The California Serengetti:
Two Hypotheses Regarding the Pleistocene Paleoecology of the San Francisco Bay Area

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I. Introduction

Today, a drive across the Golden Gate Bridge fills the senses with the sights and sounds of the San Francisco Bay area. Large ships move slowly out to the open sea while small sailboats glide delightfully about the bay. The tall buildings and famously-steep streets of San Francisco reflect the sunlight while in the distance, far across the bay, other cities stand miniature upon the watery horizon, reminders of the vastness of San Francisco Bay. It is a grand thing to see.

A visit to the Golden Gate during the time of the last Ice Age would have been a very different experience. There was no San Francisco Bay fifteen thousand years ago. Instead, what is now bay was then a wide grassy valley teeming with exotic wildlife. There were herds of mammoth and mastodon, camel and horse. Herds of bison darkened the areas they grazed. There were llamas, elk, tapirs, and maybe even a moose or two. And mingling with these great herbivores were fierce predators such as the short-faced bear and saber-tooth cat, packs of the dire wolf, and prides of the California lion. Large condors and various other vultures busied themselves disposing of the dead. To the west, where we normally expect to see the Pacific Ocean, there was a broad coastal prairie covered with grasses and tree-lined streams. And there was ample wildlife there, too. From the Golden Gate, the beach was far too distant to see as the coast was then about 30-35 km west of San Francisco. Long darkened lines of wild bison and horse, and occasionally the mammoth, moved back and forth through the Golden Gate, journeying to and from the coast. It would have been an awe-inspiring sight.

What we would have seen in the San Francisco Bay area during the late Pleistocene was grander than anything imaginable. The closest comparison might be the famous Serengetti Plains of East Africa as described in early historic times. The great mosaic of Serengetti wildlife is legendary, as are the great seasonal migrations and the interactions of predator and prey (cf. Mari and Croze 1999; Scott 1988). But in truth, the African Serengetti pales in comparison to the Bay Area at 15,000 yrbp. The California Serengetti, as I have come to think of the Bay Area during the late Pleistocene, was one of the greatest natural phenomena of all time. It is the subject of this paper and the focus of two hypotheses that address the paleoecology of wildlife and wild lands.

It is proposed herein that the San Francisco Bay area sustained an exceptionally-large and diverse population of Rancholabrean megafauna during the late Pleistocene. I propose that one large herbivore was found for every 4 ha of land and one large predator per 560 ha. Thus, I believe that the optimum megaherbivore/predator relationship was about 140 to 1.

Furthermore, it is proposed herein that a seasonal round characterized the wildlife of the San Francisco Bay area during the late Pleistocene Epoch (ca. 100,000-10,000 yrbp). Participating in the seasonal round were various and now extinct Rancholabrean megaherbivores, such as the Columbian mammoth (*Mammuthus columbi*), ancient bison (*Bison antiquus*), camel (*Camelops hesternus*), and western horse (*Equus occidentalis*). Northern and southern rounds are identified. It is likely that certain of the predators (e.g., dire wolf and American lion) accompanied the megaherbivores in their sojourns.

To the north of the Golden Gate, the primary residence of the megaherbivore herds centered on the Santa Rosa Plain, which included the Laguna de Santa Rosa, and the Petaluma Valley extending south to the "California River" (Howard 1979). The California River is a name given to the once combined flow of the San Joaquin and Sacramento Rivers that is now muted by the drowning of San Francisco Bay.

To the south of the Golden Gate, the primary residence of the megaherbivore herds centered on the "Franciscan Valley" (Axelrod 1981:848). The Franciscan Valley is a long north-south trending trough of which most is now submerged beneath San Francisco Bay (Fig. 1). I consider the Santa Rosa Plain to be the northern end of the Franciscan Valley and the area near the town of San Juan Bautista to be the southern end.

Seasonal migrations were likely made from the Franciscan Valley to the "Farallon Plain" (Parkman 2004:28). During the late Pleistocene, the Farallon Plain consisted of the then exposed Continental Shelf. It extended from near Rockport north of the mouth of the Russian River south to the mouth of the California River, and from there, further south to the town of Moss Landing and the upper Monterey Canyon. Most of the Farallon Plain is now submerged beneath the Pacific Ocean.

Large mammals visited the coast in order to acquire salt and dietary minerals, to escape the heat of summer and the annoyances it brought with increased pests such as flies and mosquitoes, and to consume the lush summer grass, sedge, and browse that resulted from the increased precipitation of the seasonal fog drip.[1] It is likely that the main "migration" routes followed natural passages that allowed for easy travel.[2] In the north, migration was probably made along one of two courses, a northern route along the narrow Russian River drainage, or a more open southern route that linked the Petaluma Valley with the Bodega Bay and Tomales Bay areas via the Estero Americano and Estero de San Antonio. Ancient ancestral game trails would have marked the migration routes, much like they do in East Africa today. Mammoth trails, resembling those of modern elephants, would have been especially prominent:

> Proboscidean trails are well used, clearly identifiable, and easy to follow. They tend to be flat-surfaced (because elephants have flat feet and great weight which compresses the ground so much), measure about 45 cm wide or more, and are consistently placed year to year (Haynes 2006:22).

Migrating herds of bison and horses would have created their own trails leading to and from the coast. The landscape alongside the trails would have been altered by the presence of the megafauna. These game trails would have provided early Paleoindians with ample signs when on hunting forays (Ibid).

The Bay Area migrations were relatively short, as the greatest distance separating the interior and coast was less than 60 km. This would have been a short walk for a mammoth. In comparison, mammoths on the Great Plains are thought to have traveled distances of 300-600 km (Hoppe 2004:142). Of course, it should be noted that the Great Plains during the late Pleistocene lacked the variety and seasonal contrast of pastures that were available to megafauna in the San Francisco Bay area. The Bay Area's status as an Ice Age coastal refugium and the local Mediterranean climate combined to ensure comfortable weather and year-round lush pastures.

The total acreage of the northern Interior and Coastal Zones was large, measuring approximately 203,000 ha (502,000 acres) and 280,000 ha (692,000 acres), respectively. The southern Interior and Coastal Zones were even larger, measuring 464,525 ha (1,147,863 acres) and 437,500 ha (1,081,086 acres) respectively. Proximity between the Interior and Coastal Zones made the seasonal round a viable foraging strategy during the late Pleistocene.

II. Modeling a Seasonal Round

An examination of the Bay Area's modern-day landscape allows for certain insights into the former presence and movement of the Rancholabrean megafauna. The topographic feature known as the "Golden Gate" stands out as a key landmark for determining the ancient movements of such animals. The Golden Gate is more or less marked by the famous bridge of the same name. This is the point where the former California River flowed out of the Franciscan Valley and onto the Farallon Plain. The river was undoubtedly deep and swift at this point and it likely posed a formidable barrier to animal movement. As such, the movement of animals would have been periodically or permanently limited to one side or the other of the river in this area. The seasonal movement of megafauna between their favorite pastures would have involved an east-west migration as dictated by environmental factors. Thus, the California River would have served as a boundary separating a northern and southern seasonal migration round.

The Northern Model

Zone 1: Interior Plain and Valley

Area 1: Santa Rosa Plain North: Cloverdale south to Windsor. Approximately 38 km N-S, 19 km E-W. 722 square km = 72,200 ha (178,410 acres).

Paleontological Sites:[3]

1. Five Oaks Ranch, Cloverdale (mastodon) [UCMP V52013] [Note that this may be in the local highlands].

Area 2: Santa Rosa Plain South: Windsor south to Cotati Hill. Approximately 19 km N-S, 27 km E-W. 513 square km = 51,300 ha (126,765 acres).

Paleontological Sites:

1. Crandall, Santa Rosa (ground sloth) [UCMP V36050];

2. Yardbirds, Santa Rosa (various species including mammoth and saber-tooth cat) [Raj Naidu, personal communication 2001].

Area 3: Petaluma Valley North: Cotati south to San Antonio Creek. Approximately 27 km N-S, 20 km E-W. 540 square km = 54,000 ha (133,436 acres).

Paleontological Sites:

1. Cardinaux, east of Petaluma (bison) [UCMP V80005];

2. Ducker Ranch, Petaluma (mastodon) [UCMP V65017];

3. Eureka School, Petaluma (horse and bison) [UCMP V36046];

4. McGrew's Ranch, Petaluma (ground sloth) [UCMP 3023];

5. Petaluma site (mastodon) [UCMP V67075];

6. Brazil Ranch, east of Petaluma (bison and mammoth) [Rolfe Erickson, personal communication 2002].

Area 4: Petaluma Valley South: San Antonio Creek to California River. Approximately 8 km N-S, 6 km E-W. 48 square km = 4,800 ha (11,861 acres).

Paleontological Sites:

1. Central Channel, Vallejo (bison, shrew, mole, cottontail rabbit, ground squirrel, pocket gopher, kangaroo rat, mouse, woodrat, and vole) [UCMP V71001];

2. Northern Cove, Vallejo (pocket gopher, rabbit, etc.) [UCMP V71003];

3. Hamlet Station (Marin County) (ground sloth) [UCMP V65147];

4. Weisman Locality (Marin County) (horse) [UCMP V51006].

Area 5: Sonoma Valley: Approximately 10 km N-S, 10km E-W. 100 square km = 10,000 ha (24,710 acres).

Paleontological Sites: None known.

►Total for Areas 1-5 = 192,300 ha (475,183 acres).

Zone 2: Coastal Plain

Area 6: Farallon Plain North: Russian River south to the mouth of the California River. Approximately 75 km N-S, 20 km E-W. 1,500 square km = 150,000 ha (370,658 acres).

