

Historical Biogeography of Longhorn Cactus Beetles: The Influence of Pleistocene Climate Changes on American Desert Communities

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Abstract—Mitochondrial sequence data from three species of flightless cactus beetles, *Moneilema gigas*, *M. armatum*, and *M. appressum*, were analyzed. The coalescent models implemented in the program FLUCTUATE were used to test the hypothesis that these species experienced range changes following the end of the last glacial period. The two desert species *M. gigas* and *M. armatum* both showed significant evidence of population growth, particularly in northern populations; however, the montane species *M. appressum* did not show evidence of range fragmentation and population decline as predicted from paleoclimate data.

Introduction

The arid regions of the intermontane American West experienced dramatic changes following the end of the most recent glacial period. Many desert plants and animals experienced range changes to higher elevations where they had been absent during glacial periods, and many cool-climate organisms that previously dominated these regions retreated to isolated mountaintops, including the Madrean Sky Islands (Van Devender 1990a,b). The range changes seen in these cases are among the best-documented examples of plant responses to Pleistocene climate changes, and have prompted a number of phylogeographic studies that looked for genetic signatures of these events (Barber 1999; Maddison and McMahon 2000; Masta 2000; Smith 2003; Sullivan 1994). Although these studies have revealed much about population structure in species within these regions, evidence for a direct impact of late Pleistocene climate changes on biogeography or demography is still lacking.

The flightless cactus beetles *Moneilema* are an appropriate place to look for evidence of such an impact. *Moneilema* spp. are large, black, flightless beetles distributed throughout the North American deserts. They feed exclusively on cacti, their larvae burrowing into the pads, where they complete their development (Linsley and Chemsak 1984). Previous research has demonstrated that these extremely sedentary animals show significant biogeographic structure (Smith 2003), and retain genetic signatures of past range changes.

There are three species of *Moneilema* that occur in the Madrean Sky Islands and the surrounding deserts. *M. gigas* LeConte occurs in the Sonoran Desert below ca 1,500 meters, and is distributed from central Arizona southwards to northern Sinaloa. *M. armatum* LeConte occurs in the Chihuahuan Desert below 1,500 meters from western New Mexico, east to the

Gulf of Mexico, and southward to Central Mexico. Finally, *M. appressum* LeConte is a sky islands endemic that occurs above 1,300 meters elevation in semi-desert grassland and oak woodlands throughout Arizona, New Mexico, Texas, Sonora, and Chihuahua, and exists in sympatry with each of the two desert species at lower elevations in the western and eastern edges of its range, respectively.

Given the packrat midden evidence for changes in the distribution of desert organisms following the end of the last ice age (Van Devender 1990a,b), we might expect that these organisms would have undergone similar range shifts, and that that history might be retained in their population genetic structure. Indeed, previous phylogenetic and Nested Clade analyses suggest that the two desert species, *M. gigas* and *M. armatum*, have undergone progressive northward range expansions, from source populations in southern Sonora, and the Bolson de Mapimi in Coahuila, into the northern edge of their current distribution (Smith 2003; Smith and Farrell, in review). Likewise, Nested Clade Analysis suggests that the Sky Island species, *M. appressum*, has undergone a range fragmentation, leading to local differentiation of isolated populations (Smith 2003). However, coalescent and molecular-clock-based estimates suggest that in all three species these dramatic range changes on a continental scale occurred between 0.3 and 2 million years ago, long before the end of the last glacial period (Smith and Farrell, in review).

Clearly, these flightless animals record biogeographic history over very deep time, but we also wanted to look at range changes on a smaller time scale. It is possible that superimposed on these large scale distribution patterns, there may have been more subtle, local range changes as certain desert organisms expanded from local refugia and moved into higher elevations throughout the last 40,000 years. In order to test this hypothesis, we examined mitochondrial DNA sequences drawn

from multiple populations in each of these species. We used coalescent models to test the hypothesis that populations of the two desert species, *M. gigas* and *M. armatum*, have undergone recent growth, and that populations of the sky island species, *M. appressum*, have undergone recent decline.

