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FACTORS INFLUENCING THE DISTRIBUTION OF THE NEOTROPICAL VINE SNAKE (*Oxybelis aeneus*) IN ARIZONA AND SONORA, MÉXICO

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Abstract. In southern Arizona and northern Sonora, the neotropical vine snake (*Oxybelis aeneus*) lives in temperate oak woodland, canyon riparian woodland, desert-grassland, and pine-oak woodland communities at 1160 to 1650 m elevation. Perennial plants in an oak woodland habitat in the Atascosa Mountains in the center of the Arizona distribution of the species, have strong biogeographical affinities with the grasslands and woodlands of the southwestern United States and the northern Sierra Madre Occidental in México. The plant communities are wholly different in vegetation structure and only 2.2% of the Atascosa site perennials reach tropical lowlands near Alamos in southern Sonora. The restricted area occupied by *O. aeneus* in southern Arizona is characterized by relatively mild winter temperature and relatively high annual precipitation that falls mainly as summer monsoon rain. The northerly limit of *Oxybelis* in southern Arizona is apparently limited by winter freezing above 1650 m and by summer aridity below 1160 m. The northward range limit is associated with final failure of tropically-evolved morphology, physiological tolerances, and behavior under continental physiographic-climatic constraints.

Resumen. En el sur de Arizona y en el norte de Sonora, la culebra bejuquillo neotropical *Oxybelis aeneus* vive en ambientes no tropicales—en comunidades de bosques de encino, cañones con vegetación riparia, pastizales desérticos, y bosques de pino y encino entre 1160 y 1650 m. Las plantas perennes en las comunidades de bosques de encino en un sitio en la Sierra Atascosa, cuya extensión está localizada en el centro de distribución de la especie en Arizona, tienen fuertes afinidades biogeográficas con los pastizales y bosques del suroeste de los Estados Unidos y el norte de la Sierra Madre Occidental en México. Estas comunidades de plantas son totalmente diferentes en cuanto a estructura de la vegetación y solo un 2.2% de las plantas perennes en las Atascosas sitio llegan a las tierras bajas tropicales cerca de Alamos en el sur de Sonora. La limitada área ocupada por *O. aeneus* en el sur de Arizona está caracterizada por una temperatura invernal relativamente moderada y una precipitación anual relativaménte alta que calle principalmente como lluvias monzónicas veraniegas. El límite norte de *Oxybelis* en el sur de Arizona está determinado por temperaturas invernales heladas encima de elevación de 1650 m y por una aridez veraniega debajo de 1160 m. El límite norteño de distribución está asociado con la falla final de morfología, tolerancias fisiológico, y conducta que han evolucionado en los trópicos bajo restricciones fisiográficas y climáticas continentales.

Key words: *Oxybelis aeneus*; Natural history; Ecology; Habitat; Distribution; Arizona; Sonora; Range limits; Biogeography.

Oxybelis aeneus (neotropical vine snake, guirotillo, bejuguillo, or chicotera) is an extremely elongate, slender snake found in much of the Neotropics from Brazil to southern Arizona (Bogert & Oliver 1945). It is a superb example of a species that is well-adapted to tropical forest and shrub communities

(Henderson & Binder 1980). However, in local areas, especially in north-central Sonora and southern Arizona, it lives in non-tropical desert-grassland and woodland habitats. Although *O. aeneus* was reported from Arizona more than 60 years ago (Barbour & do Amaral 1926; Vorhies 1926), it is a secretive snake that is only occasionally encountered in the northernmost part of its wide distribution in the Americas. Here, we summarize its distribution and habitat in Arizona and Sonora, discuss environmental parameters and ecological constraints, and propose hypotheses on the controls of its northern range limit.

METHODS

Locality records for *Oxybelis aeneus* from Arizona and Sonora were compiled from specimens deposited and other museum records on file in the University of Arizona and Arizona State University herpetological collections, from the literature, and reliable personal observations (Fig. 1). Table 1 summarizes the Arizona localities and lists the various collections surveyed. Habitat summaries were derived from these sources and our field knowledge of the localities.

The perennial flora of an *Oxybelis* locality in the Atascosa Mountains east of Nogales was analyzed to assess the biogeographical affinities of a typical Arizona habitat. Climatic records from stations in Arizona (Sellers & Hill 1974) and Sonora (Hastings & Humphrey 1969) were analyzed in determining characteristic climatic parameters in the northern range of *O. aeneus.*

DISTRIBUTION AND HABITAT

Oxybelis aeneus is a widespread tropical snake found throughout the Neotropics from South America to southern Arizona (see Keiser 1982). This snake is most abundant in various tropical and subtropical communities at lower elevations, but has been taken up to 2500 m in oak forest, at 1700 m in Michoacan, and in second growth timber at 1710-1830 m in Oaxaca (Keiser 1967, 1982). In Arizona, it is only found in the extreme south-central part of the state (Lowe et al. 1986; Fig.1). The names of the mountains in this area west of Nogales in Santa Cruz County are confusing. The Atascosa Mountains are a prominent northwest-southeast ridge that includes Atascosa Peak. The Tumacacori Mountains are the northern portion of this ridge. The Pajarito Mountains are the ridges along the border that include Calabasas, Walker, and Peña Blanca canyons, which drain easterly to the Santa Cruz River. Some authors have extended the Pajarito Mountains as far as Sycamore Canyon although Sycamore drains the western slopes of the Atascosa Mountains and flows south into the Río Concepcion drainage in Sonora (Toolin et al. 1979). Mule Ridge and Montana Peak near Ruby, California Gulch, and Warsaw Canyon form a separate area just to the west. Brown & Lowe (1980) assigned the entire area to the Pajarito Mountains. For convenience here we will refer to the entire area as the Atascosa Mountains.

Most of the Arizona records for *O. aeneus* in Table 1 are in Santa Cruz County. New records in this paper that expand the range are from Arivaca Lake northwest of Ruby (UAZ 46646; K. Stim pers. comm. 1989), from Agua Caliente Cave (W. D. P. Peachey, pers. comm. 1988) and Montosa Canyon (J. Palting, pers. observ. 1987) in the Santa Rita Mountains, and from Thomas Canyon in the Baboquivari Mountains (K. Cumming, pers. comm. 1989). An early presumption by Stebbins (1954) that *Oxybelis* occurred in the mountainous parts of Cochise County has not been verified; his latest distribution map (Stebbins 1985) is quite accurate.