Paleontological Sites:

1. Bodega Head (mammoth and fossil conifers) [James West, personal communication 2001; Parkman 2005];

2. Millerton Point (bison, fossil conifers and plants) [Savage 1951:285];

3. Jasper Rock (rubbing rock) [Parkman 2002a, 2002b, 2004, 2006e, 2006f];

4. Mammoth Rocks (rubbing rocks) [Parkman 2002a, 2002b, 2004, 2006a, 2006b, 2006e].

Area 7: Mendocino Plain: Russian River north to Rockport. Approximately 122 km N-S, 10-18 km E-W (average 12 km). 1,464 square km = 146,400 ha (361,762 acres).

Paleontological Sites: None known.

►Total for Areas 6 and 7 = 296,400 ha (732,420 acres).

Zone 3: Migration Routes

Area 8: Estero San Antonio: An area linking the coastal plain with the interior Santa Rosa Plain and Petaluma Valley. Area includes the Estero Americano and Estero San Antonio, Americano Creek, Stemple Creek, and San Antonio Creek. Approximately 10 km N-S, 20 km E-W, 200 square km = 20,000 ha (49,421 acres). Note: This would have been an easy route to travel, and would have also served as an "Interior Zone" habitat.

Paleontological Sites:

1. Estero San Antonio (mammoth, mastodon, and bison) [UCMP V28042];

2. Ebibias Creek, Valley Ford (horse and bison) [UCMP V72107].

Note: Another option for travel would have been from Petaluma to Stemple Creek to Keys Creek past the town of Tomales and down Keys Creek to current Tomales Bay.

Area 9: Russian River: The Russian River drainage from Windsor to Jenner. Approximately 0.5 km N-S, 30 km E-W, 1500 square km = 1500 ha (3705 acres). Note: This would probably have been a more difficult route to travel due to steep hillsides and lush forests.

Paleontological Sites:

1. Griffith Park [14 km west by north of Santa Rosa on Monte Rio Highway] (Proboscidean) [Savage 1951:285];

2. Morningstar Ranch, Graton (mastodon) [Raj Naidu, personal communication 2001].

Area 10: Valley of the Moon: From Santa Rosa south to Sonoma along Hwy 12. Approximately 22 km N-S, 2 km E-W, 44 square km = 4,400 ha (10,872 acres).

Paleontological Sites: None known.

Area 11: The Slot: From Petaluma east to Sonoma along Hwy 116. Approximately ½ km N-S, 10 km E-W, 5 square km = 500 ha (1,235 acres).

Paleontological Sites: None known.

►Total for Areas 8-11 = 26,400 ha (65,234 acres).

The Southern Model

Zone 4: Interior Valleys

Area 12: Franciscan Valley: The California River south to San Jose. Approximately 92 km N-S, 34 km E-W, 3,128 square km = 312,800 ha (772,946 acres).

Paleontological Sites:

1. Alameda Canal (ground sloth) [UCMP V69168];

2. Alameda Creek (mastodon) [YPM – Hay 1927];

3. Alameda County (bison, *Ursidae*) [UCMP V67098];

4. Alameda County (mammoth) [WC – Hay 1927];

5. Alameda County (ground sloth) [YPM – Hay 1927];

6. Alameda Tube Excavation (ground sloth, short-faced bear, mammoth, camel, and bison) [UCMP V62027];

7. Aquatic Park, Berkeley (bison) [UCMP V40007];

8. Arroyo Agua Fria, Milpitas (horse) [UCMP V72003];

9. "Auchenia," north of Castro Valley (camel?) [UCMP V66142];

10. Bay Bridge Caisson, Oakland (horse) [Savage 1951:284];

11. Berkeley Municipal Wharf (mammoth) [UCMP V36013];

12. Boomer Hill, Newark (mastodon) [UCMP V69199];

13. Calaveras Dam, Calaveras Reservoir [just south of Mission San Jose] (mastodon) [UCMP V69199] [Note that this location is in the foothills.];

14. Centerville, Newark (horse and Proboscidea) [UCMP V53070 ?];

15. Centerville Gravel Pit, Newark (mastodon, camel, deer, and bison) [UCMP V53070];

16. Harris Street Tunnel, Oakland (mammoth) [UCMP V28041];

17. Hayward Freeway (bison) [UCMP V52058];

18. Hayward Motel (horse) [UCMP V63004];

19. Mission San Jose, Fremont (mastodon, mammoth, horse, camel, bison, and elk?) [YPM 905 – Hay 1927];

20. Montclair Playground, Oakland (mammoth and camel) [UCMP V39033];

21. Newark (camel) [UCMP V69195];

22. Niles Community (mastodon and bison) [UCMP V59033];

23. Oak Knoll Hospital View, Oakland (horse, deer, vole, and squirrel) [UCMP V58034];

24. Oakland Coliseum (ground sloth) [UCMP V64020];

25. Reiche Number 1, Hayward (horse) [UCMP V48004];

26. San Lorenzo Creek, Hayward (horse) [Savage 1951:284];

27. Shattuck Avenue, Number 1, Berkeley (ground sloth) [UCMP V67194];

28. University Avenue, Berkeley (mastodon) [UCMP V66044];

29. Yerba Buena Island, Bay Bottoms (horse) [Hutchison 1967];

30. 81st Avenue, Oakland (mammoth) [UCMP V40045];

31. Hercules Number 2, Pinole (bison, etc.) [UCMP V3002 (0302), V65288];

32. Hipparion Point Number 2, Pinole (ground sloth, mammoth, and horse) [UCMP V52032];

33. Lone Tree Point Numbers 1-2 (Rodeo Pecten Point) San Pablo Bay (mammoth, horse, camel, deer, pronghorn, ground sloth, llama, rabbit, and bison) [UCMP 1355, V12001, V40005];

34. Pinole, Orleans Drive (horse, pronghorn?, and ground sloth?) [UCMP V63013];

35. Pinole (mastodon, mammoth, horse, pronghorn, and bison) [UCMP 1361, 1378, V63013, V65660, V67106];

36. Pinole Beach, Pinole (horse and camel) [UCMP V65660];

37. Pinole R.R. Numbers 1 and 3, Pinole (mastodon, horse, and bison) [UCMP 1361, 1378, V67106];

38. Rodeo Oyster Bed, San Pablo Bay (mammoth) [UCMP 524];

39. Tormey A, Pinole (mammoth, camel, horse, and pocket gopher) [UCMP V46015, V53002];

40. Union Oil Company, Oleum Refinery (horse) [UCMP 1375];

41. Union Oil Company Tank Farm, Hercules (mastodon, mammoth, and camel) [UCMP V34028];

42. Bay Bridge, San Francisco (bison) [Savage 1951:285];

43. Bay Bridge Numbers 1-2, San Francisco (mammoth and horse) [UCMP V34011, V69186];

44. Bay Shore Southern Pacific Tunnel Number 4 North, Bay Park or Roman (mastodon) [UCMP 1076];

45. San Francisco (deer and bison) [McDonald 1981];

46. Treasure Island, San Francisco Bay (mammoth);

47. Twin Peaks Tunnel, San Francisco (ground sloth) [UCMP V65243];

48. Menlo Park Station (mastodon) [Savage 1951:285];

49. Middlefield Road, Redwood City (camel) [UCMP V74164; USGS 1302];

50. Millbrae (mastodon, mammoth, and horse) [Savage 1951:285];

51. San Francisquito Creek, Menlo Park (ground squirrel, and pocket gopher) [USGS 1206];

52. San Francisquito Creek Northwest, Menlo Park (mastodon) [USGS];

53. San Mateo (mastodon) [Hay 1927];

54. Skyline Drive, South San Francisco (moose?) [UCMP V62003] [Note that this is in the highlands];

55. South San Francisco (horse) [UCMP V63019];

56. Alma Street Underpass at Page Mill Road (mammoth, horse, and camel) [USGS 1203];

57. Milpitas (bison) [UCMP V49016];

58. Mountain View (mastodon) [Hay 1927];

59. Mountain View Dump, Mountain View (ground sloth, mammoth, horse, camel, deer, bison, etc.) [USGS 1227];

60. Rose Trombley's Back Yard, San Jose (camel) [Jefferson 1991b:88];

61. Santa Clara Valley (horse) [Jefferson 1991b:88];

62. Stanford University, Corte de Madera Creek (mammoth) [Hay 1927];

63. Sunnyvale Sewer, Sunnyvale (mammoth, horse, camel, Ursus sp., ground squirrel, and pocket gopher) [USGS 1218];

64. Veterans Hospital, Matadero Creek (ground sloth, mammoth, horse, cottontail rabbit, etc.) [USGS 1001, 1002].

Area 13: Santa Clara Valley: San Jose south to San Juan Bautista. Approximately 62 km N-S, 8 km E-W, 496 square km = 49,600 ha (122,564 acres).

Paleontological Sites:

1. San Felipe, east of Gilroy (peccary) [UCMP V65061].

Area 14: Livermore Valley: Approximately 10 km N-S, 18 km E-W, 180 square km = 18,000 ha (44,479 acres).

