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Comparison of geographic distribution models of white-tailed deer *Odocoileus virginianus* (Zimmermann, 1780) subspecies in Mexico: biological and management implications

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and Sonia Gallina¹

Abstract

The white-tailed deer (*Odocoileus virginianus*) is the most widely distributed and studied ungulate in the American continent. This species is found throughout Mexico, except on the peninsula of Baja California and some areas of northern Chihuahua and Sonora. In this study we compared three geographic distribution models (Kellogg 1956; Hall 1981; Villarreal 1999) of white-tailed deer subspecies on a national scale, by state and by principal vegetation types. We found that neither the number of subspecies (13 or 14 of the 38 recognised subspecies), nor the geographical limits between subspecies coincided completely between models. Furthermore, for several subspecies, marked differences in distribution area were found depending on the distribution model used. Using multivariate analyses, we found that the 14 subspecies can be separated into three groups associated with different vegetation types: the northern subspecies associated with shrub land, the Pacific subspecies associated with temperate forest and tropical dry forest, and the south-eastern subspecies associated with tropical evergreen forest, cloud forest and tropical semi-deciduous forest. We suggest the classification of the 14 subspecies into three ecoregions. The data analyzed here is relevant to the management and conservation of the white-tailed deer subspecies and/or geographical variations in Mexico; it is also important to avoid the translocation of individuals into inappropriate areas with respect to their evolution and adaptation to different ecoregions.

Key words: distribution, ecoregions, management, Mexico, subspecies, vegetation types.

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Resumen

El venado cola blanca (*Odocoileus virginianus*) es el ungulado con mayor área de distribución en el continente Americano. En México, se le encuentra en todo el territorio excepto la península de Baja California, algunas áreas del norte de Chihuahua y norte de Sonora. En este trabajo comparamos algunos modelos (Kellogg 1956; Hall 1981; Villarreal 1999) de distribución geográfica de las subespecies de venado cola blanca, a nivel del país, por entidad federativa y por tipos principales de vegetación. Se encontró que no coinciden totalmente ni en el número de subespecies (13 ó 14 de las 38 subespecies reconocidas), ni en los límites geográficos entre subespecies; además de que para algunas subespecies existen claras diferencias en las áreas de distribución dependiendo del modelo de distribución. Con base en análisis multivariados encontramos que las 14 subespecies pueden separarse en tres grupos asociados a diferentes tipos de vegetación: las subespecies norteadas asociadas al matorral xerófilo, las subespecies del Pacífico asociadas al bosque templado y bosques tropical seco, y las subespecies del sureste asociadas al bosque tropical perennifolio, bosque mesófilo y bosque tropical subcaducifolio. Sugerimos clasificar a las subespecies en tres ecoregiones. La información generada es relevante para el manejo y conservación de las subespecies y/o variaciones geográficas del venado cola blanca en el país, y evitar translocar individuos a sitios que no les corresponden de acuerdo a su evolución y adaptación a las diferentes ecoregiones.

Palabras clave: distribución, ecoregiones, manejo, México, subespecies, tipos de vegetación.

Introduction

The white-tailed deer *Odocoileus virginianus* (Zimmermann 1780) is the most widely distributed and studied cervid in the American continent (Gallina *et al.* 2010). It is found from a latitude of 60° N in the south of Canada, through most of the United States, except some regions of the southeast, throughout Central America, and into South America in the north of Brazil and south of Peru at a latitude of 15° S (Smith 1991; Gallina *et al.* 2010). In Mexico this species is found throughout the country, except on the peninsula of Baja California and in some areas of northern Chihuahua and Sonora (Leopold 1959). The high levels of reproductive, behavioural and ecological plasticity observed in this species, are factors that have allowed it to expand its geographic distribution (Baker 1984). As a consequence, this browser cervid inhabits an extensive variety of different plant communities. In Mexico this species is found in temperate pine, oak and fir forests, mixed oak – pine forest, shrub land, tropical dry forest, semi-evergreen and evergreen forests, subaquatic vegetation and secondary vegetation (Galindo-Leal and Weber 2005).

Thirty eight subspecies of the white-tailed deer have been described, 14 of which are found in Mexico (Smith 1991). Although the level of subspecies is frequently employed for conservation and management purposes, from a biological point of view its definition is controversial. Theoretically, subspecies are groups of local populations, within a species, that share a geographical range and common characteristics (genetic and phenotypic), that are adapted to the environmental conditions found in their habitat, and that are separated from other populations by some kind of geographical or climatic

barrier; such qualities allow for the distinction of one subspecies from another (Frankham *et al.* 2002). However, the classification of the currently recognised white-tailed deer subspecies is entirely based on morphological characteristics (e.g., size, pelage colour, size and shape of male antlers), from just a few museum specimens (Kellogg 1956), and only a limited studies exist that present detailed or quantitative morphological or genetic data (e. g., Krausman *et al.* 1978; Sheffield *et al.* 1985; Cronin 1991a, 1991b; Mathews and Porter 1993; Ellsworth *et al.* 1994; Anderson *et al.* 2002; Van Den Bussche *et al.* 2002; DeYoung *et al.* 2002, 2003). For Mexico, very little information about morphometric or genetic variability in white-tailed deer is available. Studies exist for four north-eastern subspecies (Logan-Lopez *et al.* 2006, 2007), five subspecies in the country (Calderón-Lobato 2009), and three subspecies in the state of Michoacan (Chassin, personal communication). For these reasons, there is a clear need for further research in this topic.

The range of individual variation found in white-tailed deer, especially in size, antler details, and pelage colour, is remarkable and has been used for their subdivision into subspecies (Kellogg 1956). However, one form can pass gradually into another, especially where there are no abrupt changes in physiography. Specimens from certain regions might, with equal propriety, be referred to as either of the contiguous subspecies. But where abrupt changes in physiography do occur, such as the change from plains to high mountains, the deer tend to respond along rather sharp lines of differentiation. Generally, among the subspecies of white-tailed deer, the larger forms are found in the north and the smaller forms in the south. For example, the maximum size is reached in those races extending westward from the Atlantic coast across southern Canada and northern United States. The minimum size is found in *O. v. rothschildi*, inhabiting Coiba Island off the Pacific coast of Panama. In Mexico, the largest subspecies is *O. v. texanus*, while the smallest is *O. v. acapulensis*. Variation in antler-formation seems to correlate mainly with various physical factors, among which are size, maturity, and general physical condition (Villarreal 1999). The larger northern subspecies carry larger antlers, with more numerous tines, than do the smaller southern forms. For example, in *O. v. acapulensis* the antlers, even in fully mature bucks, may be reduced to single spikes; in contrast, in *O. v. texanus* subsidiary tines are more prevalent. Individual and subspecific variations in colour are so great that they are perplexing to explain, and gradations are so numerous that they are difficult to distinguish. The pelages usually are quite different among seasons. For example, in the northern subspecies the winter and summer colour differ, while in Mexico there are variations between wet and dry seasons. In general, summer or wet season colour being predominantly brownish or greyish, while winter or dry season is tawny. The most vivid coloration, ranging from tawny to rich orange-cinnamon, is shown by some of the subspecies inhabiting the tropical lowlands in Mexico and Central America. The colours of individuals from the high mountains of these regions usually are dull and dark. A further factor confusing the situation is the widespread translocation of various subspecies of white-tails into geographic ranges properly belonging to others.

The white-tailed deer is a highly valued species in Mexico for many reasons, including: protein consumption, commerce, the elaboration of artisan crafts, and as an important component in the rituals of indigenous cultures (Mandujano and Rico-Gray

1991; Greenberg 1992; Gonzalez-Perez and Briones 2000; Naranjo *et al.* 2004). Today the hunting of this species continues to be important, both for subsistence and trophy hunting. The white-tailed deer is the most important game species in Mexico and its cynegetic exploitation has increased notably in Wildlife Conservation, Management and Sustainable Utilization Units (in Spanish: Unidades de Manejo y Aprovechamiento para la Conservación de la Vida Silvestre, or UMAs, Montiel *et al.* 1999; Gonzalez-Marin *et al.* 2003; Segovia and Hernandez 2003; Villarreal-Espino 2006), providing an important source of income, particularly in the north of the country (Villarreal 1999). In consequence, UMA management has led to a greater national demand for the hunting of white-tailed deer and an urgent need for reliable biological and ecological data in order to sustainably manage the different populations and subspecies. In this sense, Natural Protected Areas (in Spanish ANPs) have proven to be important areas for such studies (Gallina *et al.* 2007).