One of the first *O. aeneus* from Arizona was collected "by Mr. W.W. Akers of Tucson, who states that it was captured in the edge of this city" (Vorhies 1926). Subsequent authors have tended to discount the Tucson record as doubtful if not erroneous (Lowe 1964; Fowlie 1965; Keiser 1967; Lowe et al. 1986). It is worth noting, however, that in 1925, the Santa Cruz River, now a dry wash in its northern reaches, was a permanent stream with well developed riparian gallery forests and mesquite bosques from Nogales to north of Tucson (Hastings & Turner 1965). The Santa Cruz provided a potential riparian corridor northward for *Oxybelis* living in canyons draining the Atascosa and Santa Rita Mountains. Tucson is bounded on the north and east sides by the massive Santa Catalina and Rincon Mountains. A number of subtropical plants such as feather bush (*Lysiloma microphyllum thornberi*) have isolated, relict populations in rocky canyons and on their south and southwest slopes. A relict population of *O. aeneus* in any of these areas could well have been extirpated in the subsequent 60 years as the water table dropped, streams dried, and Tucson expanded in the valley. As for other populations of reptiles, the records in Table 1 show that *Oxybelis* may have been more common in Arizona

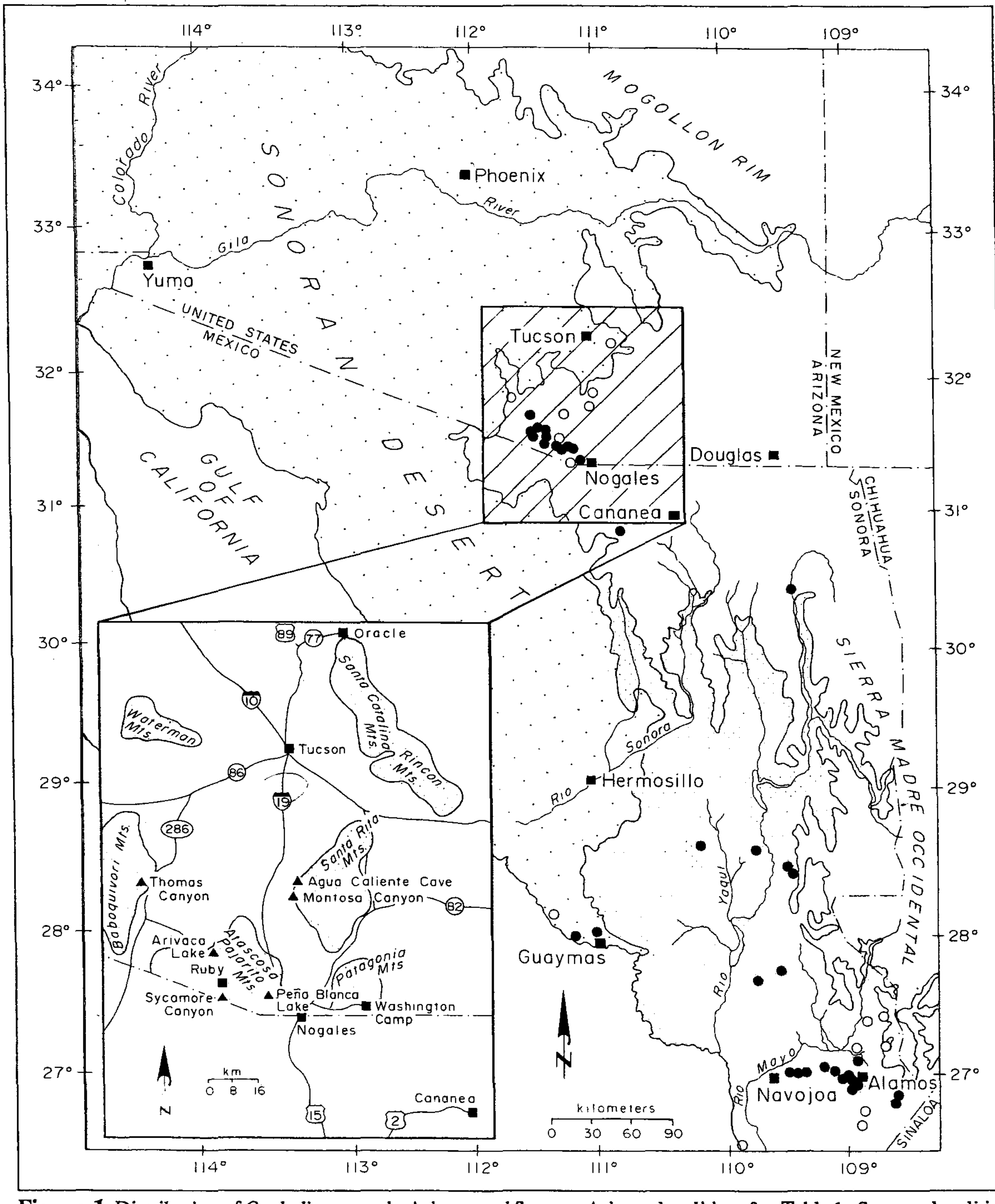

Figure 1. Distribution of *Oxybelis aeneus* in Arizona and Sonora. Arizona localities after Table 1. Sonoran localities from specimens and records on file in the University of Arizona Herpetological Collection. Solid circles = museum specimens; open circles = reliable observations; half circle = old literature record out of present range. Boundary of Sonoran Desert (light stipple) follows Shreve (1964). Subtropical and tropical areas (heavy stipple) include both Sinaloan Thornscrub and Sinaloan Deciduous Forest of Brown & Lowe (1980).

in the 1920s to 1940s than it is today.

The Arizona records of *Oxybelis* are mostly from 1160 to 1650 m elevation. The 1770 m upper elevational limit given by Lowe et al. (1986) is based on label data on the specimen from ca. 1.6 km northwest of Washington Camp in the Patagonia Mountains, which we estimate to be approximately 1650 m. Literature accounts also may be somewhat in error on the side of lower ranges: e.g. 610-1220 m in Wright & Wright (1957) and 915-1220 m in Fowlie (1965). If the species occurred historically along the Santa Cruz River (730-1035 m) or in canyons near Tucson (975-1370 m), *Oxybelis* previously reached still lower areas in riparian habitats in southeastern Arizona. However, the snake does not occur at 35-610 m elevation in the more arid Sonoran Desert in southwestern Arizona, although it reaches sea level in southern Sonora.