Paleontological Sites:

1. Arroyo Las Positas, Livermore (dire wolf, mastodon, mammoth, horse, camel, and bison) [UCMP V69167];

2. California Sand and Gravel Company Pit, Numbers 1-2, Pleasanton (mammoth and bison) [UCMP V61011 and V75112];

3. Delta Mendota, Livermore, Numbers 10-12, 18, 21-23, 26 (ground sloth, mastodon, mammoth, horse, camel, bison, and pocket gopher) [UCMP V47027-47028, V48001-48003, V48016-48018, V48060-47028, V69166];

4. Doolan Canyon, Livermore North (ground sloth, mastodon, horse, and bison];

5. Livermore (dire wolf, American lion, camel, and bison) [Harris 1985];

6. Livermore Valley (mammoth, horse, bison, llama, and elk or deer) [USNM – Hay 1927];

7. Livermore West (horse and bison) [UCMP 1077];

8. P.C.A. Pit (mammoth) [UCMP V70151];

9. Positas, Livermore (mastodon, mammoth, horse, and camel) [UMP V49001];

10. Prune Avenue, Livermore (pocket gopher, mole, ground squirrel, woodrat, vole, and mouse,) [UCMP V53001];

11. Sunol, Pleasanton (mastodon) [UCMP V65035].

Area 15: San Ramon Valley: Approximately 28 km N-S, 5 km E-W, 147 square km = 14,700 ha (36,324 acres).

Paleontological Sites:

1. Burke Ranch, Amador Valley (mammoth, bison, and horse) [UCMP V40047];

2. Alamo Creek, Number 2, Amador Valley (ground sloth and squirrel) [UCMP V44004];

3. Dinsmore Used Car Lot, Danville (mammoth) [UCMP V61008];

4. Mount Diablo, Diablo Summit Road (mammoth, bison, and horse) [UCMP V34006] [Note that this is on the side of the mountain, well above the valley];

5. San Ramon Creek (bison) [UCMP V39027].

Area 16: Concord Plain: Approximately 35 km N-S, 17 km E-W = 595 square km = 59,500 ha (147,027 acres).

Paleontological Sites:

1. Bolinas Creek (horse) [Savage 1951:284];

2. Lafayette (Proboscidea) [Savage 1951:284] [Note that this is downtown Lafayette, in hilly terrain – thus, this is probably mastodon];

3. Las Trampas Creek, east of Lafayette (Proboscidea) [Savage 1951:284];

4. Antioch Numbers 2-3 (ground sloth, mastodon, mammoth, horse, camel, bison, deer, and badger) [UCMP V16004, V40008, V60007];

5. Antioch Dam, Antioch (mastodon) [UCMP V66050];

6. Bulls Head Point, Martinez (ground sloth, and horse) [LACM 4626, MCZ, UCMP 1359, 1363];

7. Byron (horse) [Savage 1951];

8. Charles Hill, Orinda (bison) [UCMP V36009] [Note that this is hilly terrain];

9. Concord Numbers 1-2 (mammoth, bison, and horse) [UCMP V51016, V65310];

10. Garretson, Oakley (mammoth, horse, shrew, pocket gopher, rabbit, etc.) [UCMP V63012];

11. Heidorn, Oakley (horse) [UCMP V47019];

12. Highway 40, Number 1, Oakley (ground sloth, pocket gopher, mammoth, camel, elk, deer, bison, fox, etc.) [UCMP V52025];

13. Jersey (mammoth) [Hay 1927];

14. Jersey Island (bison) [Hay 1927];

15. Las Juntas Number 1, Concord (ground sloth) [UCMP V57005];

16. Pacheco Numbers 1-2, Concord (mastodon and mole) [UCMP V77117, V78027];

17. Mokelumne Aqueduct Numbers 1 and 3, Pittsburg (pocket gopher) [UCMP V60030];

18. Pleasant Hill High School (ground sloth) [UCMP V60006];

19. Sand Mound Slough, Oakley (mammoth), [UCMP V65254].

►Total for [Bay] Areas 12-13 = 362,400 ha (895,510 acres).

►Total for [Interior] Areas 14-16 = 92,200 ha (227,831 acres).

►Total for Areas 12-16 = 454,600 ha (1,123,341 acres).

Zone 5: Coastal Plain

Area 17: Farallon Plain South : Mouth of the California River south to the Monterey Canyon (San Benito River? [See Savage 1951:223, citing Allen 1946]). Approximately 132 km N-S, 8 ($1/5^{th}$ of coastline or 162 square km) -35 km ($4/5^{th}$ of coastline or 3,675 square km) = 3,837 square km = 383,700 ha (948,143 acres).

Paleontological Sites:

1. Cliff House Beach (mammoth) [Hay 1927];

2. Fleishhacker Beach, San Francisco (mastodon, mammoth, horse, and bison) [UCMP V39001];

3. Ocean Beach (mastodon) [Savage 1951:285];

4. Pacific Street, San Francisco (ground sloth) [Hay 1927] [Pacific Ave.? This is probably the hilly and/or sand dunes area of the San Francisco];

5. Ano Nuevo State Reserve (mammoth, horse, and camel) [Jefferson 1991b:83];

6. Half Moon Bay, Arroyo de Leon (mastodon and mammoth) [Hay 1927];

7. Laguna Alta, Pacifica (horse and elk) [UCBMVZ; USGS 1230];

8. Montara Beach (mammoth and saber-tooth cat) [USGA 1483];

9. Mussel Rock Number 2 (ground sloth, mammoth, horse, camel, and bison) [UCMP V40018];

10. Mussel Rock, South San Francisco (Proboscidea and bison) [UCMP V35005];

11. Seven Mile Beach, San Francisco (bison) [UCMP V36006];

12. Aptos (mammoth) [Hay 1927];

13. Santa Cruz (mammoth) [Hay 1927];

14. Moss Landing (camel) [UCMP V49015].

Zone 6: Migration Routes

Area 18: Fort Point: South bank of California River at the Golden Gate. Essentially, the Interior and Coastal Zones connect where the City of San Francisco is located. Animal herds could have moved from one zone to the other by moving along the riverbank. They may have also crossed through the sand dunes that San Francisco was later built upon. Approximately 3 km N-S, 5 km E-W = 15 square km = 1,500 ha (3,706 acres).

Paleontological Sites: None known.

Area 19: Crystal Springs Reservoir: It was possible for megafauna to travel from Palo Alto to South San Francisco by accessing the modern-day Crystal Reservoir (San Andreas Fault) which allowed for a NW-SE movement from the Franciscan Valley over to the coastal plain via San Andreas Lake and the Lake Merced area of San Francisco. Approximately 42 km N-S, 1 km E-W = 42 square km = 4,200 ha (10,378 acres).

Paleontological Sites: None known.

Area 20: Pilarcitos Creek: From modern day Crystal Springs Reservoir (San Andreas Fault) just west of Belmont, it may have been possible for herds to move west to the Half Moon Bay area via Pilarcitos Creek (modern day Hwy 92). Approximately 1 km N-S, 10 km E-W = 10 square km = 1,000 ha (2,471 acres).

Paleontological Sites:

1. Pilarcitos Lake (Pilarcitos Valley) (bison) [Hay 1927].

Area 21: Rodeo East: From the south bank of the California River near Rodeo east to Martinez. Animal herds could have moved from the Franciscan Valley to the Concord Plain by moving along the riverbank. Approximately 1.25 km N-S, 7.5 km E-W = 9 3/8 square km = 937 ha (2,316 acres).

Paleontological Sites:

1. Rodeo (ground sloth, American lion, saber-tooth cat?, mammoth, horse, camel, and bison) [UCMP V66042];

2. Rodeo Station, Number 2, Rodeo (ground sloth, mammoth, horse, camel, deer, bison, and mouse) [UCMP V66042];

3. Port Chicago (horse) [UCMP Online Catalog].

Area 22: Niles Canyon: From Niles to the Livermore Valley via Niles Canyon. Approximately 1.25 km N-S, 7.5 km E-W = 9 3/8 square km = 937 ha (2,316 acres).

Paleontological Sites: None known.

Area 23: Crow Canyon: From Castro Valley to the San Ramon Valley via Crow Canyon. Approximately 1 km N-S, 12 km E-W, 12 square km = 1,200 ha (2,965 acres).

Paleontological Sites:

1. Crow Canyon, Edenvale (horse and camel) [Savage 1951:284].

►Total for [Western] Areas 18-20 = 6,700 ha (16,556 acres).

►Total for [Eastern] Areas 21-23 = 3,074 ha (7,596 acres).

►Total for Areas 18-23 = 9,774 ha (24,152 acres).

►Total for [Interior Plain/Valley] Areas 1-5 and 12-16 = 646,900 ha (1,598,525 acres).

►Total for [Coastal Plain] Areas 6, 7, and 17 = 680,100 ha (1,680,564 acres).

►Total for [Migratory Corridor] Areas 8-11 and 18-23 = 36,174 ha (89,386 acres).

►Total for Interior and Migratory Areas (Areas 1-5, 8-16, 18-23) = 683,074 ha (1,687,911 acres).

►Total for Coastal Plain (Areas 6, 7, & 17) = 680,100 ha (1,680,564 acres)

►Total for Areas 1-23 = 1,363,174 ha (3,368,475 acres).[4]

III. A Rancholabrean Bestiary

Perhaps the greatest diversity and concentration of wildlife in existence today is found on the Serengetti Plains of East Africa. Paleontologists note that the Serengetti of the late Pleistocene was many times richer in terms of its wildlife. The California Serengetti is thought to have been even richer yet. Indeed, a magnificent array of wild animals characterized the San Francisco Bay area during the late Pleistocene. While some of the Rancholabrean species still exist in the area (e.g., deer and mountain lion), many others went extinct between 13,000-10,000 yrbp (e.g., mammoth and saber-tooth cat). The animals of the late Pleistocene can be categorized by whether they were predator or prey species and whether they were loners or moved in packs, prides, and herds. The following is a description of some of the more important of these animals.

Large Predators - Pack or Pride Animals (Canids):

The Wolf

●Dire Wolf (*Canis dirus*) [Extinct type] [Found at Rancho la Brea and in the San Francisco Bay area] The dire wolf was comparable to a good-sized timber wolf. It apparently hunted in packs and had a powerful neck and jaws for dragging downed game (Moratto 1984:36-37).