Methods

Specimens of *Moneilema* spp. were collected from across the range of the Sonoran and Chihuahuan Deserts, and from

across the Madrean Sky Islands Archipelago. The coordinates of each collection locality were recorded using a hand-held Garmin GPS 12, or E-map GPS unit (see tables 1, 2, and 3). Collection sites were chosen by consulting previous collections data in published accounts (Linsley and Chemsak 1984; Raske 1966) and by examining museum specimens at the Museum of Comparative Zoology at Harvard, the University of Arizona insect collection, the Essig Museum at University of California-Berkeley, the California Academy of Sciences, and the Instituto de Biología at the Universidad Nacional Autónoma

Table 1—Populations and collection localities information for *M. gigas*.

Population	Collection localities	Location	Coordinates	Individuals sequenced
Rio Mayo	Alamos Monte	Southeast of Alamos, Sonora, on the road towards the Rio Cuchijaqui	26 59 00 N 108 54 12 W	3
Rio Sonora	San Carlos	In the town of San Carlos, Sonora	27 50 00 N 110 54 00 W	6
	Las Guásimas	Mexico Hwy 15 East of Guaymas, Sonora, Mexico	27 54 24 N 110 34 24 W	2
	Playa Del Sol	Mexico Hwy 15, 20 Km East of Guaymas, Sonora, Mexico	27 54 24 N 110 45 00 W	1
	San Nicolas, Sonora	260 Km Southeast of Hermosillo, Sonora, Near Intersection with Road to Ciudad Obregon	28 25 00 N 109 15 00 W	3
	Moctezuma Sonora	160 Km Northeast of Hermosillo, Near Moctezuma River	29 30 00 N 109 30 00 W	4
	Ures Son	60 Km Northeast of Hermosillo	29 30 00 N 110 30 00 W	6
	Mazocahui Sonora	104 km North east of Hermosillo, Near Road to Cananea	29 31 43 N 110 09 15 W	1
	Km 100	Mexico Hwy 15, 100 KM north of Hermosillo, Sonora, Mexico	30 00 00 N 111 08 00 W	5
Rio Bavispe	Husabas Sonora	200 Km Northeast of Hermosillo, Sonora near Rio Bavispe	29 50 00 N 109 25 00 W	4
Cholla Bay	Cholla Bay	Cholla Bay, west of Puerto Peñasco, Sonora, Mexico	31 15 00 N 114 40 00 W	7
Ajo Mountains	Sonoita	Off Mexico Hwy 2, Just east of Sonoita, Sonora, Mexico	31 41 18 N 112 50 48 W	5
	Bull's Pasture	Bull's Pasture in the Ajo Mountains, Organ Pipe National Monument, Pima County, Arizona	32 00 55 N 112 41 36 W	3
	Table Mts	South of Interstate 8, Near Table Top Wilderness, Pinal County, Arizona	32 39 54 N 112 12 36 W	3
Altar Valley	Black Mt	Black Mountain, South of Ajo, Pima County, Arizona	32 20 32 N 112 44 30 W	2
	Baboquivari	Brown Canyon, East of Baboquivari Mountain, Pima County, AZ	31 45 00 N 111 30 00 E	2
	Altar Valley	Intersection of Arizona Hwy. 86 and 286 Pima County, AZ	32 03 00 N 111 19 00 W	2
	Sheriff's Mesa	Between Amado and Arivaca on Batamote Rd., Santa Cruz County, Arizona	31 45 00 N 111 11 00 W	2
Santa Rita Mts	Florida Canyon	Santa Rita Mountains, Above Santa Rita Experimental Range Station, Santa Cruz County, Arizona	31 46 00 N 110 51 00 W	7
	Box Canyon	Box Canyon Road between Greaterville and the Santa Rita Experimental Range Station, Santa Cruz County, Arizona	31 47 00 N 110 50 18 W	10
Santa Catalina Mts	Catalina State Park	Catalina State Park Group Use Area, Pima County, Arizona	32 26 00 N 110 55 00 W	3
	Biosphere II	Biosphere II Center, Pinal County, Arizona	32 34 20 N 110 51 30 W	3
	Oracle, Arizona	Arizona Trail off Mt. Lemon Road, Oracle, Pinal County Arizona	32 36 30 N 110 45 00 W	2
	Tiger Mine	Off AZ HWY 77, North East of Oracle, Arizona, Pinal County, Arizona	32 38 18 N 110 44 20 W	1
	Willow Springs Rd	Off AZ Hwy 77, West of Oracle, Arizona.	32 44 54 N 110 53 50 W	5

Table 2—Populations and collection localities information for *M. armatum*.