From a cynegetic management point of view, in Mexico only five of the 14 white-tailed deer subspecies enter into the current international trophy record books, such as those organised by the Boone and Crockett Club and Safari Club International. For this reason, these are the subspecies that are given the most attention and protection by ranchers and land owners. These subspecies are: *O. v. texanus*, *O. v. couesi*, *O. v. carminis*, *O. v. miquihuanensis* and, in recent years, *O. v. mexicanus* (Villarreal-Espino 2002). The remaining subspecies have not been considered as recognised trophies by national or overseas sport hunters, owing both to their smaller sized antlers and their lack of an individual category in the trophy record books. Notwithstanding, the situation is beginning to change and a greater regional importance is being placed on the hunting of each individual subspecies (Villarreal 2009). As a result, one worrying aspect of white-tailed deer management is the translocation of subspecies to different parts of the country other than those areas where they are historically found. Given this problem, the Wildlife Department of SEMARNAT (the Mexican office for the Environment and Natural Resources) requires that any animals that are translocated are of the same subspecies as those found in the local area. This legislation forms part of Article 81 of the General Wildlife Law of Mexico (Diario Oficial de la Federación 2006). This is particularly important in large UMAs, where animals are often released with little control. For this reason there is an urgent need for a database of geographic information that allows both the authorities and farm owners to gain a better understanding of the subspecies they manage, and to maintain the genetic variability of the species and, in turn, its conservation prospects. See Appendix 1 to detail description of each subspecies in Mexico.

Based on information from the Smithsonian Institution, Kellogg (1956) published an interesting map, now little known, in Taylor's (1956) book, which has been considered a classic for decades. Interestingly, the author only recognised 13 white-tailed deer subspecies in Mexico and presented geographical limits between subspecies which were discontinuous. That is, he left empty spaces in which it is difficult to define which subspecies are distributed (Fig. 1a). The distribution map by Hall (1981) presents the continuous distribution of 14 subspecies, based on records from limits of the distribution of each subspecies (Fig. 1b). This map appears to be the basis of others, such as that published by Baker (1984) which, in turn, served as the basis of the map presented

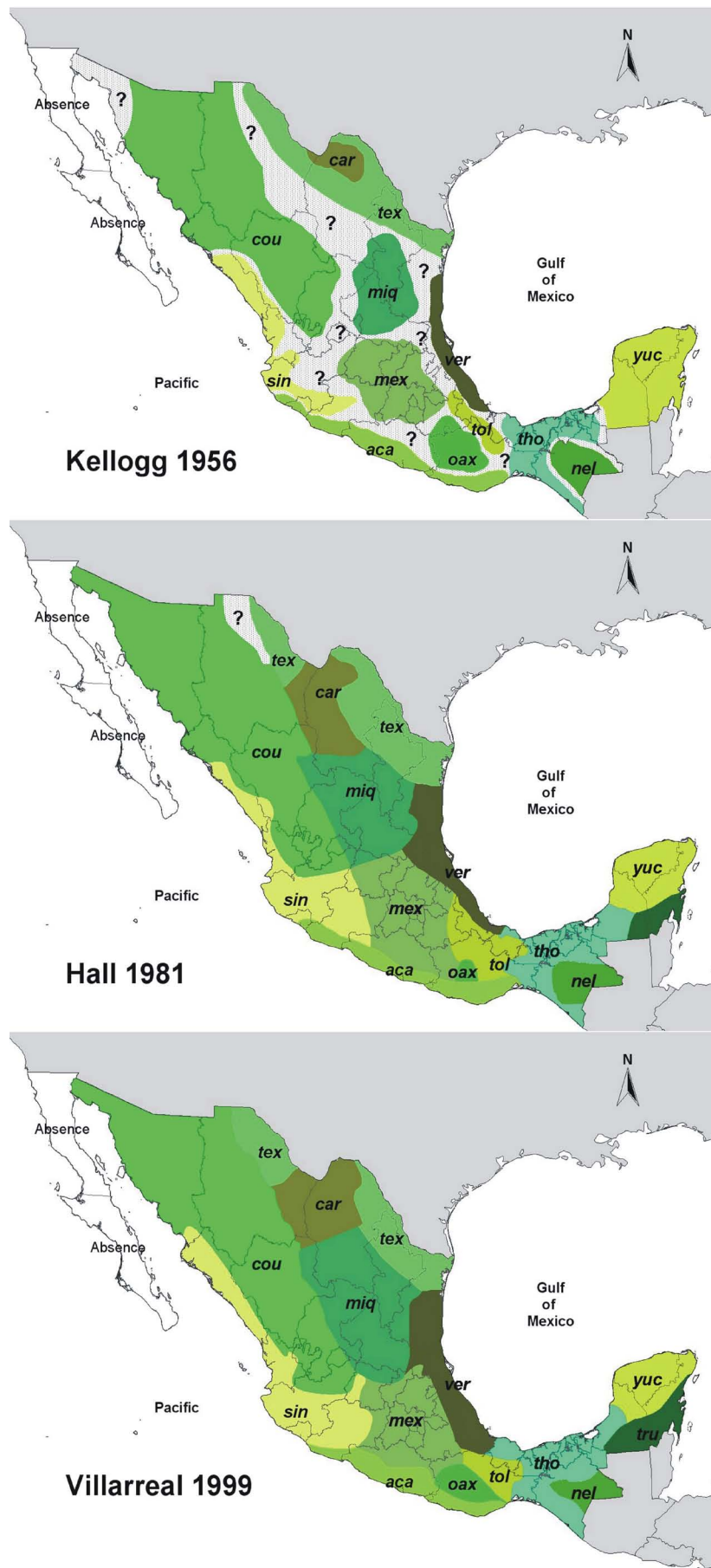


Figure 1. Distribution models of the white-tailed deer subspecies in Mexico, proposed by Kellogg (1956), Hall (1981) and Villarreal (1999). ? Indicates the regions with doubt as to which subspecies are present. In the three models, each subspecies is presented by the same colour.

by Smith (1991) in a monograph of the species, a mandatory reference. For Mexico, Villarreal (1999) published a distribution map of the subspecies which contains some important differences with respect to the other maps previously mentioned (Fig. 1c). This book is frequently consulted by deer managers in Mexico, and the author based the map on that proposed by Baker (1984), but introduced significant changes based on field experience with the species. How comparable are these distribution models? Could differences be expected in the number of subspecies and distribution surface in each federal entity depending of the distribution model used? Considering not the taxonomic characteristics, could the 14 subspecies be classified different according with the ecological conditions where they inhabit? Which are the conservation and management implications of this distribution models comparison? The objective of this study was to compare the biogeographic distribution maps for the subspecies of white-tailed deer in Mexico (Kellogg 1956; Hall 1981; Villarreal 1999), in order to: 1) Estimate the distribution areas of the subspecies on a national scale, by state and by vegetation type. 2) Identify related groups of subspecies in function with the principal vegetation types found in the country in order to define possible ecoregions, and 3) Analyse the implications of our results for the biology and management of the 14 subspecies found in Mexico. Since a model is a graphical, mathematical, physical, or verbal representation or simplified version of a concept, phenomenon, relationship, structure, system, or any aspect of the real world, and a species distribution map is a visual representation in which a biological taxon is spatially arranged in an area, in this paper we used distribution model as a synonym for distribution map.

Sources of information used.- Information relating to the distribution of the subspecies **Methods** of white-tailed deer in Mexico was gathered by consulting the maps of Kellogg (1956), Hall (1981), and Villarreal (1999). Information additional was consulted in Goldman and Kellogg (1940), Miller and Kellogg (1955), Hall and Kelson (1959), Taylor (1956), Rue (1979), Hall (1981), Smith (1991), Villarreal (1999) and Heffelfinger (2006). We also obtained the bibliographical databases published in Mandujano (2004) and Gallina *et al.* (2008, 2009). Biogeographic models of physiographic regions and vegetation in Mexico were taken from Rzedowski and Reina-Trujillo (1990), Arriaga *et al.* (1997), Palacio *et al.* (2000) and Morrone (2005). Further, several digital maps of the 32 federal entities of Mexico (31 states and one Federal District; hereinafter 'states') were obtained from several sources, including: State Political Divisions of INEGI (National Institute of Statistics and Geography), Biogeographic Regions (Arriaga *et al.* 1997), National Forest Inventory (Palacio *et al.* 2000), and Floristic Divisions (Rzedowski and Reyna-Trujillo 1990). All of the maps on which this study was based were obtained from the databases if INEGI (<http://mapserver.inegi.org.mx>) and CONABIO (National Commission for the Understanding and Use of Biodiversity, <http://www.conabio.gob.mx/informacion/gis/>).