Predators rather than prey species are the most common animals found at Rancho La Brea, and the dire wolf is the most common predator of all to be found there (Stock 1956:32). The dire wolf was almost the size of the largest timber wolves alive today. The gray wolf of Denali National Park may give some idea as to carrying capacity. Denali National Park measures 1,880,000 ha in size. There are thought to be12-19 wolf packs currently residing within the park (and about 1,500 packs in the State of Alaska). Wolves

are legally trapped in portions of the park, so total numbers vary from year to year. According to the park staff, there were 150-200 wolves in the park in the early 1990s, and 100-130 in 1995-1996. The higher numbers of wolves (i.e., 150-200) suggests that wolf packs might range from about 8-16 animals, with 10 perhaps being an average number for the ideal pack size. If we place 200 wolves at Denali National Park, that amounts to 1 wolf per 9,000 ha. Using this same ratio for the San Francisco Bay area, it would mean that there may have been 156 wolves in Areas 1-23 (or about 15 wolf packs).[5] However, since there would have been wolves in the Bay Area's uplands and forested areas, the true number would have been about 200 wolves or 20 packs of 10 animals each. Of course, this is based on the present Denali National Park ecosystem. The Bay Area ecosystem of the late Pleistocene would have been different in terms of prey animals, competing predators, landscape, and climate, thus there would have been a different carrying capacity for wolves. I suspect that there would have been considerably more wolves in Pleistocene San Francisco than currently found at Denali. Therefore, I would propose a total of 400 wolves, in 40 packs, for the late Pleistocene Bay Area. That would mean 1 wolf per 3,500 ha (of Areas 1-23).

The dire wolf equaled a large gray wolf in size (Kurtén and Anderson1980:171). There were at least 1,646 individuals found at Rancho La Brea (Ibid:172). The absence of true hyenas in the Rancholabrean faunal record may account for the hyena-like specializations such as the dire wolf's very robust carnassials (Ibid:171). A hyena-like hunting-scavenging mode of life would explain why so many dire wolves were found in the tar pits at Rancho La Brea (Ibid:172). Apparently, the dire wolf sometimes turned to eating carrion (Stock 1956:32).

Californian and Mexican dire wolves (found in California and the Southwest during the late Pleistocene) were smaller than those wolves found further east. The eastern wolves had longer legs, perhaps being an adaptation for faster running on the Great Plains, although they would have not been as fleet footed as the timber wolf (*Canis lupus*). The dire wolf became extinct about 10,000-9,000 yrbp (Ibid:172).

The size of modern-day gray wolf packs depends on the availability of food and proximity of other wolf packs. In Alaska, packs that prey on deer number 5-10 animals, while packs that prey on moose have 10-20 members and occasionally as many as 29 members in the pack. Thus, in areas characterized by larger-bodied prey, wolf packs are larger accordingly. Rancholabrean packs probably mirrored the bigger packs of Alaska with at least 10 and probably as many as 20 animals per pack. In Rancholabrean times, the dire wolf apparently played a similar role as that of the modern-day hyena on the Serengetti Plain. In other words, the dire wolf was a hunter-predator-scavenger. The wolf probably competed with the American lion for prey. With skill and bravery, wolf packs probably drove lion prides off kills (especially those without an adult male lion present) just as hyena packs do in Africa today.

The carrying capacity of a wolf pack depends on the environment, presence of year-round prey animals (large ungulates such as deer, elk, moose, and bison), and the amount of competition from other packs. One wolf requires anywhere from 20-600 square miles

(5,180-155,399 ha) for its range. Thus, a wolf pack numbering ten adults would require 200-6,000 square miles (51,800-1,553,990 ha). These range numbers are based on landscapes less productive than the Rancholabrean-era Bay Area, so I would assume the low end of 5,180 ha (20 square miles) needed per wolf as a figure for the Bay Area's Rancholabrean dire wolves. That would mean that the Bay Area's 1,410,499 ha of prime land would have sustained 272 wolves. However, this does not take into account the possibility that the dire wolf filled a somewhat different niche from that of the modern-day wolf. The dire wolf was a predator-scavenger (as suggested by their great numbers at Rancho La Brea), thus it may have increased its numbers (and decreased its range requirements) by filling this niche. Therefore, a better figure for the range of the dire wolf would be around 3,500 ha per dire wolf. That would give us an optimum number of 389 dire wolves in the Rancholabrean Bay Area. These wolves undoubtedly filled niches somewhere intermediate between that of the modern-day Alaskan gray wolf and African hyena.

●Gray Wolf (*Canis furlongi*) (also known as Timber Wolf) [Extinct type] [Found in Rancho La Brea] Compared to the numerous remains of the dire wolf, very few specimens of the gray wolf were found at Rancho La Brea (Stock 1956:33).

The Coyote

●Coyote (*Canis orcutti*) [Extinct type] [Found in Rancho La Brea] The coyote probably assumed a much more important role as predator in the Holocene, following the extinction of the wolf and other large predators. The coyote is the second most common predator found at Rancho La Brea, occurring about $1/10^{th}$ as often as the dire wolf (Stock 1956:33). The coyote may be less numerous than the wolf at Rancho La Brea due to some superior intelligence on its part for avoiding the tar, or because they were not as common. Following the extinction of the other predators (especially the dire wolf), the coyote assumed a greater role as predator, and, undoubtedly, increased its population to its historic levels. Like its modern counterpart, the Pleistocene coyote hunted small game.

Large Predators - Pack or Pride Animals (Felines):

Late Pleistocene felids in North America in fall into two main groups. Most belong to the modern cat types, including the genera *Panthera* (great cats in leopard to lion range) and *Felis* (pumas, lynxes, and smaller cats). *Panthera atrox* was an enormous plains-living cat. A second group of felids is formed by the dagger-toothed cats, represented by the saber-toothed form, *Smilodon* (Kurtén 1972:207).

The American Lion

●American lion (*Panthera atrox*) [Extinct type] [Found at Rancho La Brea and in the San Francisco Bay area] The American lion was enormous, being about ¼ larger than the living cats of Eurasia (Stock 1956:39). At the peak of its success, the lion ranged from Africa through Eurasia and North America into South America, and it appears to have been the most wide-ranging wild land mammal species of all time (Kurtén and Anderson 1980:191). Given its high degree of cephalization, it is probable that the American lion hunted in groups, as do the living lions of Africa (Kurtén and Anderson 1980:191). It had a larger brain than any of the Pleistocene or modern-day lions. It is found in large numbers only at trap sites; the minimum number estimated at Rancho La Brea is 76 individuals (Ibid). That is a relatively-small number when compared to the 1,646 dire wolves that have been found in these same tar pits. The lion's extinction in the New World appears to have occurred around 10,000 yrbp (Ibid:192).

Based on historic East African lion numbers (cf. Estes 1999:318), there were probably about 800 American lions in the Bay Area at any one time. About 230 lions may have occupied the North Bay and 570 lions in the South Bay. This would mean that there was about 1 lion per 1,700 ha of the Bay Area (i.e., Areas 1-23). There may have been resident lions living on the Farallon Plain (i.e., Areas 6 and 16) although it seems more likely that lions would have occupied the coast seasonally along with the migrating herbivores from the interior. Assuming that there were few if any megaherbivores residing year-round on the coast, there should have been no lions living there permanently as well.

The American lion would have occupied grassland, savanna, and the margins of forestlands. It is not as represented at Rancho La Brea as the saber-tooth cat, but it is certainly more common than the cougar (Stock 1956:40). The American lion probably preferred open country, as seen by its absence in the fossil record in the East and peninsular Florida (Kurtén and Anderson 1980:191). It is possible that the number of lions should be lowered due to the presence of "competing" predators during the Pleistocene. In other words, did the lions of the California Serengetti fill a sole niche, or did they have competitors? It is probably safe to assume that the American lion competed in its niche with the short-faced bear and dire wolf, and perhaps the saber-tooth cat as well.

The Saber-Tooth Cat

●Saber-tooth Cat (*Smilodon californicus*) [Extinct type] [Found at Rancho La Brea and in the San Francisco Bay area] This famous predator was about the size of the modern African lion (Stock 1956:36). It was common at Rancho La Brea indicating that it hunted out in the open, although it was likely found also in the forest margins. It does not appear to have been fleet-footed like the lion or tiger, and thus would have necessarily preyed on

large slow-moving animals, such as the mammoth, mastodon, and ground sloth (Stock 1956:36).

The saber-tooth cat may have been a pride animal. If so, then it probably competed with the American lion (i.e., shared the same ecological niche). On the other hand, if the saber-tooth was not a pride animal but hunted alone instead, it may have complemented the lion. Both cats probably hunted the giant ground sloth, and both would have taken infant mammoths if the opportunity arose. The saber-tooth may have been adept at hunting the mastodon, using its large saber teeth to impale the animals from their topsides. If so, then the saber-tooths may have specialized in hunting mastodons. The American lion would have specialized on prey animals that required a communal or pride approach, such as the bison, horse, and camel. If the saber-tooth was a solitary hunter, then it would have gone after prey a single cat could bring down. Saber-tooth cats were not built for great speed, thus they apparently used cunning and stealth to ambush their prey. Whereas they undoubtedly hunted on the plains, it is also likely that they hunted in the highlands and forests as well, places where they could ambush mastodons and other browsers in thick cover. Prides of American lions may have preferred the open plains where their communal approach to hunting allowed them to isolate and capture fleet-footed prey such as the bison and antelope. Apparently, the saber-tooth cat preyed on large, slow-footed animals, which it stabbed in the neck or belly to produce heavy bleeding and death (Kurtén and Anderson 1980:188). Many saber-tooth specimens were found at Rancho La Brea, including many with signs of injuries. Apparently, injured saber-tooths hung out at the tar pits looking for easier prey (Ibid). The saber-tooth cat went extinct about 9,000-8,000 yrbp (Kurtén and Anderson 1980:188).