Habitat in Arizona

In Arizona, *Oxybelis aeneus* has been found in a number of habitats including desert-grassland, oak woodland, and canyon riparian woodland; there are no tropical habitats in southern Arizona. The Patagonia Mountains locality supports a more mesic pine-oak woodland dominated by oaks in association with border pinyon (*Pinus discolor*) and Chihuahua pine (*P. leiophylla*). A northern Sonoran specimen from 58 km west of Cananea on the road to Imuris was from a similar habitat at 1430 m with oak woodland in a creek bottom and grassy hillsides above (T. Walker, pers. comm. 1988; UAZ 1679). Other observations for northern Sonora are in oaks and junipers (J. T. Marshall, pers. comm. 1956). Records and observations of *O. aeneus* in central and southern Sonora are all in montane tropical deciduous forest or lowland subtropical communities even though woodlands dominated by tropical oaks such as Chihuahua (*Quercus chihuahuensis*) and cusi (*Q. albocincta*) oaks occur as low as 760 to 915 m in southern Sonora (Gentry 1942).

Most authors have associated *Oxybelis* in Arizona with trees, shrubs, or woody vines (Vorhies 1926; Campbell 1934; Goodding 1946, 1961; Wright & Wright 1957; Lowe 1964; Fowlie 1965; Lowe et al. 1986); a few have been found crossing open ground in Arizona and adjacent Sonora including both dirt and asphalt paved roads. Lowe (1964) and Lowe et al. (1986) noted that it lives in both upland and riparian communities. Arizona observations and reports of *Oxybelis* have been in riparian plants including Arizona sycamore (*Platanus wrightii*) and willow (*Salix* sp.; Goodding 1946, 1961), canyon grape (*Vitis arizonica*; Wright & Wright 1957), oak woodland plants such as Arizona and emory oaks (*Q. arizonica*, *Q. emoryi*; D. Cumming, pers. comm. 1989) and oak (*Quercus* sp.; Campbell 1934; Groschupf & Lower 1988), and desert-grassland plants such as whitethorn (*Acacia* cf. *constricta*; K. Stirn, pers. comm. 1989), wolfberry (*Lycium* sp.), and velvet mesquite (*Prosopis velutina*).

Although many records are from Peña Blanca and Sycamore canyons, a strong emphasis placed on riparian habitats for this animal would be unwarranted for several reasons. Non-riparian observations and records are from hillsides and ridgetops in desert-grassland and open oak woodland. Although the densities of brushy habitats and semi-arboreal food lizards, especially *Urosaurus ornatus* (tree lizard), are often greatest in riparian areas, *Oxybelis* is a facultative riparian species. Moreover, the non-riparian communities often begin on steep slopes within a few meters of canyon bottoms. Canyon bottoms are one of the coldest winter microhabitats in the area due to cold air drainage. In Sycamore Canyon, these cool shady areas support the lowest known populations of woodland plants such as border pinyon, netleaf (*Quercus reticulata*) and silverleaf (*Q. scytophylla*) oaks, Arizona honeysuckle (*Lonicera arizonica*), and red columbine (*Aquilegia triternata*; Goodding 1946, 1961; Toolin et al. 1979). *Oxybelis* is undoubtedly on sunny slopes above the canyon bottom in the winter time as it is in other seasons.

Wildlife is often more abundant in riparian habitats in Arizona because water and nutrients from broad drainage areas concentrate to form habitats that are more mesic and productive than the surrounding area. The slopes above the *O. aeneus* canyons are not so dry (see below) that moisture is a limiting factor. Well-developed riparian communities composed of trees and shrubs restricted to canyon bottoms are much more important in temperate latitudes than more tropical areas. In southern Sonora, the difference between slope and riparian communities is somewhat less than in temperate areas as the common trees in Sinaloan Tropical Deciduous Forest extend into the canyon bottoms as well. Only sabino or Mexican bald cypress (*Taxodium mucronatum*), guásima (*Guazuma ulmifolia*), and locally Bonpland willow (*Salix bonplandiana*) form riparian gallery forests along

TABLE 1. Localities for *Oxybelis aeneus* in Arizona. Elevations estimated from topographic maps. Collection abbreviations: ASDM-Arizona-Sonora Desert Museum; ASU-Arizona State University; CAS-California Academy of Sciences; CM-Carnegie Museum; CJM-C. J. May; CU-Cornell University; ILL-University of Illinois; MCZ-Museum of Comparative Zoology, Harvard University; SDNHM-San Diego Natural History Museum; UAZ-University of Arizona; UCMVZ-University of California Museum of Vertebrate Zoology; UMMZ-University of Michigan Museum of Zoology.

Specific Area	General Area	Locality	Elevation (m)	Date	Time	Collector/ Observer	Specimen Number	Habitat	Vegetation	Source
Pima Co.	Tucson Basin	Edge of Tuscon	?975	June 1925		W. W. Akers	—			Vorhies 1926
	Baboquivari Mts.	Thomas Canyon	1400	Summer 1978			—	In vines on porch	Canyon riparian scrub at lower edge of oak woodland	K. Cumming, pers. comm. 1989
Santa Cruz Co.	Santa Rita Mts.	Aqua Caliente Cave	1220	1969		R. Buescher	—	In dark cave	Desert-grassland on limestone	W. D. Peachey, pers. comm. 1989
			1220	1970		R. Buescher	—	In dark cave		
			1220	Mar.-Apr. 1988		V. Omori	—	In twilight zone in cave		
		Montosa Canyon	1305	25 Sept. 1987	0300 h	J. Palting	—	In *Lycium*, rocky canyon	Desert-grassland/ canyon riparian scrub at lower edge of oak woodland	J. Palting, pers. comm.
	Patagonia Mts.	ca. 1.6 km NW Washington Camp	1645	28 July 1968		C. Coughanour, M. S. Keasey	UAZ 39544		Pine-oak woodland	
	Pajarito Mts.	General		June 1936		C. T. Vorhies	—			Wright & Wright, 1957
		General		June 1949		G. W. Harvey	CAS 84947			
		3.2 mi. W. IH 10 on AZ 89		14 Aug. 1991		R. Babb	—	Crossing paved road	Desert-grassland	R. Babb, pers. comm. 1991
		Calabasas Canyon, 3-5 km above border		April 1925		S. H. Beattie, C. T. Vorhies	MCZ 22417			
		Walker Canyon	1370	17 April 1950		W. H. Woodin	UAZ 39545	Rocky hillside	Oak woodland/ desert-grassland	Stebbins 1954
		Walker Canyon at border	1365	1 May						
		29 km W Nogales		7 Oct. 1949		G. W. Harvey	CM 29739			
		1.6 km E. Peña Blanca spring	1210	11 Oct. 1949		J. Gorman, C. Lorsythet	UCMVZ 52240			
		Peña Blanca Spring/Lake	1170-1220	1 July, 1932		S. H. Beattie	UAZ 16793			Wright & Wright, 1957