Analysis of geographic and statistical data.- The three distribution maps used were digitalised using ArcView ver. 3.2 (ESRI 1999) and homogenised into a plane coordinate system in order to simplify the area calculations into. The metadata used were from a map generated by CONABIO (<http://www.conabio.gob.mx/informacion/>). The resulting

maps were geo-referenced to allow for simple, comparative referencing. Each of the distribution models was broken down into section by state and vegetation type, as mentioned earlier. Later, the areas of the different sections were calculated for each distribution model: the total area occupied by each subspecies, the area occupied by each subspecies in each state, and the area occupied by each subspecies in each vegetation type.

With the data we generated with regard to the area occupied by each subspecies within each vegetation type in each distribution model, we obtained percentages for each subspecies. With the percentage data for each vegetation type, we carried out Cluster Analyses (with the algorithm Euclidean Paired Group Similarity Index and Principal Component Analyses (PCA)), using correlation matrices and Euclidean Similarity Index for each distribution model using, in both cases, the statistics program PAST (Hammer *et al.* 2001). The results of both multivariate analyses allow related groups of subspecies, sharing similar vegetation types, to be defined. We defined these groups as possible ecoregions.

Based on the studies by Kellogg (1956) and Villarreal (2009), in Appendix 1. We show a description of the subspecies found in Mexico. However, it is important to note that the data presented are based on measurements taken from one, or just a few individuals. In the case of *O. v. toltecus* no data are available. We analysed the data from Appendix 1 using PCA with a correlation matrix, in order to know the relationships of the 13 Mexican subspecies (excluding *O. v. toltecus*, for which data was unavailable) in function of their size.

Results

Geographic distribution of subspecies. - The total distribution area for any given subspecies differed markedly, depending on the distribution model used (Table 1). The subspecies that differed in their distribution area, depending on the model were: *O. v. carminis*, *O. v. oaxacensis*, *O. v. miquihuanensis*, *O. v. nelsoni*, *O. v. toltecus*, *O. v. veraecrucis* and *O. v. yucatanensis*. If we do not consider the model used by Kellogg (1956), that underestimates distribution area, the subspecies with the greatest distribution area was *O. v. couesi*, which inhabits >500,000 km², followed by *O. v. miquihuanensis* (~200,000 km²), *O. v. sinaloae*, *O. v. mexicanus*, *O. v. texanus*, and *O. v. thomasi* (~172,000 to 106,000 km²). Other subspecies that varied between 60,000 and 106,000 km² were: *O. v. carminis*, *O. v. veraecrucis*, *O. v. yucatanensis* and *O. v. acapulcensis*. Finally, the remaining subspecies, *O. v. truei*, *O. v. toltecus*, *O. v. oaxacensis*, *O. v. nelsoni*, and were found to have the most restricted distribution areas (< 62,000 km²).

Distribution by federal entity. - The number of subspecies that could apparently be found in each state (federal entity) varied depending on the distribution model used, primarily varying with the use of the Kellogg (1956) model, which could be considered over-conservative (Table 2). The state with the greatest number of subspecies was Oaxaca, with 5 or 6, followed by Durango, Guanajuato, Guerrero, Jalisco and Veracruz with 3 or 4. Those states that contained only one subspecies were: Distrito Federal, Estado de México, Morelos, Tabasco, Tlaxcala and Yucatán. Of the 30 states considered, only in 13 did the number of subspecies found coincide among the three models. In the case

of the state of Aguascalientes, in Kellogg's (1956) model no subspecies are reported to be found because is considered problematic to define the geographic limits between subspecies (Fig. 1).

The subspecies that inhabited the greatest number of states was *O. v. mexicanus* (13 of

Subspecies	Distribution Model		
	Kellogg+	Hall	Villarreal
<i>O. v. acapulcensis</i>	66,014	69,248	64,077
<i>O. v. carminis</i>	26,315	94,031	102,390
<i>O. v. couesi</i>	451,518	548,802	528,928
<i>O. v. mexicanus</i>	121,544	171,574	143,697
<i>O. v. miquihuanensis</i>	94,250	175,221	223,362
<i>O. v. nelsoni</i>	38,142	40,500	27,750
<i>O. v. oaxacensis</i>	44,751	7,820	30,223
<i>O. v. sinaloae</i>	86,047	135,536	168,225
<i>O. v. texanus</i>	147,558	167,518	141,026
<i>O. v. thomasi</i>	76,939	105,737	117,363
<i>O. v. toltecus</i>	24,654	62,186	32,455
<i>O. v. truei</i>	-	26,378	46,189
<i>O. v. veraecrucis</i>	37,296	76,257	95,505
<i>O. v. yucatanensis</i>	127,965	84,612	71,753

Table 1. Surface (km²) occupied by each of the white-tailed deer subspecies, depending on the distribution model used. + According with the delimitation of the geographic distribution of each subspecies, this model sub-estimated the distribution surface for some subspecies; see text.

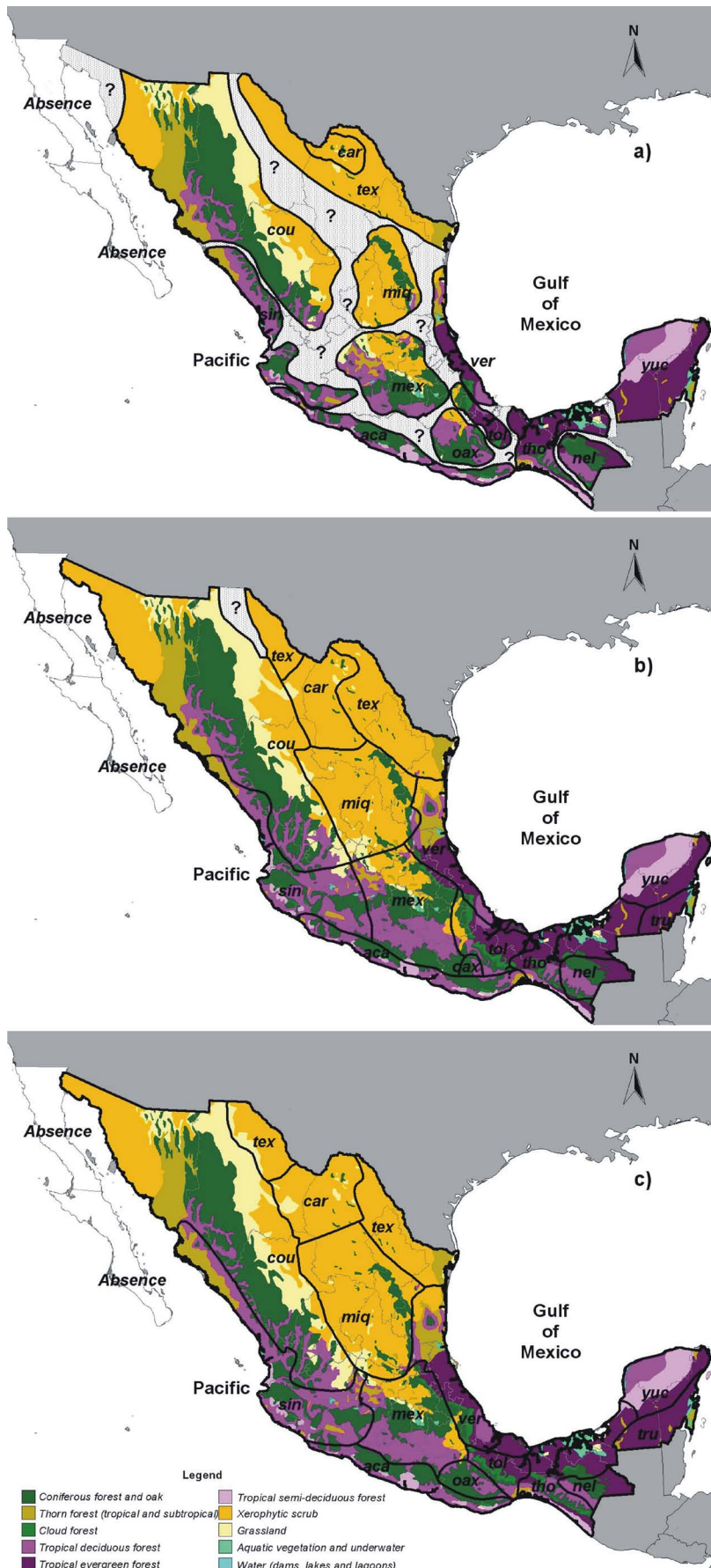
30, including Distrito Federal), followed by *O. v. couesi*, *O. v. miquihuanensis* and *O. v. sinaloae*. The only subspecies limited to just one state was *O. v. nelsoni*; while *O. v. oaxacensis* and *O. v. truei* were limited to two states (Fig. 1). Although we do not present the data, given the differences in the distribution of subspecies between models, the area inhabited by each subspecies in each state varied considerably.