If there were indeed 802 American lions in the Bay Area, there was probably half that number of saber-tooth cats in the area. I would suggest a total number of 454 saber-tooth's in the Bay Area, with about 150 of them residing in the North Bay. That would mean about 1 saber-tooth for every 3,000 ha of the Bay Area (i.e., Areas 1-23). The number of saber-tooths would have been less than the lions due to the likelihood that they were solitary hunters and thus they needed a larger territory to subsist. To their advantage was the probable fact that they included the lion's grassland range in their own, as well as a greater amount of forestland. Still, the number of saber-tooths should have been smaller than that of the lions.

The Scimitar Cat

●Scimitar Cat (*Homotherium serum*) [Extinct type] [Found at Rancho La Brea] The scimitar cat is closely related to the saber-tooth cat. It also occurs throughout the Rancholabrean, although the animal is much rarer than the saber-tooth. Kurtén and Anderson (1980:190) have described the hunting habits of the scimitar cat:

> Apparently, the scimitar cat preyed mainly on mammoth (and mastodont) calves…. The cat may have attacked from ambush, inflicting a quick, slashing stab which caused the prey to bleed profusely, and then have gone into hiding

until the parents left the dead animal. The extinction of the scimitar cat is probably linked to that of the mammoth, its favorite prey.

The Jaguar

●Jaguar (*Panthera onca*) [Extinct type] [Found at Rancho La Brea] Now extinct in California, jaguars are thought to have existed as far north as San Francisco until the 1820s and in the Palm Springs area until about 1860 (Edwards 1996:16).

The American Cheetah

●American cheetah (*Acinonyx trumani*) [Extinct type] Remains of the American cheetah have yet to be found in the San Francisco Bay area, although they do occur in Nevada (Adams 1979; Kurtén and Anderson 1980:194). Thus, they were likely present in the Bay Area (cf. Edwards 1996:16). This species was similar in size to the living cheetah of Africa, and its mode of life probably resembled the modern-day cheetah (Kurtén and Anderson 1980:194). A cheetah is described from the Serengetti as hunting gazelles, and following them to the woodlands at the onset of the dry season (Scott 1988:55). The North American cheetah was smaller than the American lion, and capable of pursuit speeds of about 35m/second (Moratto 1984:36).

Predators - Non-Pack or Pride Animals (Felids):

The Cougar

●Cougar (*Felis daggetti*) (also known as puma and mountain lion) [Extinct type] [Found at Rancho La Brea] Remains of the cougar are found less often at Rancho La Brea than are the remains of the American lion and saber-tooth cat (Stock 1956:40). This may be because the cougar tended to inhabit hilly and rocky terrain instead of open grasslands. It is doubtful whether the cougar and lion competed for the exact same prey (i.e., occupied the same ecological niche). Nor did the saber-tooth cat occupy the same niche as the lion (or cougar). In the late Pleistocene Bay Area, it is likely that the cougar was restricted to the more remote and mountainous regions and played a lesser role as a predator (in terms of its numbers) than it did in historic times. Also, it probably did not include much of the 1,409,499 ha of prime Bay Area landscape in its late Pleistocene range. However, upon extinction of the great predators (American lion, saber-tooth cat, and short-faced bear), both the cougar and grizzly would have expanded their territory dramatically. By preying on deer and elk, these two animals would have opened up their range as their prey opened up their range (i.e., deer and elk would have increased as they filled the spaces) abandoned by the megaherbivores (mastodon, camel, horse, bison, etc.). The relationship that existed between the cougar/grizzly and deer/elk was one of rapid increase in both population numbers and available range during the early Holocene.

In modern-day Colorado, cougars need 40-360 square miles (10,360-93,240 ha) of range depending on the prey base. Males tend to have a considerably larger range than do females.

The Lynx

●Lynx ["Bobcat"] (*Lynx rufa fischeri*) [Extinct type]. [Found at: Rancho La Brea]. The modern lynx hunts small prey.

Predators - Non-Pack or Pride Animals (Ursids):

Three species of bears called California home during the late Pleistocene. These were the short-faced bear, brown (grizzly) bear, and black bear. Only the black bear remains in existence today.

The Short-faced Bear

●Giant Short-faced Bear (*Arctodus simus*) [Extinct type] [Found at Rancho La Brea and in the San Francisco Bay area]

The giant short-faced bear was the largest carnivorous mammal ever to live in the New World. It stood 130 cm high at the shoulder (compared to 100 cm for the grizzly bear) and weighed over one ton. It was armed with a battery of shearing teeth unlike those of omnivorous true bears and it had long legs designed for great speed (Moratto 1984:37). It was the "most powerful carniverous mammal which has ever lived on our continent" (Cope 1891:998). It is thought "to have been more fleet of foot, as well as more rapacious, than living types of bears" (Kurtén 1969:23-24).

Because the short-faced bear had legs built for running, it is likely that this predator lived out on the grasslands and ran down fleet-footed prey. It may have overlapped the ecological niche occupied by the American lion, as the lion was probably a competitor of the great bear. The short-faced bear is more common at Rancho La Brea than the grizzly or black bear (Stock 1956:34-35).[6] I estimate that the Bay Area sustained a short-faced bear for every 3,000 ha of land. If so, then there would have been at least 454 of the bears present at any one time. Following the extinction of the short-faced bear, the grizzly and black bear undoubtedly expanded their ranges and importance as predators. The giant short-faced bear was "…the most powerful predator of the Pleistocene fauna of North America" (Kurtén and Anderson 1980:180). Its demise may be associated with invading grizzly bears, although this is not certain (Ibid: 182).

The Brown Bear

●Brown Bear (*Ursus arctos*) [Extinct type] [Found at Rancho La Brea and in the San Francisco Bay area]

The brown bear is known as the grizzly bear in California. It went extinct in the historic period (1920s). The grizzly probably occupied grasslands, savanna, forest, and mountain land, just as they did in the historic period. However, it is likely that they were more restricted during the late Pleistocene, and were perhaps found primarily in the uplands along with the cougar. Following the extinction of the giant short-faced bear, American lion, and saber-tooth cat, the grizzly became the major predator, and probably at that time expanded out onto the grasslands and valley floors, occupying the ecological niches given up by the extinct predators. Although some grizzlies were undoubtedly on the flatlands along with the short-faced bears and lions, it seems unlikely that their numbers would have been significant until after the time of extinction.

In Pleistocene times, the grizzly may have primarily inhabited the uplands where it preyed on deer and other medium-size game. In late prehistoric times, it is estimated that there were about 10,000 grizzlies in California (Storer and Tevis 1955). That means that there was a bear for every 4,500 ha throughout California, including the desert, forest, and high mountains. Because some of the state was not good brown bear country, it is likely that only half of the state was inhabited, meaning there was one bear per 2,250 ha. However, some areas were more attractive to bears, including the San Francisco Bay area, where the numbers would have been higher. If the Bay Area was twice as populated as the state as a whole, there would have been 1 bear per 1,125 ha for a total of 1,252 bears in the Bay Area (i.e., Areas 1-23). This number, however, does not account for the forested and uplands areas that were not computed in Areas 1-23. Thus, the total number of grizzlies should be adjusted upwards to account for this additional bear country.

I would suggest that there were probably a total of 1,500 grizzlies living in the Bay Area during protohistoric times. However, it seems likely that there would have been considerably fewer grizzlies living in the Bay Area during the late Pleistocene. In fact, I would suggest that there were fewer than 500 grizzlies in the Bay Area at 15,000 B.P., with the majority of them relegated to the uplands along with the deer and cougars. After 10,000 yrbp (i.e., following the Rancholabrean extinctions), though, the grizzly moved into abandoned ecological niches left behind by the American lion, saber-tooth cat, short-faced bear, and perhaps the dire wolf (which probably had a somewhat later date of extinction). Upon occupying additional ecological niches, the overall number of grizzlies would have increased accordingly.

The Black Bear

●Black Bear (*Ursus optimus*) [Extinct type]. [Found at Rancho La Brea]
The black bear would have occupied the upland forests during the late Pleistocene, and would have represented a minor predator.

Predators - Non-Pack or Pride Animals (Other):

The Gray Fox

●Gray Fox (*Urocyon californicus*) [Extant type]. [Found at Rancho La Brea]. Like the modern gray fox, the Pleistocene fox is thought to have hunted small game.

Large Prey - Herd Animals (Ungulates - Grazers)

The Mammoth

●Columbian Mammoth (*Mammuthus columbi*) [Grazer] [Extinct type] [Found at: Rancho La Brea and in the San Francisco Bay area] The Columbian mammoth had molars comparable to those of the modern Indian elephant, which is a mixed grazer-browser (Edwards 1992:4). The mammoth stood as high as 13 feet (3.9 m) at the shoulder (Harris and Jefferson 1985:26). It could weigh up to 11,000 kg (24,250 lb) (Moratto 1984:37).

Given the mammoths' great weight, it is very likely that they broke some of the rocks they tread upon while walking on trails and when crossing streams. Many of these broken rocks would resemble the rocks broken by people during stone tool-making activities. But instead of being artifacts, the mammoth creations are considered to be zoofacts. I have estimated that mammoths created more than 70 billion zoofacts in the northern San Francisco Bay area alone (Parkman 2006c).[7]

Elephant herds normally average 10-20 animals (Owen 1981:45). A cohesive herd of 9-11 females and their calves is the basic social unit, led by the biggest and oldest female. Groups that grow larger tend to split into two or three family units, but they normally stay in the same vicinity and often associate (Alden *et al.* 1995:520). Mammoth herds were probably very similar in their composition.