TABLE 1. Extended

Specific Area	General Area	Locality	Elevation (m)	Date	Time	Collector/ Observer	Specimen Number	Habitat	Vegetation	Source
				24 July, 1933		B. Campbell	—	In *Quercus*, ridgetop	Oak woodland/ desert-grassland	Campbell 1934
				June 1934		Kimmel	—	In *Vitis*, on house		Wright & Wright , 1957
							UMMZ 75779			Keiser 1967
				4 Oct., 1937		G. W. Harvey	CU 2655			Wright & Wright, 1957
				17 April, 1946		G. W. Harvey	CU 4072			
				9 Sept., 1969		W. R. Garstska	SDNHM 57054			
	Atascosa Mts.	Atascosa Lookout Trail	1370	1950		D. Cumming		On ground	Oak woodland	D. Cumming, pers. comm 1989
		8 km E. Sycamore Canyon; T23S, R11E, S29, SE 1/4	1340	1 Sept., 1980	0940 h	H. E. Lawler T. R. Van Devender	ASDM 87203 ♀SVL=859 mm	Open rocky hillside; temperature 26.2° in shade at 1 m, 26.4° in shade on ground, 35.0°C in sun on ground; sunny with winds to 30 kph.	Oak woodland/ desert-grassland	
		Jct. Summit Motorway-and Ruby Road	1400	2 Nov.,1963	0900 h	D. West	ILL 80501	Rocky ridgetop	Desert-grassland	
		Sycamore Canyon	1195	Before 1946		L. N. Godding, C. G. Reeder	— —	In *Salix*, rocky stream canyon	Canyon riparian woodland	Goodding 1946, 1961
			1170	12 April,1970		C. J. May	CJM 1211 (lost)	Rocky stream canyon	Canyon riparian woodland	
				9 June, 1970		F. R. Gehlbach	USNM 201622			
			1160	20 Sept., 1980	Midday	F. W. Reichenbacher, J. Kaiser	—	On *Platanus* trunk, rocky stream canyon	Canyon riparian woodland	
			1215	20 May, 1988		K. Groschupf, S. Lower	—	In *Quercus*, rocky stream canyon	Oak/riparian woodland	Groschupf & Lower, 1968
		4.5 km NNW Sycamore Canyon	1315	5 Sept., 1965		M. W. Larson	UAZ 47314		Oak woodland/ desert/grassland	

TABLE 1. Extended

Specific Area	General Area	Locality	Elevation (m)	Date	Time	Collector/ Observer	Specimen Number	Habitat	Vegetation	Source
Tumacacori Mts.	Peck Canyon tributaries	1200-1370		1939-1984		D. Cumming	ca. 10 individuals	In *Quercus arizonica* or *Q. emoryi*	Oak woodland/ desert-grassland	D. Cumming, pers. comm. 1989
	Ruby Area	Near Ruby	1285	14 May, 1963		C. H. Lowe, J. J. Reed	UAZ 16787	On ground, grassy/ shrubby area	Oak woodland/ desert grassland	
		4 km SW Ruby	1310	2 June, 1932		D. H. Fairchild	UAZ 16792			
		5 km SSW Ruby		3 May, 1950		D. H. Fairchild	UAZ 16786 (lost)			
		California Gulch		21 July, 1991		J. & S. Levy	—	On ground, shrubby area	Oak woodland/ desert grassland	S. Levy, pers. comm. 1991
		Arivaca Lake (Chimney Creek)	1195	April 1986		K. Stim	—	In *Prosopis*, edge of lake	Desert-grassland	C. Schwalbe, pers. comm. 1989
			1195	20 May, 1986		M. Clark, P. Rose	UAZ 46646	In *Prosopis*, edge of lake	Desert-grassland	
			1195	14 May, 1989	0100 h	K. Stim	—	In *Acacia*, edge of of lake	Desert-grassland	K. Stim, pers. comm. 1989

TABLE 2. Analyses of habitats of *Oxybelis aeneus* in Arizona (see Table 1).

Habitats		Localities		Specimens	
		No.	%	No.	%
Primary					
Pine-oak woodland		1	5.0	1	2.3
Oak woodland		1	5.0	1	2.3
Canyon riparian woodland		2	10.0	6	14.0
Desert-grassland		4	20.0	8	18.6
	Totals:	8	40.0	16	37.2
Ecotones					
Oak woodland/desert-grassland		8	40.0	19	44.2
Oak woodland/canyon riparian woodland		2	10.0	2	4.7
Oakwoodland/canyon riparian woodland/ desert-grassland		2	10.0	6	14.0
	Totals:	12	60.0	27	62.8
	Totals:	20		43	
Combined Habitats					
Pine-oak woodland		1	2.9	1	1.4
Oak woodland		13	38.2	26	35.1
Canyon riparian woodland		6	17.6	14	18.9
Desert-grassland		14	41.2	33	44.6
	Totals:	34	99.9	74	100.0

streams.

Data associated with 43 specimens from 20 localities listed in Table 1 permit a quantitative characterization of *Oxybelis* habitat in Arizona (Table 2). Primary habitats account for only 40.0% of the localities and 37.2% of the specimens. The majority of the localities and specimens are from ecotonal combinations of oak woodland, desert-grassland, and canyon riparian woodland. The oak woodland/desert-grassland ecotone is particularly important with 40.0% and 44.2% of the localities and specimens, respectively. Combining the habitat data from primary and ecotonal records for habitats provides a different view of the overall abundances of *Oxybelis*. Together oak woodland and desert-grassland elements account for 79.4% of the localities, and 79.7% of the specimens, whereas canyon riparian woodland is involved in only 17.6% of the localities and 19.9% of the specimens.

Inherent biases in the analyses are primarily due to the complex vegetational mosaic in the region, the wide spacing of trees in the open oak woodlands, and the difficulty of precisely relocating localities in a complex mountainous terrain. The importance of desert-grassland as habitat is somewhat over estimated in view of the fact that its ecotonal partners are tree communities.