Population	Collection localities	Location	Coordinates	Individuals sequenced
Gulf Coast	China	Mexico Hwy 40, Near China Reservoir, Nuevo Leon, Mexico	25 41 00 N 99 13 60 W	2
	Reynosa	Mexico Hwy 40, 10 km south of Reynosa, Tamaulipas	26 01 00 N 98 13 00 W	2
	Monterrey	Mexico Hwy 53, 7 KM Northwest of Monterrey, Nuevo Leon, Texas	25 40 00 N 100 19 00 W	2
East of Rio Grande	Cox Mts	Off County Hwy 1111, North of Sierra Blanca, Hudspeth County, Texas	31 16 45 N 105 13 48 W	4
	Franklin Mts	Franklin Mountains in County Road 375 Loop, North of El Paso, El Paso County, Texas	31 52 33 N 106 29 34 W	5
	Hueco	County Road 001 and US 180, Near Hueco, Hudspeth County, Texas	31 58 00 N 105 58 00 W	2
	Bernalillo	Interstate 25 at exit 242, Bernalillo, Sandoval County, New Mexico	35 18 58 N 106 31 54 W	5
	Doña Ana Mts	Doña Ana Peak, off County road 64, North of Las Cruces, Doña Ana County, New Mexico	32 28 24 N 106 45 54 W	3
	Valley of Fire	Off US 380, Northeast of Carrizozo, Lincoln County, New Mexico	33 40 55 N 105 55 05 W	3
Pecos River Valley	Correo	Interstate 40, Exit 126 Near Correo, New Mexico, Cibola County, New Mexico	34 59 27 N 107 05 54 W	6
	Bear Mt	Davis Mountains, Texas, Jeff Davis County	30 43 27 N 104 13 32 W	2
	Medley Draw	Texas Rt 166 near windfarms east of Fort Davis, Jeff Davis County, Texas	30 31 50 N 104 11 59 W	1
Continental Divide	Old Hachita	Old Hachita Road and New Mexico Hwy 9, West of Hachita, Grant County, New Mexico	31 55 48 N 108 24 12 W	1
	Granite Gap	Arizona/New Mexico State Line at NM Hwy 80. Hidalgo Cty, New Mexico	32 05 20 N 108 58 25 W	4
	Antelope	New Mexico Hwy 9, east of Animas, New Mexico near Continental Divide, Hidalgo Cty, New Mexico	31 55 30 N 108 43 00 W	4
	Tres Hermanas	Near Tres Hermanas Mountains off New Mexico Hwy 11, South of Deming, Luna County, New Mexico	31 57 15 N 107 45 40 W	9
	Sierra Las Uvas	Off New Mexico Hwy 185, South of Hatch, Doña Ana County, New Mexico	32 32 29 N 107 07 38 W	2

de México (UNAM). Additionally, biotic communities maps (Brown 1994) and published accounts of paleovegetation in the region (Elias and VanDevender 1992; Van Devender 1990a,b; Van Devender and Bradley 1994) were consulted to identify potential new populations and determine which would be most informative in reconstructing Pleistocene climate changes.

Approximately 1,000 base pairs of mitochondrial DNA sequence data from the Cytochrome Oxidase 1 (COI) gene was obtained by PCR and thermal cycle sequencing using the methods described in Smith (2003) from 59 individuals of *M. appressum*, 57 individuals of *M. armatum*, and 92 individuals of *M. gigas*. Sequence data were easily aligned by eye using MacClade version 4.03 (Maddison and Maddison 2001).

Coalescent modeling of changes in population size were performed using the program FLUCTUATE (Kuhner et al. 1998). Samples were grouped into populations based on previous estimates of migration rates between collection localities (Smith 2003) obtained from the program MDIV (Nielsen and Wakeley 2001); if there was evidence of significant migration between collection localities, these localities were combined and analyzed as a single population (see tables 1 through 3). FLUCTUATE was used to estimate the parameters “ Θ ” (= $2N\mu$) and “ g ” (= the exponential rate of population growth or decline relative to the neutral mutation rate) for each species. We set the program to compute the Watterson estimate of theta,

and allowed the population to change in size, with an initial value for “ g ” set to 0.1. We used 10 short Markov Chain Monte Carlos of 200 generations each, and two long Markov Chain Monte Carlos of 20,000 generations each. The probability that “ g ” is different from zero was determined by referring to plots of the likelihood surface and the confidence intervals about g and theta output by FLUCTUATE.

