	FAUNMAP REFERENCE
Skull Point	Lincoln	McGuire 1977
Spring Creek Cave	Washakie	Frison 1965
Taliaferro Site	Lincoln	Smith and Creasman, 1988
Wardell Buffalo Trap	Sublette	Frison 1973; Hill 1991
Post-Columbian (0-550 Yrs B.P.)		
48AB301	Albany	Zeimens 1975
48TE1107	Teton	Cannon 1991
Boar's Tusk	Sweetwater	Fritz 1984; Fisher and Frison, this volume
Bugas - Holding Site	Park	Rapson 1990
Glenrock Buffalo Jump	Converse	Frison 1970; Hill 1991
Rock Ranch Trading Post	Goshen	Zeimens et all 1987
River Bend	Natrona	Buff 1983; McKee 1988
Vore	Crook	Walker 1975, 1980