Oxybelis is more or less well distributed in both upland and bottomland habitats within its narrow elevational zone of approximately 490 m. There does appear to be a preference for oak woodland on steep rocky slopes where temperatures are buffered by cold-air drainage and relatively large trees form a more continuous canopy. Even here, the number of *Oxybelis* specimens was increased significantly by Douglas Cumming's 10 sightings over 45 years on Peck Canyon Ranch in the Tumacacori Mountains. Considering how rarely *Oxybelis* has been observed in Arizona, and differences in visitation and accessibility of different habitats, a more accurate habitat sampling is unlikely.

Biogeographical Analysis of a Typical Arizona Habitat

To assess how unexpected, if not unusual, *Oxybelis* may be in an Arizona habitat, we analyzed the perennial flora from a typical oak woodland/desert-grassland locality 8 km east of Sycamore Canyon on the Ruby-Peña Blanca road in the Atascosa Mountains. The vegetation on the moderately steep rhyolitic slopes is transitional between oak woodland or encinal communities in the Madrean Evergreen Woodland Series and grama grass-scrub community in desert-grassland (Brown & Lowe 1974). Dominant trees were alligator bark juniper (*Juniperus deppeana*), Mexican blue oak (*Quercus oblongifolia*), and velvet mesquite. The grasses were dominated by five species of grama (*Bouteloua*) grasses.

The distributions of the perennial plants reflects the biogeographic affinities of *Oxybelis aeneus* and its habitat at the northern end of its range. A total of 24 perennial plants was observed (see Table 3) including eight trees and shrubs (33.3%), five succulents (cacti and Agavaceae, 20.1%), three forbs (12.5%), and eight grasses (33.3%). General distributions for each species were determined using regional floras (Gentry 1942; Kearney & Peebles 1964; Shreve & Wiggins 1964; Correll & Johnston 1970; Gould 1951) and label data on University of Arizona Herbarium specimens. Three species (*Quercus oblongifolia*, *Juniperus deppeana*, and *Rhus choriophylla*; 12.5%) are restricted to woodlands in the southwestern United States and the northern Sierra Madre Occidental in Chihuahua and Sonora, Mexico. All of the remaining taxa occur in open woodlands at the upper edges of their elevational ranges.

Fully 70.8% of the species have ranges centered on the grasslands of the Southwest inclusive of the Mexican Plateau. Five of these species (*Opuntia phaeacantha*, *Bothriochloa barbinodis*, *Bouteloua curtipendula*, *B. gracilis*, *B. hirsuta*; 20.8%) extend into the Great Plains and to higher elevation Rocky Mountain forests. One species (*Bouteloua eludens*) is a regional endemic only found in desert-grasslands at 1220-1525 m in Arizona and adjacent Sonora.

Fifteen (62.5%) species also occur in the Sonoran Desert although few (12.5%) occur in the hotter, drier areas below about 610 m. These species usually reach lower elevations to the south in Sonora as summer rainfall increases and becomes more reliable and as maritime humidity increases along the Gulf of California. As the climate becomes more tropical to the south and east in central and southern Sonora, Sonoran desertscrub is replaced by Sinaloan Thornscrub and Tropical Deciduous Forest (Shreve 1964; Brown & Lowe 1980; Turner & Brown 1982). Only five plants (2.2%) in the Arizona Ruby Road habitat also occur in the vicinity of Alamos in southernmost Sonora, 525 km to the south: coral bean (*Erythrina flabelliformis*), fairy duster (*Calliandra eriophylla*), saya (*Amoreuxia palmatifida*), sprucetop grama (*Bouteloua chondrosioides*), and tanglehead (*Heteropogon contortus*). In response to colder temperatures and increased incidence of freezing, coral bean changes growth-form southward from a 1-2 m shrub restricted to south-facing slopes to a 15 m tree in tropical deciduous forest. Tanglehead occurs throughout the Neotropics as well as tropical areas of Africa and Australia.

LIMITING FACTORS

Climates

Although the climatic stations in the range of *Oxybelis aeneus* are scattered, of short duration, or only record precipitation (Sellers & Hill 1974), some patterns are clearly evident. The winter temperatures are relatively warm for the elevation. Ruby (1310 m) has an annual mean of 16.9°C, a January mean of 9.3°C, and a record low of -10.6°C compared to Nogales (1160 m) with 16.8°C, 7.4°C, and -14.4°C and Oracle (north of Tucson, 1385 m) with 16.7°C, 7.8°C, and -16.6°C. Even Tucson (710 m), with warmer annual (19.2°C) and January (9.7°C) means, has recorded lower temperatures (-12.8°C). The Atascosa, Santa Rita, and Patagonia Mountains are partly effective in blocking Arctic air masses from the north and buffering winter lows.

Precipitation means for three *O. aeneus* stations (Bear Valley, Ruby, and Ruby 4NW) range from 418 to 507 mm/yr which is relatively high for desert-grassland and typical of woodland. Rainfall in the Santa Cruz River Valley declines from ca. 400 mm/yr at Nogales (1160 m) to 275 mm/yr in Tucson (770 m). Most of the Sonoran Desert to the southwest at

TABLE 3. Distributions of perennial plants observed or collected on Sept. 1, 1987, 8 km E. of Sycamore Canyon on Peña Blanca-Ruby Road, Atascosa-Pajarito Mountains, Santa Cruz County, Arizona. *=University of Arizona Herbarium specimen.

Species	Common Name	Vegetation: Forest	Woodland	Grassland	Desertscrub	Thornscrub	Tropical Deciduous Forest	Distribution: Great Plains	Rocky Mountains	Chihuahuan Desert	Colorado Plateau	Sonoran Desert	Mohave Desert	Sierra Madre Occidental	Tropical México	Central México
Trees And Shrubs																
Calliandra eriophylla	Fairy duster		X	X	X	X	X			X		X				
Erythrina flabelliformis	Coral bean		X	X	X	X	X					X			X	
Fouquieria splendens	Ocotillo		X	X	X					X		X				
Juniperus deppeana	Alligator bark juniper	X	X							X				X		
Mimosa dysocarpa	Gatuño		X	X	X					X		X		X		
Prosopis velutina	Velvet mesquite		X	X	X							X				
Quercus oblongifolia	Mexican blue oak		X							?				X		
Rhus choriophylla	Evergreen sumac		X	X						X				X		
Succulents																
Agave palmeri	Century plant		X	X	X					X		X		X		
Echinocereus pectinatus	Rainbow cactus		X	X						X				X		
Nolina microcarpa	Beargrass		X	X						X				X		
Opuntia phaeacantha	Variable prickly pear	X	X	X	X	?		X	X	X	X	X	X	?		
Opuntia spinosior	Cane cholla	X	X	X	X							X		?		
Subshrubs And Herbs																
Amoreuxia palmatifida	Saya		X	X	X	X	X					X		X	X	
Macrosiphonia brachysiphon	Rock trumpet		X	X	?							?		X		
*Salvia parryi**	Parry sage		X	X	X							X		X		

TABLE 3. Extended.