Results

FLUCTUATE found evidence of population growth in all three species, in most of the populations (table 4). Estimates of “ g ” were positive for all populations analyzed, but were generally low, with per-generations growth rates between 1.0×10^{-4} and 1.0×10^{-7} . Estimates of “ g ” were significantly greater than zero ($p < 0.05$) in all but four populations.

Discussion

Both of the desert species show evidence of population growth as we had predicted. Additionally, as we might expect, the most dramatic rates of population growth were seen in populations on the northern periphery of the range of *M. gigas* (i.e., the Catalina Mountains, Altar Valley, and Ajo Mountains,

Table 3—Populations and Collection Localities information for *M. appressum*.

Population	Collection localities	Location	Coordinates	Individuals sequenced
East of Rio Grande	Bernalillo	Interstate 25 at exit 242, Bernalillo, Sandoval County, New Mexico	35 18 58 N 106 31 54 W	2
	Organ, NM	US 70 Between Las Cruces and White Sands Missile Range. Doña Ana Cty, New Mexico	32 24 51 N 106 37 53 W	5
Continental Divide	Mt Riley	East Portillo Mts. Cty Road A005 north of Cty Road A003 near US/Mexico Border. Doña Ana Cty, New Mexico	31 52 55 N 107 05 45 W	4
	Old Hachita	Old Hachita Road and New Mexico Hwy 9, West of Hachita, Grant County, New Mexico	31 55 48 N 108 24 12 W	3
	Saddlerock Canyon	Big Burro Mts. Saddlerock Canyon Rd. off US 180 west of Silver City, Grant Cty, New Mexico	32 47 04 N 108 29 48 W	1
	Las Playas Valley	Las Playas Valley Rd. South of Intersection w/ NM Hwy 9 Hidalgo Cty, New Mexico	31 51 21 N 108 37 09 W	4
	Antelope	New Mexico Hwy 9, east of Animas, New Mexico near Continental Divide, Hidalgo Cty, New Mexico	31 55 30 N 108 43 00 W	3
	Granite Gap	Arizona/New Mexico State Line at NM Hwy 80. Hidalgo Cty, New Mexico	32 05 20 N 108 58 25 W	4
	Skeleton Canyon	Peloncillo Mts. Skeleton Canyon	31 35 25 N 109 03 48 W	3
	Tollhouse Canyon	Peloncillo Mts. Hwy 191 west of Clifton, Greenlee Cty, Arizona	33 46 25 N 109 18 41 W	2
	San Simon	Pinaleño Mts. Hwy 191 South of Safford, Graham Cty, Arizona	32 32 58 N 109 40 31 W	1
	Willcox Playa	Railroad Avenue, Southwest of Willcox, Cochise Cty, Arizona	32 12 05 N 109 52 02 W	5
	Cochise Stronghold	Dragoon Mts. Ironwood Rd, East of Cochise Ranger Station, Cochise Cty, Arizona	31 56 55 N 109 55 59W	9
Dragoon	Dragoon Mts. Forest Service Rd 795, North of Intersection w/ Ironwood Rd. Cochise Cty, Arizona	31 58 36 N 109 57 50 W	1	
Santa Cruz River Valley	Oracle, Arizona	Arizona Trail off Mt. Lemon Road, Oracle, Pinal County Arizona	32 36 30 N 110 45 00 W	3
	Greaterville	Santa Rita Mts. Greaterville Rd. West of AZ Hwy 83	31 46 31N 110 45 06 W	2
	Nogales, Arizona	Pajarito Mts. Forest Service Rd 222 Near Arizona Hwy 289, east of Interstate 19. Sta Cruz Cty. Arizona	31 23 34 N 110 48 57 W	4
	Box Canyon	Box Canyon Road between Greaterville and the Santa Rita Experimental Range Station, Santa Cruz County, Arizona	31 47 00 N 110 50 18 W	3

where post-glacial range changes in desert organisms were greatest), whereas three populations from Sonora, including one on the Sea of Cortez (i.e., putative desert refugia) did not show rates of population growth that were significantly different from zero. Although this latter observation may in part be an artifact of small sample size, the geographic component, and the fact that “g” was of similar sign and magnitude across all populations offer further support for a common extrinsic cause of these demographic changes.