Distribution by vegetation type.- It is important to note that of the 14 subspecies found in Mexico, only two (*O. v. texanus* and *O. v. carminis*) did not inhabit tropical forests; while all of the other 12 subspecies included at least some tropical forest within their distribution areas (Fig. 2 and Table 3). The subspecies *O. v. miquihuanensis* and *O. v. couesi*, considered to be principally found in shrub land and temperate forest respectively, were also found to marginally inhabit dry tropical forests. However, those subspecies with a greater part of their total distribution area occupied by deciduous or tropical dry forests were: *O. v. sinaloae*, *O. v. mexicanus*, *O. v. acapulcensis* and *O. v. yucatanensis*. In contrast, the subspecies *O. v. veraecrucis*, *O. v. toltecus*, *O. v. thomasi*, *O. v. nelsoni* and *O. v. truei*, inhabited tropical evergreen forest, tropical semi-deciduous forest and cloud forest.

Table 2. Distribution of the white-tailed deer subspecies in each state or federal entity in Mexico. + In these states, the number of subspecies is the same in the three models used

State	Distribution model		
	Kellogg	Hall	Villarreal
Aguascalientes		<i>cou, miq</i>	<i>cou, miq</i>
Campeche	<i>tho, yuc</i>	<i>tho, tru, yuc</i>	<i>tho, tru, yuc</i>
Chiapas+	<i>nel, tho</i>	<i>nel, tho</i>	<i>nel, tho</i>
Chihuahua+	<i>car, cou, tex</i>	<i>car, cou, tex</i>	<i>car, cou, tex</i>
Coahuila	<i>car, cou, miq, tex</i>	<i>car, miq, tex</i>	<i>car, miq, tex</i>
Colima	<i>aca, sin</i>	<i>aca, sin</i>	<i>sin</i>
Distrito Federal+	<i>mex</i>	<i>mex</i>	<i>mex</i>
Durango	<i>cou, sin</i>	<i>car, cou, miq, sin</i>	<i>car, cou, miq, sin</i>
Guanajuato	<i>mex</i>	<i>cou, mex, miq, sin</i>	<i>cou, mex, miq, sin</i>
Guerrero	<i>aca, mex, oax</i>	<i>aca, mex, sin</i>	<i>aca, mex, oax, sin</i>
Hidalgo	<i>mex</i>	<i>mex, ver</i>	<i>mex, ver</i>
Jalisco	<i>aca, cou, mex, sin</i>	<i>aca, cou, miq, sin</i>	<i>cou, miq, sin</i>
México+	<i>mex</i>	<i>mex</i>	<i>mex</i>
Michoacán+	<i>aca, mex, sin</i>	<i>aca, mex, sin</i>	<i>aca, mex, sin</i>
Morelos+	<i>mex</i>	<i>mex</i>	<i>mex</i>
Nayarit	<i>sin</i>	<i>cou, sin</i>	<i>cou, sin</i>
Nuevo León+	<i>miq, tex</i>	<i>miq, tex</i>	<i>miq, tex</i>
Oaxaca	<i>aca, oax, tho, tol</i>	<i>aca, mex, oax, tho, tol</i>	<i>aca, mex, oax, tho, tol, ver</i>
Puebla	<i>mex, oax, tol, ver</i>	<i>mex, tol, ver</i>	<i>mex, tol, ver</i>
Querétaro	<i>mex</i>	<i>mex, ver</i>	<i>mex, miq, ver</i>
Quintana Roo	<i>yuc</i>	<i>tru, yuc</i>	<i>tru, yuc</i>
San Luis Potosí	<i>mex, miq</i>	<i>mex, miq, ver</i>	<i>mex, miq, ver</i>
Sinaloa+	<i>cou, sin</i>	<i>cou, sin</i>	<i>cou, sin</i>
Sonora	<i>cou</i>	<i>cou</i>	<i>cou, sin</i>
Tabasco+	<i>tho</i>	<i>tho</i>	<i>tho</i>
Tamaulipas+	<i>miq, tex, ver</i>	<i>miq, tex, ver</i>	<i>miq, tex, ver</i>
Tlaxcala+	<i>mex</i>	<i>mex</i>	<i>mex</i>
Veracruz	<i>tho, tol, ver</i>	<i>mex, tho, tol, ver</i>	<i>mex, tho, tol, ver</i>
Yucatán+	<i>yuc</i>	<i>yuc</i>	<i>yuc</i>
Zacatecas+	<i>cou, miq</i>	<i>cou, miq</i>	<i>cou, miq</i>

Groups of subspecies by vegetation type.- Both PCA (Fig. 3) and Cluster Analysis (Fig. 4) gave similar results for all three distribution models. In general, PCA revealed a clear order of the subspecies *O. v. texanus*, *O. v. miquihuanensis*, *O. v. carminis* and *O. v. couesi* in function with the presence of shrub land in the north of Mexico; although *O. v. couesi* is more clearly associated with temperate forests. The subspecies *O. v. mexicanus*, *O. v. sinaloae*, *O. v. oaxacensis* and *O. v. acapulcensis* formed a group associated with temperate pine-oak forest and tropical dry forest, mostly in the Pacific region and the centre of the country. The subspecies *O. v. veraecrucis*, *O. v. thomasi*, *O.*



a).-Kellogg model

b).-Hall model

c).-Villarreal model

Figure 2. Distribution models of the white-tailed deer subspecies in Mexico within the principal vegetation types proposed by Rzedowski and Reyna-Trujillo (1990).

Table 3. Distribution potential (km²) of the white-tailed deer subspecies in each of the vegetation types by Rzedowski and Reyna-Trujillo (1990) and modified by CONABIO.