Species	Common Name	Forest	Woodland	Grassland	Desertscrub	Thornscrub	Tropical Deciduous Forest	Great Plains	Rocky Mountains	Chihuahuan Desert	Colorado Plateau	Sonoran Desert	Mohave Desert	Sierra Madre Occidental	Tropical México	Central México
		Vegetation						Distribution								
								Grasses								
Bothriochloa barbinodis	Cane beardgrass		X	X	X			X	X	X	X	X	X	X		
Bouteloua chondrosioides	Sprucetop grama		X	X	X					X		X		X	X	X
Bouteloua curtipendula	Sideoats grama	?	X	X	X		?	X	X	X	X	X	X	X		
*Bouteloua eludens**	Santa Rita grama		X	X												
Bouteloua gracilis	Blue grama	X	X	X				X	X	X	X			X		
Bouteloua hirsuta	Hairy grama		X	X				X	X	X	X			X		
Heteropogon contortus	Tanglehead		X	X	X	X	X			X		X		X	X	X
*Hilaria belangeri**	Curly mesquite		X	X	X					X	X	X		X		

lower elevations receives less than 275 mm/yr precipitation with very high evaporation rates.

Moving south in the Sonoran range of *Oxybelis*, the climate becomes increasingly tropical. The eastern and southern boundaries of the Sonoran Desert in central Sonora approximate the penetration of freezing temperatures (Hastings & Turner 1965). Most of the range of *Oxybelis* in Sonora is in the frost-free zone. Means for Guaymas (8 m), Navojoa (38 m), and Alamos (389 m) are annual temperatures of 24.9°C, 25.2°C, and 23.5°C; January temperatures of 18.0°C, 17.8 °C, and 16.6°C; and annual precipitations of 238 mm, 383 mm, and 639 mm/yr (Hastings & Humphrey 1969). The low precipitation values for Guaymas and Navojoa compared to the *O. aeneus* range in Arizona are misleading; high relative humidity and reduced evapotranspiration along the coast of the Gulf of California significantly offset general aridity.

Descriptions of *Oxybelis* habitats in various regional vegetational contexts from throughout its Neotropical range such as "xeric," "semi-arid," or "arid" (see Keiser 1967) simply reflect seasonally dry tropical communities that are not arid on the basis of annual climate. During the tropical dry season with lower humidity and warmer temperatures, *Oxybelis* and other surface foraging snakes experience potential water stress for a few months. At Alamos, monthly mean temperatures from November to March in the winter range from 16.4°C to 20.4°C (average of 18.5°C). The usual tropical dry season is from November into June with 0.9-46.3 mm monthly means and 156 mm total rainfall, 24.2% of the annual mean (Hastings & Humphrey 1969). In response, summer reptile activity becomes reduced variously, according to species, during November-December-January, gradually increasing in February-March-April reaching maximum surface activity with the onset of summer rains in July.

In comparison, the monthly means for Ruby are 16.4°C to 21.2°C with an average of 18.3°C for November to March, 4.6 mm to 49.3 mm totaling 212 mm for November to June (41.7% of annual mean; Sellers & Hill 1974). The main difference in temperatures is the increase in winter minima to the south until winters are frost-free. From southern Sonora southward, the aridity of the tropical dry season becomes the dominant climatic factor in "winter" rather than cooler temperatures.

Physiology and Behavior

The northern limits of *O. aeneus* in Arizona are apparently set by a combination of interrelated factors. The climatic window for it approximates the area where winters are relatively mild (January mean >9°C, minimum >-10°C) and rain-fall is relatively high (>415 mm/yr) and predominantly during summer. The behavioral and physiological adaptations that allow *O. aeneus* to be such a highly successful arboreal snake in the tropics do not serve well in more temperate environments (see discussion in Lillywhite & Henderson 1994). The winter retreats used in the tropical dry season such as hollow tree trunks and branches, and shallow rock crevices and ledges, are likely less adequate to protect it from the extremely low temperatures of more northern latitudes. The elongate body with its very high surface area to volume ratio functions well in cooling through evaporation but does not aid retention of heat in winter or of moisture when relative humidity is low. Estimated surface area/volume of an adult *O. aeneus* with a tail/snout-vent ratio of 0.69 (Keiser 1974) is more than twice that of a sympatric adult *Masticophis bilineatus* (Sonoran whipsnake) or *M. flagellum cingulum* (Sonoran coachwhip; P. C. Rosen, pers. comm. 1992). As noted above, in central and southern Sonora, increased humidity accommodates *Oxybelis* in areas with lowered rainfall because of reduced evapotranspiration.

In tropical forests, the leafy canopy intercepts a great deal of sunlight, buffering the temperatures in the understory and on the ground (Lillywhite & Henderson 1994). With canopy reduction in thornscrub, desertscrub, and desert-grassland, temperature extremes and diurnal fluctuations increase greatly due to direct diurnal radiative heating and radiative cooling at night. In such open habitats, surface temperatures are a more difficult problem for ground snakes than for arboreal snakes; the snake moving slowly on the ground is more prone to overheating than when on a shrub or tree. In the northern non-tropical part of its range, *Oxybelis* more often crosses open ground (see habitat discussion below) where it meets thermal stresses that generate problems in thermoregulation and water balance. It is of interest here that the bark-like skin with non-reflective scales likely absorbs heat from sunlight more rapidly than a snake skin with a highly reflective surface.

Although climate is variable throughout the range of *Oxybelis*, rapid changes in winter temperatures present greater risks in temperate latitudes. In Arizona, it has been found active from April to November, an activity period typical of many reptiles in the northern tropics. From late fall to spring, temperatures in Santa Cruz County vary enormously depending on the frequency and distribution of Arctic air masses penetrating to these latitudes. Recorded highs and lows for Ruby for December to February from 1931-1944 were 27.8°C to -10.6°C (Sellers & Hill 1974). Unlike snakes of temperate and boreal climates, the tropical *Oxybelis* does not have a fixed inactivity period in the winter tied into the annual daylength cycle. Lillywhite & Henderson (1994) pointed out that slender arboreal snakes typically pass food through the digestive system much faster than heavier-bodied species. Our observations indicate that *Oxybelis* could feed on *Urosaurus ornatus* and a few hours later face a storm with temperatures quickly dropping low enough to interfere with digestion for many days.