Using a variety of information, including historic elephant data from Africa, I estimate that the Bay Area sustained one mammoth per 1,879 ha of land (i.e., Areas 1-23). If accurate, it would mean that at any one time, about 725 mammoths called the Bay Area home. This seems reasonable given the rich environment that was found in the Bay Area fifteen thousand years ago. It is conceivable that there were far more than 750 mammoths present in the Bay Area. For modern elephants, home range size is correlated with their habitat. In lush habitats, an elephant's home range may be no more than 15 square km (1500 ha), while in very arid regions individuals might range over more than 3,000 square km (300,000 ha) (MacClintock 1984:48). If the home range of the mammoth was as low as 1500 ha in the Bay Area, then there could have been as many as 908 herds of mammoth living there at any one time. Assuming that mammoth herds were each comprised of 10-20 animals, this model then suggests that there could have been 9,080-

18,160 mammoths living in the Bay Area at one time. Those numbers sound exceedingly high to me. Therefore, for the time being, a total of 725 mammoths seems more appropriate for the San Francisco Bay area during the late Pleistocene.

The mammoth was the premiere keystone species of the California Serengetti. As is true with the modern elephant, the mammoth's behavior would have altered ecosystems (Haynes 2006:20). They destroyed forests and helped convert them to grasslands. They dug and enlarged waterholes, dug pits for mineral-rich earth, and created wallows that may have led to vernal pools. The created well-established trail systems that were used by other species, including the first Paleoindians. Some of these mammoth trails became Indian trails and later the trails of Euro-American pioneers. More than a few of these trails are probably well-traveled highways today, such as State Highway 12 through the Valley of the Moon and perhaps State Highway 1 from Rockport south to Bodega Bay.

Like modern elephants, the mammoth was undoubtedly an intelligent and caring animal. Their brains were probably designed for a rich emotional life similar to that of humans. The brain of almost every mammal is already about 90 percent of its adult weight at birth. Humans are exceptional, as our brains at birth weigh only about 25 percent of their adult weight. Elephants are right behind us, with brains weighing about 35 percent of their adult weight. Therefore, we can assume that elephants live as rich an emotional life as any creature on earth (Page 1999:202). The life of the mammoth should have been just as rich and rewarding.

The Bison

●Long-Horned Bison [*Bison latifrons*) [Grazer] [Extinct type] [Found at: Rancho La Brea and in the San Francisco Bay area]. The long-horned bison went extinct about 25,000 yrbp.

●Ancient Bison (*Bison antiquus*) [Grazer] [Extinct type] [Found at: Rancho La Brea and in the San Francisco Bay area]. The ancient bison went extinct between 12,000-10,000 yrbp.

Like mammoths, bison were grazers. Grass comprised 80-90% of the diet of American plains bison (*Bison bison*) studied under natural conditions (Guthrie 1990:176; Lott 2002). Modern bison consume some forbs and woody browse, but browse appears to be their lowest choice. A skull of *Bison antiquus*, collected in Sonoma County, has a broad snout suggestive of a grazer (Edwards 1992:4). Late Pleistocene bison dung from Cowboy Cave, Utah was found to contain mostly grasses and sedges (Hansen 1980). At Rancho La Brea, however, the epidermal fragments recovered from bison teeth suggest that *B. antiquus* was primarily a browser, perhaps with a seasonal emphasis (Akersten *et al.* 1988).

A modern-day male bison (*Bison bison*) stands about 6 feet (1.8 m) high at the shoulder (Elms 1986:42). In comparison, *Bison antiquus* stood 7 (2.1 m) feet high and *Bison latifrons* stood 8 (2.4 m) feet high.

The long-horned bison probably lived alone or in very small groups whereas the ancient bison was clearly a herd animal. Their herds probably averaged 50-200 animals, but they could have been much larger at certain times of the year, when seasonal migrations were underway. Certain evidence from Rancho La Brea suggests that the bison was a migratory animal and appeared at the famous tar pits at particular times of the year (Jefferson and Goldin 1989). I estimate that the Bay Area sustained 1 bison (i.e., *Bison antiquus*) per 6 ha of land. This is an optimum number that assumes a number of things primarily that the Franciscan Valley and Farallon Plain were grasslands with very little woodlands. It also assumes that the grasslands had a nutrition level closer to that of tall grass prairies instead of short grass. If there was a bison for every 6 ha of land, then there would have been about 227,196 of these animals roaming about the Bay Area.

Herds of bison had a tremendous effect on the landscape. Their collective hooves cut deep and helped to aerate the soil much like a gardener's rototiller. On the Great Plains, the visual reminders of the bison were still everywhere to see not so long ago:

> Buffalo wallows made by the wild plains buffalo can still be seen today in many areas of the Dakotas, Wyoming, Montana, Kansas, Nebraska, Oklahoma, and the Texas Panhandle on grazing land that has yet to be touched by the plow. In some of these areas, rubbing stones are also visible. These are large boulders standing alone on the prairie against which the buffalo would rub themselves. Around some are depressions, several feet deep, made by the buffalo. The animals literally "walked the ground away" in a circle around the boulders as they rubbed.
>
> Where trees were available on the plains, buffalo would rub against the bark, sometimes causing the sides of the trees to be smooth. It was not uncommon for the animals, particularly the large bulls, to rub so hard that it would knock younger trees to the ground (Dary 1989:41).

Monaghan (1963:432) elaborates on why bison rubbed trees and rocks:

> Fully as permanent as the buffalo wallows were the "rubbing places" where the shaggy beasts sought to relieve itching caused by loose hair and insect bites. The irritated animals often debarked trees and polished solid rock until it became smooth and round.

The Horse

●Western Horse (*Equus occidentalis*) [Grazer] [Extinct type] [Found at: Rancho La Brea and in the San Francisco Bay area] The western horse stood about 4 feet and 10 inches tall (1.5 m).

●Giant Horse (*Equus pacificus*) [Grazer] [Extinct type] [Found in the San Francisco Bay area]. The giant horse was considerably larger than the western horse.

The ancient horse was a herd animal, and similar to those of today. It stood about 150cm high at the shoulder. Using data on the zebra from the Serengetti Plains, I estimate that there was a horse for every 39 ha of the Bay Area. Thus, there would have been about 34,953 horses living in the Bay Area at any one time.

The Llama

●Large-headed llama (*Hemiauchenia macrocephala)* [Grazer] Extinct type] [Found at Rancho La Brea and in the San Francisco Bay area] The large-headed llama is thought to have been a swift, open-country grazer (Edwards 1996:18).

Large Prey - Herd Animals (Ungulates - Browsers)

The Mastodon

●American Mastodon (*Mammut americanum*) [Browser] [Extinct type] [Found at: Rancho La Brea and in the San Francisco Bay area] The American mastodon, only distantly related to the elephant and mammoth, stood 2-3 m tall at the shoulder. It was shorter and stockier than the mammoth and differed from it in a number of other features.

Like the mammoth, the mastodon was a herd animal. It probably inhabited the forest edge and may have been little more than a casual visitor to the more expansive grasslands. When it did venture out into the grasslands, it probably fed on browse obtained from the riparian zones found alongside the streams that drained the valleys and plains. Mastodons may have migrated considerable distances if in need of food. For example, Florida mastodons are thought to have migrated north into Georgia (Hoppe *et al*. 1999).

I estimate that there was a mastodon for every 940 ha of the Bay Area. Thus, there would have been about 1,450 of these animals living in the Bay Area at any one time.

The Camel

●Camel (*Camelops hesternus*) [Browser/Grazer] [Extinct type] [Found at Rancho La Brea and in the San Francisco Bay area] This large camel had very high-crowned teeth, which are strongly suggestive of some degree of grazing, though it may have been mostly a browser (Edwards 1992:4). *Camelops* was as large as or larger than the modern dromedary. It was a herd animal and herds may have numbered about 12-20 animals.

Camels probably visited the valley grasslands seasonally, spending other times of the year in the highlands. I estimate that there was a camel for every 196 ha of the Bay Area. Thus, there would have been about 6,955 camels living in the Bay Area at any one time.[8]

The Antelope

●Antelope ["Pronghorn"] (*Antilocapra americana*) [Browser] [Extant type] [Found at Rancho La Brea and in the San Francisco Bay area]

●Antelope ["Pronghorn"] (*Antilocapra pacifica*) [Browser] [Extinct type] [Found in the San Francisco Bay area]

●Dwarf Antelope ["Pronghorn"] (*Capromeryx minor*) [Browser] [Extinct type] [Found at Rancho La Brea and in the San Francisco Bay area]

Modern pronghorns are browsers (Jones and Hanson 1985:15). While preferring shrubs and forbs, they are also known to eat some grass. "They benefit from fresh growth on forbs and grasses that results from earlier activity of grazers" (Edwards 1996:18). Modern pronghorns travel in small groups. In winter, their herds can include 50-100 animals (Kurtén and Anderson 1980:325).

The Deer

●White-tailed Deer (*Odocoileus virginianus*) [Extant type] [Browser] [Found at Rancho La Brea and in the San Francisco Bay area]. The white-tail deer is an inhabitant of woodlands, forest edges, and stream borders (Ibid:312).

●Mule Deer (*Odocoileus hemionus*) [Extant type] [Browser] [Found at Rancho La Brea and in the San Francisco Bay area]. "Mule deer are found in a variety of habitats, ranging from woods to open plains and broken terrain" (Ibid.).

The deer may have assumed more importance as a prey animal in the Holocene, after the extinction of the megafauna. Their numbers should have increased at that time.