Subspecies	Vegetation types	Distribution model		
		Kellogg	Hall	Villarreal
<i>O. v. acapulcensis</i>	Temperate forest	26,038	26,592	29,751
	Thorn forest	969	2,408	156
	Cloud forest	1,221	1,225	1,221
	Tropical dry forest	26,874	28,986	23,692
	Tropical semi-deciduous forest	10,002	8,691	8,894
	Tropical rainforest	-	-	-
	Grassland	207	312	384
	Shrub land	-	-	-
<i>O. v. carminis</i>	Aquatic vegetation	-	-	-
	Temperate forest	783	1,429	1,585
	Thorn forest	-	-	-
	Cloud forest	-	-	-
	Tropical dry forest	-	-	-
	Tropical semi-deciduous forest	-	-	-
	Tropical rainforest	-	-	-
	Grassland	1,037	4,107	7,021
<i>O. v. couesi</i>	Shrub land	24,444	88,487	93,359
	Aquatic vegetation	-	-	-
	Temperate forest	146,339	173,891	173,912
	Thorn forest	57,047	56,989	42,842
	Cloud forest	-	-	-
	Tropical dry forest	31,342	57,725	46,453
	Tropical semi-deciduous forest	-	-	-
	Tropical rainforest	-	-	-
<i>O. v. mexicana</i>	Grassland	100,917	110,364	120,832
	Shrub land	115,426	149,177	143,746
	Aquatic vegetation	-	-	-
	Temperate forest	41,525	66,415	46,190
	Thorn forest	7,461	6,501	4,592
	Cloud forest	614	1,970	1,738
	Tropical dry forest	30,406	55,707	53,063
	Tropical semi-deciduous forest	-	811	-
<i>O. v. miquihuanensis</i>	Tropical rainforest	658	4,183	5,680
	Grassland	9,601	4,833	3,995
	Shrub land	29,139	28,955	26,195
	Aquatic vegetation	2,140	2,198	2,245
	Temperate forest	14,841	18,259	20,598
	Thorn forest	-	1,608	375
	Cloud forest	-	142	136
	Tropical dry forest	-	2,038	1,014
<i>O. v. nelsoni</i>	Tropical semi-deciduous forest	-	350	188
	Tropical rainforest	-	-	-
	Grassland	1,783	12,839	7,881
	Shrub land	77,626	139,986	193,169
	Aquatic vegetation	-	-	-
	Temperate forest	15,091	15,814	8,958
	Thorn forest	-	-	-
	Cloud forest	1,279	949	192
<i>O. v. oaxacensis</i>	Tropical dry forest	9,850	10,749	6,950
	Tropical semi-deciduous forest	-	24	-
	Tropical rainforest	11,922	12,747	11,911
	Grassland	-	-	-
	Shrub land	-	-	-
	Aquatic vegetation	-	-	-
	Temperate forest	20,823	5,232	20,313
	Thorn forest	-	-	16
	Cloud forest	1,029	105	196
	Tropical dry forest	17,526	2,483	9,495
	Tropical semi-deciduous forest	-	-	-
	Tropical rainforest	221	-	-
	Grassland	199	-	37
	Shrub land	4,953	-	166
	Aquatic vegetation	-	-	-

continuación Tabla 3...

Subspecies	Vegetation types	Distribution model		
		Kellogg	Hall	Villarreal
<i>O. v. sinaloae</i>	Temperate forest	27,647	39,765	43,082
	Thorn forest	9,584	12,455	29,633
	Cloud forest	668	683	684
	Tropical dry forest	41,443	70,861	85,208
	Tropical semi-deciduous forest	4,984	6,221	6,862
	Tropical rainforest	-	-	-
	Grassland	-	2,854	784
	Shrub land	-	-	-
<i>O. v. texanus</i>	Aquatic vegetation	1,182	1,996	2,279
	Temperate forest	903	1,111	439
	Thorn forest	7,239	8,820	8,426
	Cloud forest	-	-	-
	Tropical dry forest	-	237	-
	Tropical semi-deciduous forest	-	-	-
	Tropical rainforest	-	-	-
	Grassland	2,980	2,787	12,960
<i>O. v. thomasi</i>	Shrub land	135,504	153,911	117,857
	Aquatic vegetation	-	-	-
	Temperate forest	5,240	6,713	13,501
	Thorn forest	1,544	1,951	2,160
	Cloud forest	2,130	3,675	3,724
	Tropical dry forest	5,353	5,687	9,766
	Tropical semi-deciduous forest	4,725	4,998	8,092
	Tropical rainforest	41,739	65,725	65,134
<i>O. v. toltecus</i>	Grassland	2,441	2,844	2,932
	Shrub land	-	-	-
	Aquatic vegetation	11,814	11,791	12,183
	Temperate forest	4,419	13,601	5,161
	Thorn forest	-	-	826
	Cloud forest	3,441	7,556	5,551
	Tropical dry forest	1,000	7,789	4,136
	Tropical semi-deciduous forest	-	-	-
<i>O. v. truei</i>	Tropical rainforest	13,667	26,767	16,768
	Grassland	-	-	-
	Shrub land	1,919	6,270	12
	Aquatic vegetation	208	202	-
	Temperate forest	-	-	-
	Thorn forest	-	2,222	49,482
	Cloud forest	-	-	-
	Tropical dry forest	-	430	-
<i>O. v. veraecrucis</i>	Tropical semi-deciduous forest	-	-	-
	Tropical rainforest	-	19,924	39,729
	Grassland	-	-	-
	Shrub land	-	-	-
	Aquatic vegetation	-	1,876	881
	Temperate forest	800	3,751	9,109
	Thorn forest	6,835	17,268	18,934
	Cloud forest	1,619	1,524	4,390
<i>O. v. yucatanensis</i>	Tropical dry forest	7,248	13,140	16,869
	Tropical semi-deciduous forest	-	123	284
	Tropical rainforest	17,302	28,339	31,293
	Grassland	657	674	970
	Shrub land	1,616	9,597	12,953
	Aquatic vegetation	816	1,123	1,048
	Temperate forest	-	-	-
	Thorn forest	4,533	859	762
	Cloud forest	-	-	-
	Tropical dry forest	16,230	16,018	18,240
	Tropical semi-deciduous forest	33,509	33,104	31,733
	Tropical rainforest	67,228	31,709	21,401
	Grassland	50	-	-
	Shrub land	-	-	-
	Aquatic vegetation	3,838	1,800	1,594

O. v. toltecus, *O. v. truei* and *O. v. yucatanensis* are associated with tropical rain forest, semi-deciduous forest, cloud forest, thorn forest and aquatic and sub-aquatic vegetation in the southeast. Finally, the subspecies *O. v. nelsoni* was an intermediate subspecies between the temperate and dry forest group and the tropical rainforest and semi-deciduous group. With slight variations, this tendency was observed in all three models (Fig. 3).

Cluster Analysis revealed similar groups of subspecies, with slight differences. The main difference being that *O. v. couesi* was associated with the temperate/dry forest group, depending on the distribution model used (Fig. 4). Consequently, both PCA and Cluster Analysis defined three distinct groups of subspecies, clearly associated with vegetation types. This classification into three groups can be considered as a proposal for distinct ecoregions, or possible ecotypes for white-tailed deer in Mexico: the ecoregion that includes the shrub land of the northeast; that which includes the temperate forests and tropical dry forests of the Pacific and central country; and that which includes the tropical rain forests, semi-deciduous forests and cloud forests of the Gulf and southeast of the country.

Size of subspecies.- Analysis by PCA demonstrated that 13 of the 14 subspecies found in Mexico (excluding *O. v. toltecus*, for which data was unavailable) can be organised by size, based on total length, chest height and antler measurement (Fig. 5). The largest subspecies was *O. v. texanus*, followed by *O. v. carminis*, *O. v. miquihuanensis*, *O. v. veraecrucis*, *O. v. mexicanus* and *O. v. couesi*; while the smallest subspecies were *O. v. sinaloae*, *O. v. thomasi*, *O. v. yucatanensis*, *O. v. truei*, *O. v. oaxacensis*, *O. v. acapulcensis* and *O. v. nelsoni*.

Discussion

Biological implications.- The maps, or distribution models, proposed by Kellogg (1956), more than 50 years ago, Hall (1981), which was widely accepted, and Villarreal (1999), which is the most commonly used map in Mexico, are not exempt from errors in their definitions of the biogeographical limits between subspecies. To reduce this, Kellogg (1956) presented distribution areas in which the geographical limits between subspecies were discontinuous. In contrast, Hall (1981) extended the geographic distribution of each subspecies and proposed clearly defined limits. However, these limits were defined on the basis of the author's own criteria and not necessarily on the basis of quantitative studies. Further, this author recognised a fourteenth subspecies, *O. v. truei* (= *nemoralis*), located in the southeast of the country. Another important difference between the models is that Hall (1981) significantly increased the distribution area of *O. v. carminis*, which Kellogg (1956) reported as found only in a highly restricted area of the Sierra del Carmen, Coahuila. Morphometric studies of *O. v. carminis* by Krausman *et al.* (1978) confirmed the difference with other subspecies; but its geographical limits its unknown. By increasing the distribution area, Hall (1981) introduced this subspecies into areas of shrub land, where *O. v. texanus* and *O. v. miquihuanensis* were also found. Another difference between the models is that, while Kellogg (1956) presents a wide-ranging distribution area for *O. v. oaxacensis*, Hall (1981) reduces this distribution to a very small area of the Valles Centrales of Oaxaca. This means that distinguishing *O. v. oaxacensis* from *O. v. toltecus* can be complicated and their areas of sympatry can be hard to define.