It is of particular interest that since about 1969, *Oxybelis* has been observed on four occasions in total and near darkness in Agua Caliente Cave in the Santa Rita Mountains (R. Buescher & W. D. P. Peachey, pers. comm. 1989). The cave is at 1220 m elevation on a xeric southwestern exposure on a limestone hill that supports a relatively barren desert-grassland community. The interior of the cave has increased relative humidity, warmer winter temperatures, and cooler summer temperatures: i.e. a more tropical microclimate. Agua Caliente Cave appears to be a special retreat that assists survival of a local relict population of *O. aeneus*.

Moving northward from southern Sonora into southern Arizona, more intense freezes have marked effects on vegetation that change the habitat of *Oxybelis*. Tropical trees, shrubs, and succulents gradually disappear as perennial, winter-dormant grasses thrive. Dense, structurally diverse thornscrub and desertscrub communities give way to desert-grassland that contains fewer trees and shrubs. Henderson (1974) found *O. aeneus* to be abundant in shrubs, especially *Mimosa*, and trees mostly less than 6.5 m in height in open, sunny situations in Belize. The mean perch height was 1.5 m in the daytime and 2-4 m at night. In Arizona desert-grasslands, shrubs including *Mimosa* are mostly less than 2 m in height. Shrubs have few of the slender elongate branches typical of plants in tropical vegetation due to shorter growing seasons, low relative humidity, less summer rainfall, and freeze-pruning. Shrubs are widely spaced, reducing the opportunity for movement through the vegetation. In general, woody vines decline to the north and almost disappear at higher elevations in the cool woodlands and forests of the Rocky Mountains and in the drier desertscrub of the Sonoran Desert. A basking vine snake at northerly latitudes is significantly less cryptic and at greater predator risk. In such open habitats, the vine snake is obviously susceptible.

Selection for a body that mimics vines produced not only an elongate form with non-reflective, bark-like skin but one with a rounded cross-section. The wavering, rigid body strongly resembles a slender branch moving in the wind. An *Oxybelis aeneus* captured in November 1993, at Camahuiroa on the Gulf of California in southern Sonora, kept its tongue extended to its maximum length and curved upward as long as it was held. A number of hypotheses have been proposed to explain prolonged extension of a rigid tongue including luring or confusing prey, a sight for visual reference in stalking prey, maintenance of continuous olfactory contact with the environment, and a defensive act to deter potential predators (Keiser 1974; Henderson & Binder 1980). Extension of a rigid, extended upturned tongue in a threat situation appears to be a different behavior than the tongue-thrusting described for *O. aeneus* in Veracruz by Kennedy (1965). We suggest that the upturned rigid tongue helps the elongate head to resemble a formidable thorn, not unlike those of boatthorn acacia (*Acacia cochliacantha*), various other trees and shrubs, and cacti in tropical dry communities.

The rounded belly further facilitates arboreal locomotion by reducing friction and allowing the animal to use gravity to "fall" rapidly from branch to branch; locomotion on the ground is more dependent on traction. *Oxybelis* is a slender sit-and-wait ambush forager that does not actively pursue its prey (Lillywhite & Henderson 1994). Although it has occasionally been observed on and near the ground in many areas, it is not a "racer" and moves relatively slowly when directly on the ground surface. *Masticophis bilineatus* and *M. flagellum*, which are sympatric with *O. aeneus* in Arizona and Sonora, are much more active, rapid, diurnal foragers. Endurance capacities in the slender *Oxybelis* are undoubtedly inadaptive for the sustained, rapid, ground locomotory performance found in racers. When crossing open areas in desert-grassland, *Oxybelis* is obviously at greater risk than in more dense tropical vegetation, being more vulnerable to predators including various mammals, raptors, both species of *Masticophis*, and other snake-eaters. The relatively low population densities of the vine snake in plant communities of southern Arizona and northern Sonora in comparison to more tropical areas to the south may, in part, reflect the much greater predator risk for *Oxybelis* in open habitats.

Food

Oxybelis aeneus faces other problems at more northerly latitudes because of shifts in food resources. It is a rear-fanged specialist on relatively small, semi-arboreal lizards, that occasionally eats frogs, birds, and insects (Henderson & Binder 1980). In the tropics, *Anolis* and its relatives are especially common. In the more tropical portions of its range, hatchlings of larger lizards (e.g. *Basiliscus*, *Ctenosaura*, and *Iguana*) emerging synchronously are an excellent dependable food resource (R. W. Van Devender, pers. com. 1988; see Keiser 1967). In Arizona, *Urosaurus ornatus* and small *Sceloporus clarki* (Clark's spiny lizard) are the only species in this semi-arboreal guild. The more active terrestrial species in the area (e.g. *Callisaurus draconoides*, *Cnemidophorus burti*, *C. sonorae*, *C. tigris*, and *Holbrookia maculata*) are more likely to be eaten by *Masticophis*. As discussed above, *Oxybelis*, with its passive dependence on camouflage to assist in catching prey, is less well-adapted in open habitats. In Arizona and Sonora, *Oxybelis* has been observed to eat *Holbrookia maculata* (lesser earless lizard), *Sceloporus clarki*, *S. spinosus* (including *S. horridus*; Sinaloan spiny lizard), *S. undulatus* (western fence lizard), *Urosaurus bicarinatus* (tropical tree lizard), and *U. ornatus* (Barbour & do Amaral 1926; Bogert & Oliver 1945; Stebbins 1954; Groschupf & Lower 1988). Our observations near Alamos in southern Sonora, suggest that *Anolis nebulosus* (Mexican bark anole), *Sceloporus nelsoni*, and *U. bicarinatus* are likely to be important prey species in tropical deciduous forest.

Reproduction

Keiser (1967) summarizes the limited information available regarding reproduction in *Oxybelis*. Most records are for eggs found within wild-caught females. The only clutch discovered in the field was from a depression in leaf litter on a hillside in undisturbed, mature open forest in Darien Province, Panama (Sexton & Heatwole 1965). Suitable egg laying sites for non-burrowing snakes apparently become less prevalent at the northern edge of the tropics for several reasons. Less leaf litter accumulates and soil moisture decreases as absolute amounts of summer rainfall decrease and the productivity and sizes of deciduous plants are reduced. Evergreen species such as alligator bark juniper, Mexican blue oak, and evergreen sumac (*Rhus choriophylla*) are widely spaced and produce little litter with leaf-fall more continuous throughout the year. Smaller tree sizes and relatively dry conditions produce fewer moist, hollow pockets in snags or logs. Although leaf litter is often greater in canyon bottoms because riparian trees are larger and usually deciduous, the habitats are inherently unstable because of flooding from spring snow melt from higher peaks and during summer monsoonal thunderstorms. If leaf litter is important, suitable egg laying sites for *Oxybelis* are scarce in southern Arizona compared to the habitat situation in the ecological metropolis of the species.