The Elk

●American elk ["Wapiti"] (*Cervus canadensis)* [Browser] [Extant type] [Found at Rancho La Brea and in the San Francisco Bay area]

●Elk ["Wapiti"] (*Cervus nannoides)* [Extant type] [Found in the San Francisco Bay area]

The elk may have been of limited number during the late Pleistocene. However, their population should have skyrocketed following the extinction of the megafauna, especially after the demise of the most formidable of the predators.

The elk, like most other deer, are primarily inhabitants of woodland and forests. They feed on twigs, bark, herbs, and grasses (Ibid:318).

The Moose

●Moose (*Alces alces*) [Browser] [Extant type] [Possibly found in the San Francisco Bay area] The modern moose inhabits coniferous forests, preferring wet and boggy ground. They browse on conifers as well as deciduous trees. They also feed on aquatic plants, grasses, and sedges (Kurtén and Anderson 1980:317).

The Peccary

●Flat-headed Peccary (*Platygonus compressus*) [Browser] [Extinct type] [Found at Rancho La Brea and in the San Francisco Bay area] The flat-headed peccary reached the size of the European wild boar and is thought to have lived in the open country (Edwards 1996:16). However, the scarcity of their remains in California might suggest they favored woodland environments (Stock 1956:44).

Large Prey - Non-Herd Animals (Grazers)

The Ground Sloth

●Harlan's Ground Sloth (*Glossotherium harlani*) [Grazer] [Extinct type] [Found at Rancho La Brea and in the San Francisco Bay area] This large sloth stood about 6 feet (2 m) tall and lived in the grasslands (Kurtén and Anderson 1980:143). It had a massive skeleton and probably used its powerful forelimbs and claws for defense against predators.

Large Prey - Non-Herd Animals (Browsers)

The Ground Sloth

●Jefferson's Ground Sloth (*Megalonyx jeffersoni californicus*) [Browser] [Extinct type] [Found at: Rancho La Brea and in the San Francisco Bay area] This sloth was the size of an ox. It was almost as big as the Harlan's ground sloth. It lived in woodlands and forests, and browsed on leaves and twigs (Kurtén and Anderson 1980:138).

The Tapir

●California Tapir (*Tapirus californicus*) [Browser] [Found at: Rancho La Brea and in the San Francisco Bay area] The California tapir was a large form similar to the modern-day tapir of South America. Modern tapirs are browsers and forest dwellers.

Other Rancholabrean Species of Interest:

- Valley Pocket Gopher (*Thomomys bottae*). The behavior of the Pleistocene pocket gopher was similar to its modern relatives.

- California Ground Squirrel (*Spermophilus beecheyi*). Like its modern relatives, the Pleistocene ground squirrel lived in colonies.

- Badger (*Taxidea taxus*). Like its modern relative, the Pleistocene badger was generally a solitary animal.

These animals, present in the San Francisco Bay area during the late Pleistocene, may have served a similar role as that of the prairie dog of the Great Plains. On the Great Plains, prairie dog burrows were visited regularly by bison that came in order to wallow in the exposed soil. The bison grazed the grass short in the vicinity of the burrows, which added to the safety of the prairie dogs. The bison also enriched the grasses with their dung and urine, guaranteeing a continuing lush growth. On their part, the prairie dogs supplied the bison with large bare earth exposures for rolling about in.

Currently, there are relatively-extensive pocket gopher and badger burrows near the Mammoth Rocks site on the Sonoma Coast. Numerous badger holes exist on a slight hillside about 200 m from Locus 1. While badgers are not communal animals like the prairie dog, their burrows would have offered a considerable amount of bare earth for wallowing in by bison. Looking at the large holes, and the surrounding mounds of soil, it is easy to imagine a herd of bison using them for dry soil wallows. Pocket gophers and ground squirrels probably provided bison with a similar resource.

On the Great Plains, prairie dog towns were most often associated with shortgrass communities (Bolen and Robinson 1995:302-304). Taller grasses provided less safety for the prairie dogs. In other words, they prefer their burrows to be in the open where they can see danger approaching. Prairie dogs are known to abandon their towns when the surrounding grass is not grazed and becomes overgrown (Ibid:303).

> Prairie dogs are associated with the early stages of plant succession and hence thrive on heavily grazed ranges where livestock suppresses taller grasses. When

grazing pressure is reduced or eliminated, prairie dogs commonly abandon their colonies as the vegetation recovers (Bolen and Robinson 1995:303).

Prairie dog burrows are marked at the surface by mounds 0.3-0.9 m high and from 0.9-3.0 m in diameter (Ibid:248). Burrows measured in Kansas were 1.5-2.4 m deep, with about 4.3 m of lateral tunneling, but others were as deep as 4.6 m with lateral tunneling to 11 m (Ibid).

The pocket gopher (*Geomys bursarius*) has been shown to transport 2,025 kg of soil to the surface each year (Ibid:248, citing Downhower and Hall 1966). In Texas, pocket gophers were estimated to bring 807 kg of soil to the surface per ha in a tall grass area (Ibid, citing Buechner 1942). Ground squirrels and pocket gophers may bring 7-9 kg of subsoil to each square meter of surface area, for a total of about 67,200-89,600 kg/ha (Ibid:249, citing Taylor 1935; Thorp 1949). In the Bay Area, that may have resulted in enough exposed bare soil to have attracted the attention of bison during the late Pleistocene.

- Condor (*Terratornis merriam)*[Extinct type] [Found at Rancho La Brea]

This giant condor-like vulture was the largest aerial inhabitant of the California Serengetti. It is estimated to have had a wingspan of 12 feet (3.7 m) (Stock 1956:57). *Terratornis* is similar to the modern California condor (*Gymnogyps californianus*) and is thought to be the ancestor of the living species.

With the great numbers of wildlife present, and the ongoing struggles of predator and prey, the Bay Area's valley floor and coastal plain would have been littered with the carcasses of dead and dying animals. Flocks of condors were probably a common sight. As with the vultures of the African Serengetti, the condors of the California Serengetti played an important role in the efficient disposal of the dead. Five additional vulture-like birds are known from Rancho La Brea and may have called the Bay Area home as well (Ibid:58).

IV. Environment and Carrying Capacity

During the late Pleistocene, the Bay Area's interior valley/plain system (i.e., the Franciscan Valley) may have had a higher carrying capacity for predator and prey animals than did the coastal plain (i.e., the Farallon Plain). It would have depended primarily on the landscape's vegetation. For example, did the area consist of forest, savanna, or grasslands or some combination of the three? Undoubtedly, vegetation is one of the most important factors to be considered when calculating an area's carrying capacity for various species of wildlife. The reconstruction of the Bay Area's Rancholabrean-era environments is informed by the analysis of the fossil pollen, the plant phytolith record, and the local paleontological record. Of special importance in the paleontological record is the distribution of grazing versus browsing megaherbivores.

An examination of the 140 paleontological sites listed above may reveal significant patterns in the distribution of grazers versus browsers. Ground sloths may be an especially important animal to examine. It should also be noted that bison, horse, mammoth, and mastodon occur much more frequently than lion, wolf, and bear. It is only natural that prey animals, especially megaherbivores, occur more often in the fossil record than large predators. It is likely that a typical area sustained hundreds of horses and bison for every large predator, thus we should find considerably more fossil remains of the prey than of the predators. That pattern is visible in the distribution of predator/prey occurrences at the sites listed above. Thus, while the American lion and short-faced bear were only found at a few San Francisco Bay area sites, it is safe to assume that these admittedly rare species lived throughout the area albeit in relatively-small numbers.

Minimum viable population (MVP) is the minimum number of animals required to survive as a short-time (50-100 year time frame) viable population. Current genetic research indicates that for long-term population viability (e.g., 1,000 years), ten times the number of animals (and thus 10 times the amount of habitat) is needed. The MVP for the grizzly bear is estimated to be 393 bears. The MVP is 148 for wolves. That means 1,965,000-7,860,000 ha (19,650-78,600 square km) are needed for 393 bears. That is for short-term viability (50-100 years). Ten times that number of bears and habitat are needed for genetic viability (1,000 years). The area required for wolf and cougar MVP's is more difficult to calculate given the greater variation in wolf and cougar densities in different areas of Canada (where the data is derived).

Areal Comparisons

The combined North and South Model Areas for the San Francisco Bay area presented above total 1,410,499 ha (3,485,418 acres) in size. Based on historic bison (*Bison bison*) population levels on the American Plains, it is estimated that as many as 420,000 bison (*Bison bison*) could have survived in the Bay Area (North and South Areas), had they been present during the Holocene with no competition from other ungulates. For the late Pleistocene Epoch, it is hypothesized that a slightly smaller number of large herbivores could have existed in the area. This number (up to 350,000) would have included not only the ancient bison, but also mammoth, camel, and horse. Of this number, it is likely that up to 120,000 large animals would have resided at any time in the North Area and up to 230,000 in the South Area. The numbers can be further reduced by species, using historic and contemporary animal associations on the Serengetti and American Plains to estimate late Pleistocene associations in the San Francisco Bay area. For example, while the accuracy of the information cannot be verified, it is hypothesized herein that the North Area was inhabited by approximately 125 mammoth at any one time, with approximately 250 mammoth residing in the South Area.

The North Area may have supported an optimum high number of 85,000 bison (*Bison antiquus*), 12,000 horses (*Equus* spp.), 125 mammoth (*Mammuthus columbi*), 2,400

camels (*Camelops*), and 21,500 deer, elk, and other herbivores. The number of animals for the North Area may have been even higher due to the increased precipitation in the area, and thus there would have been an even higher carrying capacity. Browsers such as the mastodon (*Mammut*) and, to some degree, the camel (*Camelops*) would have utilized savanna and forest habitats, and thus overlapped with grazers. Mastodon populations in the North (and South) were probably greater than that of the mammoth. There may have been considerably less competition for browse, perhaps giving the mastodon an advantage over the mammoth. Additionally, the mastodon's smaller size, compared to the mammoth, allowed for a greater carrying capacity of similar-sized pastures. Thus, it is likely that about 250 mastodons resided in the North Area at any one time.