It should be noted, of course, that population growth per se and range expansion are certainly distinct processes, but barring dramatic changes in population density, the one would seem to require the other. Additionally, while it is not possible to accurately infer when these demographic changes occurred, they must have been recent enough that the genetic signatures of these events have not been lost through genetic drift. We therefore view these results as compelling evidence that the two desert insects have undergone recent range expansions, which may have been a response to climate changes since the end of the last glacial period.

However, The montane species *M. appressum* not only does not show evidence of population decline as we had predicted, but in fact indicates strong evidence of population expansion in two of the three populations analyzed. It is possible that

grouping sequences from different localities could produce erroneous estimates of coalescent parameters, particularly if demographic histories differed between localities, or if geographic sampling were uneven. However, in this case, there was still significant evidence of population expansion when the data from particular collection localities were analyzed separately (C. Smith, unpublished). Additionally, we suspect that if grouping populations were to have biased our results at all, it would have produced lower estimates of “g” on average because sampling multiple populations should increase the mean time to coalescence in our sample.

So, it appears that the evidence of population expansion in *M. appressum* is not an artifact of the analysis. This result is somewhat confusing, however, as both phylogenetic and Nested Clade analyses indicate that this species has undergone range fragmentation, albeit much longer ago than the end of the last glacial period (Smith 2003). One possible explanation might be that more recent demographic changes have erased any evidence of prior population decline. Alternatively, it may be that this species simply did not respond to post-Pleistocene climate changes by undergoing significant range fragmentation. It has long been known that particular plants and animals responded idiosyncratically to climate change following the end of the last ice age, rather than responding en-masse as an

Table 4—Exponential growth rates estimated by FLUCTUATE.

Species	Population	Theta	g (t=1/μ)	r (t= 2Ne)	r (t=1 generation)	p
Gigas	Alamos	0.31	155.3	48.1	2.33 × 10 ⁻⁰⁶	>0.05
	Rio Sonora	0.54	80.1	43.2	1.20 × 10 ⁻⁰⁶	<0.01**
	Rio Bavispe	0.03	99.5	3.0	1.49 × 10 ⁻⁰⁶	>0.5
	Cholla Bay	0.03	117.4	3.5	1.76 × 10 ⁻⁰⁶	>0.5
	Ajo Mts	0.12	238.5	28.6	3.58 × 10 ⁻⁰⁶	<0.05*
	Altar Valley	0.6	402.1	241.2	6.03 × 10 ⁻⁰⁶	<0.01**
	Santa Ritas	0.8	203.8	163.04	3.06 × 10 ⁻⁰⁷	0.05*
	Catalinas	0.49	935.7	463.2	1.40 × 10 ⁻⁰⁵	<0.01**
Armatum	Continental Divide	0.08	201.8	16.1	3.03 × 10 ⁻⁰⁶	0.01**
	Gulf Coast	0.718	608.1	436.6	9.12 × 10 ⁻⁰⁶	<0.05*
	Pecos River	0.25	404.1	101.0	6.06 × 10 ⁻⁰⁶	<0.01**
	Rio Grande	0.18	38.8	7.0	5.82 × 10 ⁻⁰⁷	<0.01**
Appressum	East of Rio Grande	0.0435	47.681	2.1	7.15 × 10 ⁻⁰⁷	>0.5
	Continental Divide	0.83	190.6	157.6	2.86 × 10 ⁻⁰⁶	<0.01**
	Santa Cruz River	0.37	376.8	138.6	5.65 × 10 ⁻⁰⁶	<0.01**

entire community (VanDevender 1990a). Although many pine and oak woodland species did retreat to higher elevations, it may be that *M. appressum* and their hosts remained in place as the environment changed around them.

Conclusions

The results for all three of these species suggest a complex biogeographic history in which recent range changes have been overlaid on an older biogeographic history. Previous studies suggest that the desert species, *M. gigas* and *M. armatum*, have been undergoing progressive northward expansion throughout the Pleistocene, but the evidence presented here suggests that populations from across the range of both of these species have also experienced local demographic changes and population growth following the end of the last ice age. Conversely, whereas previous studies suggest that the montane species *M. appressum* underwent significant range fragmentation in the past, the evidence presented here suggests recent expansion in some populations.

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