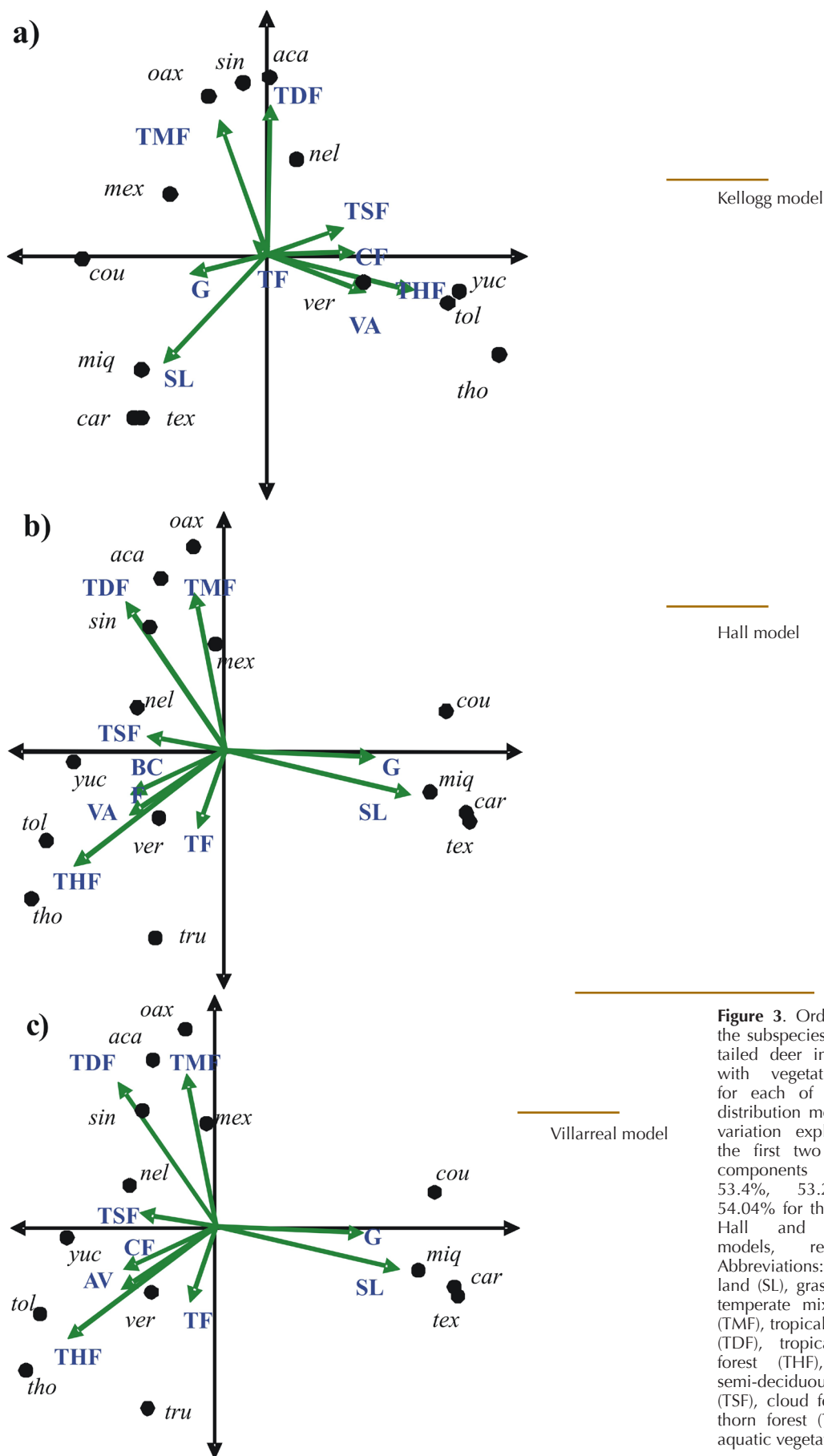


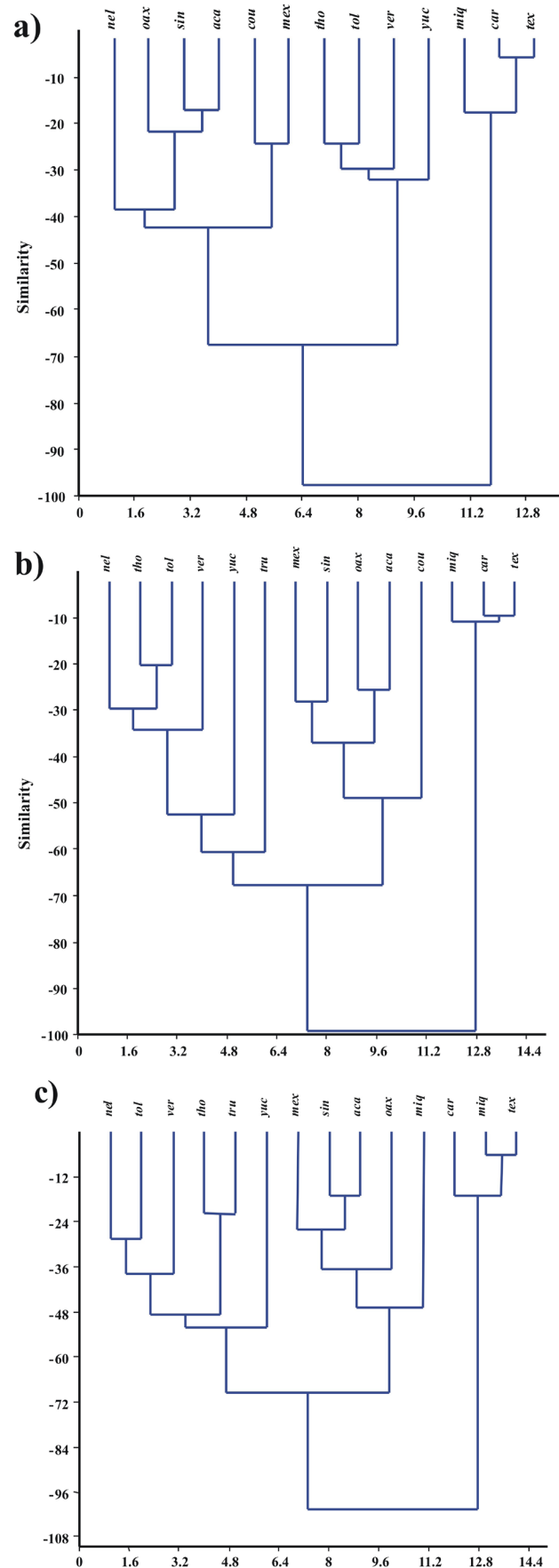
Figure 3. Ordination of the subspecies of white-tailed deer in function with vegetation type for each of the three distribution models. The variation explained by the first two principal components were 53.4%, 53.2% and 54.04% for the Kellogg, Hall and Villarreal models, respectively. Abbreviations: shrub land (SL), grassland (G), temperate mixed forest (TMF), tropical dry forest (TDF), tropical humid forest (THF), tropical semi-deciduous forest (TSF), cloud forest (CF), thorn forest (TF), semi-aquatic vegetation (AV).

Kellogg model

Hall model

Villarreal model

Figure 4. Classification of the subspecies of white-tailed deer in function with vegetation type for each of the three distribution models, following the algorithm Euclidean Paired Group Similarity Index. The coefficients of correlation were 0.93, 0.91 and 0.87 for the Kellogg, Hall and Villarreal models, respectively.



For example, Ortiz-Martínez *et al.* (2005) and Briones and García (2005) identify *O. v. oaxacensis* for the north of the state of Oaxaca. The map proposed by Villarreal (1999) identifies 14 subspecies, but modifies their distribution limits. For example, in the case of *O. v. oaxacensis* important changes are made, while the distribution of *O. v. sinaloae* is extended to the south of Sonora and the distribution limits are modified for *O. v. texanus*, *O. v. miquihuanensis* and *O. v. carminis* (Fig. 1). These differences among distribution models were evident when we estimate the area of distribution at national and federal state level (Table 2). In some cases, even the number of subspecies by federal entity was different depending of the model used (Table 1). Also, these differences are evident in the vegetation type occupied by each subspecies (Table 3).