HISTORICAL BIOGEOGRAPHY

Interesting biogeographical patterns often raise questions of antiquity and of the past environments that caused them. Axelrod (1979) places the origin of the Sonoran Desert in the latest Miocene five to eight million years ago. As the Rocky Mountains and Sierra Madre Occidental were uplifted, regional climates and biotas differentiated. The Sonoran Desert biota mostly evolved from taxa found in seasonally dry tropical forests (Madro-Tertiary Geoflora), a much older evolutionary landscape.

However, the Pleistocene, with its two million years of ice ages, had profound effects on the distributions of most organisms on the globe. Fifteen to twenty ice ages (glacial periods) perhaps 100,000 years long alternated with hot interglacials of lesser duration (Imbrie & Imbrie 1979). Woodlands dominated by junipers, pinyon pines, and shrub oaks expanded into most of the deserts of the southwestern United States and northern México during each glacial (Van Devender et al. 1987). Creosote bush (*Larrea divaricata*) desertscrub without woodland trees was restricted to below about 300 m in the Lower Colorado River Valley of Arizona and California south into the lowlands surrounding the Gulf of California although sea level lowering of about 100 m expanded this area. The impact of glacial climates on the tropical vegetation in Sonora is unknown.

Much of the insight into the vegetational dynamics in the southwestern deserts during the last glacial/interglacial cycle has been inferred from plant macrofossils in ancient packrat (*Neotoma* sp.) middens. Most climatic parameters reflect regional circulation patterns allowing regional paleoclimates to be reconstructed based on local midden macrofossil sequences. Paleoclimatic inferences from the Waterman Mountains in the eastern Sonoran Desert (Van Devender 1990) should be applicable to the nearby range of *O. aeneus* in Arizona. The Watermans are 55 km west-northwest of Tucson and approximately 95 km north-northwest of the nearest *Oxybelis* localities known today. Seventeen fossil middens from 795 m elevation provide paleoenvironmental records for the last 22,450 yr B.P. (years before 1950; Anderson & Van Devender 1991). They reveal that until the end of the last ice age (the Wisconsin glacial) about 11,000 years ago, a temperate climate with cool summers and winter rain dominance supported a woodland with singleleaf pinyon (*Pinus monophylla*), juniper (*Juniperus* sp.), shrub live oak (*Quercus turbinella*), big sagebrush (*Artemisia tridentata*-type), and Joshua tree (*Yucca brevifolia*). Similar woodlands are found today to the north and west in more temperate mountainous areas with greater winter rainfall surrounding the Mohave Desert. Subsequently, the vegetation and climate went through several stages in the present interglacial (the Holocene), before a relatively modern Sonoran desertscrub was re-established approximately 4,000 years ago with the arrival of subtropical plants including elephant tree (*Bursera microphylla*) and foothills paloverde (*Cercidium microphyllum*). Mild winters and warm summers with strong monsoonal precipitation combined to allow the maximum expansion of subtropical and desertscrub communities. In the last 500-800 years, the climate of the region has become hotter, drier, and very likely with more frequent freezes.

For widespread desert and grassland species, bones in packrat middens present a different history than do the plants. Animals that mostly live in desertscrub communities today such as *Cnemidophorus tigris* (western whiptail lizard), *Coleonyx variegatus* (banded gecko), *Lichanura trivirgata* (rosy boa), *Sauromalus obesus* (common chuckwalla), *Uta stansburiana* (side-blotched lizard), and *Xerobates agassizi* (desert tortoise) typically inhabited late Wisconsin and early Holocene woodlands and were not displaced great distances into southern refugia (Van Devender et al. 1977, 1991; Van Devender & Mead 1978). However, the equable climates with cool summers and dominant winter rainfall that allowed greater biological mixing, did not favor subtropical animals and plants closely linked to the summer monsoons. The northward dispersals of tropical animals such as *O. aeneus* and the sympatric *Gyalopion quadrangularis* (thornscrub hook-nosed snake) likely occurred after about 9,000 years ago as more subtropical climates developed. The subsequent shift to a more xeric climate after about 2,000 years ago, and especially the last 800 years, did not favor subtropical species. Thus, the northern populations of tropical species should be considered relictual only on a relatively recent and vacillating thousand-year time scale, and not the pre-Pleistocene million-year scale.

AT THEIR NORTHERN LIMITS

Many tropical animals and plants reach their northern limits between 29° and 33°N latitude as the Neotropics meet more temperate climates and communities in Sonora or Arizona. *Oxybelis aeneus* reaches approximately 31°15'N where it is restricted to a vertical range of less than 500 m at moderate elevations (1160-1650 m) in desert-grassland and oak woodland habitats. Many of the physiological, behavioral, and morphological adaptations that make this snake a highly successful tropical species do not serve well in temperate or arid environments. As the vegetation changes from a closed canopy tropical deciduous forest in southern Sonora to more open Sinaloan thornscrub and Sonoran desertscrub in coastal and central Sonora to desert-grassland in southeastern Arizona, the physical environment of *Oxybelis* becomes increasingly less optimum. Winters become colder, summers become hotter and drier, and daily temperature ranges increase. Decreases in the duration and total amount of summer rainfall coupled with reductions in humidity and cloud cover and increases in insolation, temperatures, and evaporation combine to increase aridity and lower productivity. The data available indicate that the northerly limits of the neotropical vine snake are controlled by winter freezing above about 1650 m and by summer aridity below 1160 m. As the vegetation becomes more open, there are fewer trees, few woody vines, more shrubs of lower stature with relatively few elongate branches, and little leaf litter. The cryptic values of color pattern, body morphology, and behavior in *Oxybelis* are reduced in open habitats with few vines or vine-like slender branches, likely with greatly increased predator risks. Small semi-arboreal lizards become less abundant and more seasonal. Considering the climatic regime, vegetation structure, food sources, and predators, the presence of *Oxybelis* in southern Arizona at all is remarkable, and probably represents a remanent population from a more tropical period in the Holocene.

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