From an ecological perspective, our results suggests that the 14 subspecies can be grouped into three ecoregions: north-eastern shrub land (*O. v. carminis*, *O. v. miquihuanensis* and *O. v. texanus*), Pacific and central temperate and tropical dry forests (*O. v. acapulcensis*, *O. v. couesi*, *O. v. mexicanus*, *O. v. oaxacensis* and *O. v. sinaloae*), and Gulf-southeast tropical humid, sub-deciduous and cloud forests (*O. v. nelsoni*, *O. v. thomasi*, *O. v. toltecus*, *O. v. truei*, *O. v. veraecrucis* and *O. v. yucatanensis*). An ecoregion is defined as a relatively large area of land or water that contains a geographically distinct assemblage of natural communities and environmental conditions (WWF 1999). These communities share a large majority of their species, dynamics, and environmental conditions, and function together effectively as a conservation unit at global and continental scales (Dinerstein *et al.* 1995). Several standard methods of classifying ecoregions have been developed, with climate, altitude, and predominant vegetation being important criteria (Olson *et al.* 2001). Because ecoregions are defined by their shared biotic and abiotic characteristics, they represent practical units on which to base conservation planning. For example, a map of Mexican ecoregions was presented by Dinerstein *et al.* (1995).

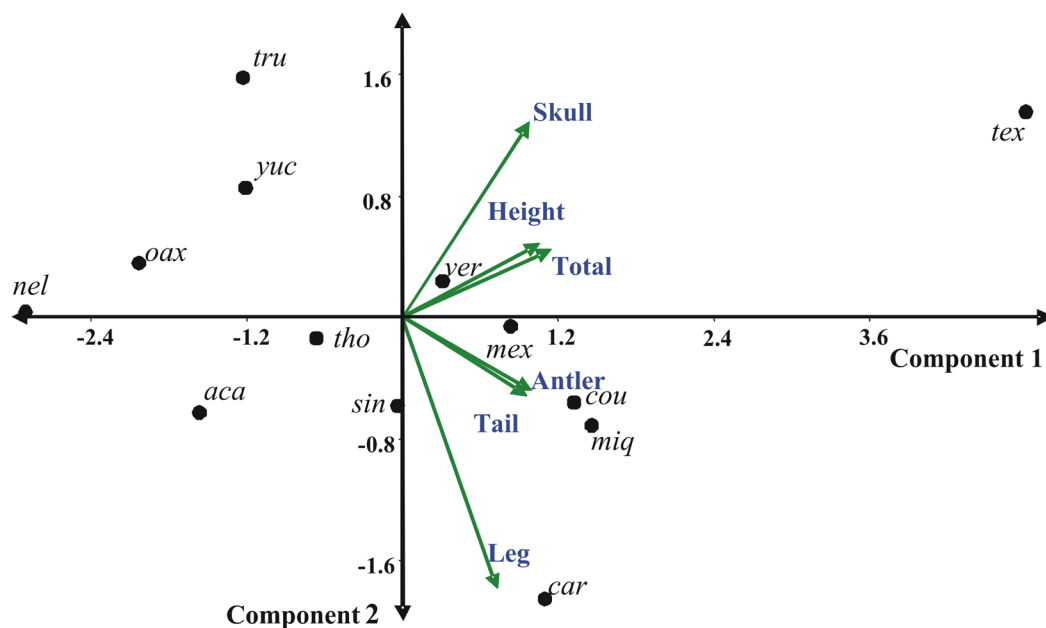


Figure 5. Ordination of the white-tailed deer subspecies in Mexico in function with the morphological characteristics described in Table 1. The variation explained by the first two principal components was 79.9%. The first component (60%) characterises, in the right side of the graph, those subspecies of greater size expressed as the total length (total), height of shoulder (height) and antler size (antler).

The use of ecoregions for deer classification and management has also been suggested for mule deer (Heffelfinger *et al.* 2006). The 11 subspecies of mule deer and black-tailed deer are distributed throughout western United States and the northern Mexican states. With this wide latitudinal and geographic range, mule deer occupy a great diversity of climatic regimes and vegetation associations, resulting in an incredibly diverse set of behavioural and ecological adaptations that have allowed this species to succeed. Within the geographic distribution of mule deer, however, areas can be grouped together into ecoregions, within which deer populations share certain similarities. With regard to the issues and challenges that deer managers face, deVos *et al.* (2003) has designated seven separate ecoregions: California Woodland Chaparral, Colorado Plateau Shrubland and Forest, Coastal Rain Forest, Great Plains, Intermountain West, Northern Boreal Forest, and Southwest Deserts. The diversity among the ecoregions presents different challenges to deer managers and guidelines for managing habitat must address these differences (Heffelfinger *et al.* 2003).

Figure 6. Classification of the subspecies of white-tailed deer in Mexico according to hunting regions by Villarreal (2009) and ecoregions proposed by Mandujano *et al.* (this paper).

Subspecies	Hunting regions	Ecoregions
<i>O. v. texanus</i> <i>O. v. carminis</i> <i>O. v. miquihuanensis</i>	Texas white-tailed deer Carminis white-tailed deer Chihuahuan Desert white tailed deer	Northeastern shrub lands
<i>O. v. couesi</i> <i>O. v. sinaloae</i> <i>O. v. acapulcensis</i> <i>O. v. mexicanus</i> <i>O. v. oaxacensis</i>	Coues white-tailed deer North Pacific white-tailed deer South Pacific white-tailed deer Mexican white-tailed deer	
<i>O. v. toltecus</i> <i>O. v. thomasi</i> <i>O. v. nelsoni</i> <i>O. v. truei</i> <i>O. v. yucatanensis</i> <i>O. v. veraecrucis</i>	Southeastern white-tailed deer Gulf white-tailed deer	

For the distribution of white-tailed deer subspecies in the United States, Deckman (2003) classified the 16 subspecies into six regions: Western Region I (*O. v. couesi*, *O. v. leucurus*, and *O. v. ochrourus*). North Central Region II (*O. v. dacotensis*). Central Plains Region III (*O. v. macrourus* and *O. v. texanus*). Gulf Coast Region IV (*O. v. clavium*, *O. v. mcilhennyi*, *O. v. osceola* and *O. v. seminolus*). Atlantic Islands and Southeastern Region V (*O. v. hiltonensis*, *O. v. nigribarbis*, *O. v. taurinsulae*, *O. v. venatorius* and *O. v. virginianus*), and Northeastern Region VI (*O. v. borealis*). However, this author also recognised that white-tailed deer subspecies could overlap in many areas and that the genetic pool in these areas is likely to be mixed.

For Mexico, the Comisión de Flora y Fauna Silvestres de Nuevo León (CEFFSNL) recently proposed to Safari Club International the inclusion of nine hunting regions, with the objective of recognising all of the 14 different subspecies of white-tailed deer in Mexico on an international scale as different sport hunting trophies (Villarreal 2009). This proposal comes from the fact that the Safari Club International and Boone and Crockett

Club only recognise five subspecies. The hunting regions were defined on the basis of antler size, in such a way that males of the different subspecies are competitive within any given geographic region with particular ecological characteristics. The hunting regions proposed by Villarreal (2009) are presented in figure 6, in which we also compare the classification of the ecoregions proposed in this article. This figure represents a synthesis of both hunting and ecological view of the 14 subspecies in Mexico, and we propose it as a framework for management and conservation actions.

The taxonomic rank of subspecies has been the subject of long-running controversy (Mayr 1982). Traditionally, subspecies have been recognised on the basis of discontinuities in the geographical distribution of phenotypic traits. It has long been established that populations on islands encounter a physical impediment to gene-flow between local populations, and it is therefore expected that such populations may diverge in isolation (Mayr and Ashlock 1991). In contrast, continental subspecies will often have geographical ranges that directly adjoin, or even overlap, those of conspecific subspecies, and thus any phenotypic adaptation to local environments will need to take place in the face of gene flow (e. g., ecotype). Throughout the geographic range of white-tailed deer in Mexico, we see a lot of variation in body size, pelage colour, antler shape, and other attributes (Kellogg 1956, Villarreal 2009). For example, subspecies in the southern latitudes are generally smaller in body size than those in the north, and those inhabiting open habitats appear lighter in colour than those in heavily forested habitats. As was the case with mule deer *O. hemionus* (Heffelfinger 2006), the geographic range of several white-tailed deer subspecies was drawn somewhat arbitrarily. In fact, the purported differences between subspecies were often based on subjective opinions regarding characteristics or measurements of only one or a few specimens. Fortunately, recent advances in DNA analysis techniques now allow researchers to evaluate genetic data in ways that provide managers with meaningful ecological management units on an ecoregion scale. Therefore, given the lack of quantitative morphometric and genetic data for the subspecies, it is impossible to confirm the taxonomic validity of the subspecies present in the country. Further, the absence of phylogeographic studies means that the redefinition of the geographic limits between subspecies is not possible. Indeed, when faced with a species with such capacity for adaptation to different environments, it is hard to define where the distribution of one subspecies ends and another begins (i.e., zones of sympatry) as, basically, some kind of geographic (mountains, rivers, drastic changes in vegetation type) or climatic barrier ought to exist in order to clearly define subspecies. However, in some cases we may expect to find a gradient of variations, or cline, from one subspecies to the next and, therefore, the distribution limits between them become arbitrary.

Management implications.- Given the lack of data supporting the validity of the biogeographic limits of the subspecies, there should be strict control over the deliberate, or even accidental, movement of subspecies to localities where they have not been historically reported. One important problem is posed by those regions where more than one subspecies converge and the criteria to define the geographic limits between the subspecies are arbitrary. The translocation of animal species has resulted in severe consequences for conservation, such as interspecific competition and the introduction of

diseases and parasites (Waldrup *et al.* 1990; Kock *et al.* 2007). For example, Galindo and Weber (1994) reported incidences of dystocia (difficulty in parturition), probably caused by the translocation of some individuals of other subspecies, such as *O. v. texanus*, into the distribution range of *O. v. couesi*, in La Michilía, Durango. Unfortunately, some programmes translocate individuals, principally of the subspecies *O. v. texanus*, to other parts of the country, with the idea of “improving the breed”, mainly the size of their antlers. In such a case, Storfer (1999) suggested that knowledge of gene flow rates and understanding ecological differences among populations is necessary before embarking on a program to artificially enhance gene flow. This situation could change in the medium term. For example, recently, the CEFFSNL stated that although they had always supported and developed cynegetic activities for the benefit of the economy, they would not agree to support the transfer of individuals of the subspecies *O. v. texanus* from the north of Mexico (Coahuila, Nuevo León and Tamaulipas) to other parts of the country, even under regulated management schemes such as in UMAs. This is to avoid cross breeding between subspecies that are adapted to differing ecological conditions and that form part of the biological heritage of the country (Villarreal 2009). Our classification of the 14 subspecies into three possible ecoregions suggests the more critical action to translocate deer among ecoregions than inside of the same ecoregion. Ecoregions classification implicates a local adaptation to similar ecological conditions.

From a conservation perspective, Phillimore and Owens (2006) suggest that subspecies may be of considerable conservation value, as proxies for the sub-structure found within species. They suggest that the conservation value of subspecies is likely to be greatest in situations where molecular data is absent, a scenario that is encountered in the white-tailed deer in Mexico. However, there is an urgent need to integrate biographic models and molecular studies (e. g., Moodley and Bruford 2007) as a framework for the conservation of white-tailed deer at the national and continental scale. Thus, it is imperative to obtain data on the geographical variation of white-tailed deer throughout the country. The studies must investigate both morphological and genetic variation. This evaluation will provide not only a basis for conservation efforts (Gallina and Mandujano 2009), but also help solidify the range of different subspecies into and among ecoregions. Clear delineation of the boundary among subspecies is an issue that the governmental offices (SEMARNAT, DGVs, CONANP, CONABIO) and international agencies such as Safari Club International must address in order to maintain the integrity of the different geographical haplotypes and for trophy record books.

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Appendix 1. Description of the subspecies of white-tailed deer present in Mexico, based on Kellogg (1956) and Villarreal (2009). In parenthesis is show the abbreviations of subspecies used in the following tables and figures.

Subspecies	Type locality	Measurements (mm)					Antler	Minimum score for trophy hunting (a= atypical, t= typical)	Pelage
		Total length	Tail	Feet	Height	Cranial length			
<i>Odocoileus virginianus acapulcensis</i> (Caton, 1877) (aca)	Acapulco, Guerrero, México	1394	195	385	677	224	Small, frequently reduced to simple spikes even in adults	70 t, 90 a	Varying from drabish Snuff Brown to Sayal Brown, the banded hairs tending to produce a grizzled effect
<i>Odocoileus virginianus carminis</i> Goldman and Kellogg, 1940 (car)	Botellas Cañón, Sierra del Carmen, northern Coahuila, México	1520	220	490	793	246	Moderately spreading with short spikes	70? t, 90? a	A drab colored subspecies. Upperparts in winter pelage a mixture of brownish black and Drab Gray.
<i>Odocoileus virginianus couesi</i> (Coues and Yarrow, 1875) (cou)	Rancho Santuario, northwestern Durango, México	1530	270	415	890	241	8-10 spikes, with the tendency of the main branches to form oval in the front part	70 t, 90 a	Brownish gray or drab to dull cinnamon or cinnamon buff. In winter pelage the individual hairs, especially on the back, are black at tips with a grayish sub-terminal band, below which they are dark brown
<i>Odocoileus virginianus mexicanus</i> (Gmelin, 1788) (mex)	Valley of México, México	1550	235	410	915	241	4 to 8 spikes, branches curve to the front	60? t, 70? a	General coloration of upperparts Mummy brown to Cinnamon brown
<i>Odocoileus virginianus miquihuensis</i> Goldman and Kellogg, 1940 (miq)	Sierra Madre Oriental, near Miquihuana, southwestern Tamaulipas, México	1530	270	420	820	247	similar to "texano" but small and short spikes	80? t, 90? a	Darker, especially over median dorsal area. A grizzled Drab subspecies; with conspicuous brownish black upper side of tail; upperparts in worn winter pelage a mixture of Snuff Brown and Buff. Summer pelage more brownish.
<i>Odocoileus virginianus nelsoni</i> Merriam, 1898 (nel)	San Cristobal, highlands of Chiapas, México	1346	170	371	658	224	Antlers with main beam straighter, directed backward, instead of curving forward.	40? t, 50? a	A dark brownish gray high mountain subspecies

continuación **Appendix 1...**

<i>Odocoileus virginianus oaxacensis</i> Goldman and Kellogg, 1940 (oax)	Mountains 15 miles west of Oaxaca, México	1340	170	362	750	230	4 to 8 spikes, branches curve to the front	60? t, 70? a	Present a grizzled pattern of coloration
<i>Odocoileus virginianus sinaloae</i> J. A. Allen, 1903 (sin)	Escuinapa, southern Sinaloa, México	1490	223	415	820	234	Antlers longer with more numerous points	unknown	Varying in color from near Sayal Brown to drabdish dilute Snuff Brown, mixed with black over back
<i>Odocoileus virginianus texanus</i> (Mearns, 1898) (tex)	Fort Clark, Kinney County, Texas, USA	1829	254	420	1048	288	The biggest sized of antlers of all Mexican subspecies	100 t, 125 a	Pelage short, color of upper parts in winter pelage inclining toward gray, usually with grizzled pattern approaching grayish light cinnamon drab
<i>Odocoileus virginianus thomasi</i> Merriam, 1898 (tho)	Huehuetan, Chiapas, México	1544	180	425	800	238	4 to 8 spikes, vertical branches slightly to back	40? t, 50? a	Predominant tone of upperparts Tawny or Cinnamon Brown
<i>Odocoileus virginianus toltecus</i> (Saussure, 1860) (tol)	Orizaba, Veracruz, México	1440		71			4 to 8 spikes, vertical branches slightly to back	40? t, 50? a	Characterized by dark
<i>Odocoileus virginianus truei</i> Merriam 1898 (tru)	Sibube, Panamá	1422	178	360	825	253	Antlers in adults varying from simple spikes to those having two or three points near the tip.		
<i>Odocoileus virginianus veraecrucis</i> Goldman and Kellogg, 1940 (ver)	Chijol, northern Veracruz, México	1560	220	400	800	247	small and closer	60? t, 70? a	with tail usually more or less distinctly blackish bone brown on upper side sub terminally.
<i>Odocoileus virginianus yucatanensis</i> (Hays, 1872) (yuc)	Throughout Yucatán and the southern part of México	1470	228	365	647	251	Relatively straight, simply branched.	40? t, 50? a	Paler less. Finely grizzled wood brown to Mikado brown upperparts