The South Area may have supported an optimum high number of 160,000 bison (*Bison antiquus*), 24,000 horses (*Equus* spp.), 250 mammoth (*Mammuthus columbi*), 4,800 camels (*Camelops*), 43,000 deer, elk, and various other herbivores. It is also likely that about 500 mastodons (*Mammut*) resided in the South Area at any one time.

Historic Predator/Prey Comparisons

The Great Plains measures 202,000,000 ha (500,000,000 acres) in size. Historically, as many as 60,000,000 bison (*Bison bison*) are thought to have lived on the Plains. During the late Pleistocene, the Plains were home to various megaherbivores, including mammoth (*Mammuthus* spp.), horse (*Equus* spp.), camel (*Camelops*), and ancient bison (*Bison antiquus* and *B. latifrons*). All of these animals became extinct between approximately 12,000-9,000 yrbp. It is likely that the modern bison (*Bison bison*) of the Holocene Epoch multiplied to its historic numbers due to the lack of competition from other megaherbivores (and made easier by the absence of large predators other than for gray wolves and grizzlies).

The Serengetti Plains measures 10,359,953 ha (25,600,001 acres) in size. Today, there are approximately 1,300,000 blue wildebeest (*Connochaetes taurinus*), 200,000 plains zebra (*Equus burchelli*), and 400,000 Thomson's gazelle (*Gazella thomsoni*) living on the Serengetti Plains. The herds migrate each year between the Serengetti Volcanic Grasslands ecoregion and the *Acacia-Commiphora* Bushlands ecoregion.

The Arctic National Wildlife Refuge measures 8,012,775 ha (19,800,000 acres) in size. The Refuge has a migratory herd of caribou that currently numbers 129,000 animals.

If the number of bison that were sustained on the historic Great Plains is used as a model, then the San Francisco Bay area might have sustained a herd of about 420,000 bison. That would have been about one bison for every 3 ha of land. Using the modern day Arctic caribou herds as an example, the Bay Area might have had a herd of 22,764 caribou or one caribou for every 62 ha (if caribou had lived in the Bay Area, which they did not do). Using the modern day Serengetti Plains as an example, the Bay Area would have had a total of 278,635 large herbivores or one large herbivore for every 5 ha. The Pleistocene Bay Area probably had an herbivore population numbering somewhere in

between the historic Great Plains and the modern day Serengetti Plains, perhaps numbering about 350,000 large herbivores. This number may be too high, though. The population of *Bison bison* on the Great Plains represented a somewhat different situation than was found in the Pleistocene Bay Area due in large part to the difference in predators. Also, *Bison antiquus* had not evolved toward larger communal behavior as did the later *Bison bison*. So there may have been less bison in the Pleistocene Bay Area than I have calculated.

Estimated Optimum Carrying Capacities for Various Rancholabrean Species for Combined Areas 1-23 at 15,000 yrbp

Species	Carrying Capacity	Total Population
●American Lion:	1 per 1,700 ha	N = 802
●Saber-tooth Cat:	1 per 3,000 ha	N = 454
●Dire Wolf:	1 per 3,500 ha	N = 389
●Short-faced Bear:	1 per 3,000 ha	N = 454
●Brown Bear:	1 per 2,818 ha (1 per 940 ha by A.D. 1776)	N = 484
●Mammoth:	1 per 1,879 ha	N = 725
●Mastodon:	1 per 940 ha	N = 1450
●Bison:	1 per 6 ha	N = 227,196
●Horse:	1 per 39 ha	N = 34,953
●Camel:	1 per 196 ha	N = 6955
●Deer, Elk, & Antelope	1 per 21 ha	N = 64,913

I suggest that there was one large herbivore (bison, horse, camel, mammoth, mastodon, elk, deer, or antelope) for every 4 ha in the San Francisco Bay area during the late Pleistocene. Furthermore, I suggest that there was one large predator (lion, cat, wolf, brown bear, or short-faced bear) per 560 ha. Thus, the megaherbivore/predator relationship was about 140 to 1.

At a Rancholabrean site near Fairbanks, Alaska, it was estimated that there was 1 wolf per 130 ungulates and 1 lion per 250 ungulates; these are numbers that are close to the

predator-prey ratio found in East Africa today (Kurtén and Anderson 190:41, citing Guthrie 1968).

During the late Pleistocene, there were probably up to 125 mammoths, 250 mastodons, 32,000 bison, 4,900 horses, 980 camels, 68 brown bears, 64 short-faced bears, 55 dire wolves, 113 American lions, and 64 saber-tooth cats at any one time in the North Bay Interior (Areas 1-5). In other words, there were about 364 large predators (not counting cougars) to 38,180 large herbivores (not counting deer, elk, and antelope).[9] These are minimum numbers that do not reflect the optimum populations discussed above, nor do they account for those animals resident on the Farallon Plain, in transit to and from the Plain, and/or resident in the mountainous areas not covered by the formal "Areas."

The Serengetti Plains Ecosystem

The Serengetti-Mara ecosystem is 9,600 square miles (2,486,389 ha) in size (Line and Ricciuti 1985:24). In terms of its wildlife, it is one of the natural wonders of the world. At the very mention of the Serengetti, people quickly imagine the elephant, zebra, wildebeest, and lion.

The lion is at home on the Serengetti Plains. The African lion (*Panthera leo*) lives out in the midst of the grasslands and not in the jungle or deep forest. They must be out where the large herds of animals are located. Large mammals are rare in forests (Line and Ricciuti 1985:17-18). A lion has a maximum weight of 500 pounds, being second in size to only the tiger among cats (Ibid:18).

In Africa, the typical lion pride ranges from a low of 3-4 individuals to as many as a few dozen (Ibid). The pride includes about 5 adult female animals (but the number can be 2-20), 2 adult males (it can be 1-8), and their young, thus a pride averages about 7 adults (Kingdon 1997:284). The lion is a cooperative hunter. It usually takes prey animals weighing 50-300 kg, but when food is rare, it will take animals weighing 15-1,000 kg.

On the plains and savanna where there are large numbers and variety of hoofed mammals, there can be 1 lion per 3 mi^2 (12/100 km^2) (1 lion per 800 ha). Where prey density is very low, there may be only 1 lion per 50-100 mi^2 (1 lion per 13,000-26,000 ha) (Estes 1999: 318).

In some African populations, the ratio of predator to prey is 1:1,000; in such case, predation has little impact on the prey population (Bolen and Robinson 1995:350-351). In Kruger National Park (South Africa), the ratio is 1 lion per 110 prey animals (Ibid:351). In 1975, Kruger had 700 lions requiring about 2,500 wildebeest as kills per year.

The lion is unique among cats in the extent of its social life (Schaller 1972:33). Serengetti lion prides varied from 4 to 37 individuals and averaged 15 individuals (Ibid:34). Lion prides on the Serengetti average about 15 individuals, although you only tend to see groups of 3-6 animals (Schaller 1973:45). The members of a pride may be widely scattered, as much as 10 miles apart, and yet they still maintain their pride ties (Ibid). In a

sample of 14 days, a pride of females averaged 2.8 miles of walking a day, with a variation of 0.8-5.6 miles (Ibid:69). In a sample of 5 days, males in a pride averaged 5 miles of walking, with a variation of 1.2-9 miles (Ibid). "Both the Masai and Loliondo prides used about 150 square miles of terraine; the Seronera pride roamed over at least 70 square miles…" (Ibid:93). In comparison, two large prides in Manyara National Park each needed only 8 square miles of woodlands due to the presence of several large buffalo herds (Ibid:93-94).

The Ngorongoro Crater has a large hyena population whose presence has an influence on the number of lions the area can support since both species compete for the same resources. The Serengetti also has fewer lions than might be otherwise expected as the migratory herds are unavailable to most lions for much of the year. Schaller (1973:94) presents the following information regarding lions in Africa:

Area	Prey Biomass Lbs./Square Mile	Square Miles per Lion
Ngorongoro Crater	58,000 (224 ha)	1.4 (363 ha)
Manyara Peak	45,000 (174 ha)	1.0 (259 ha)
Serengetti Unit	24,000 (93 ha)	4.1-4.8 (1,062-1,243 ha)
Nairobi Park	17,000 (66 ha)	1.7 (440 ha)
Kruger Park	6,000 (23 ha)	6.5 (1,683 ha)

Obviously, the more food that is available to lions, the more lions there will be in a given area. That is true of other animals as well. In addition to the lions, other inhabitants of the Serengetti include the following:

- Leopard [Resident] [in hills]
- Cheetah (*Acinonyx jubatus*) [Resident] [on plains]
- Striped Hyena (*Hyèna hyaena*) [Resident]
- Common Jackal (*Canis aureus*) [Resident]
- Wild Dog (*Lycaon pictus*) [Resident]
- African Elephant (*Loxodonta africana*) [Resident] [Herds = 5-20 animals]
- Grevy's Zebra (*Equus grevyi*) [Migrant]
- Wildebeest (*Connochaetes taurinus*) [Migrant]
- Thomson's Gazelle (*Gazella rufifrons*) [Migrant]
- Eland (*Taurotragus oryx*) [Migrant]
- Topi (*Damaliscus lunatus*) [Resident]
- African Buffalo (*Syncerus caffer*) [Resident]
- Giraffe (*Giraffa camelopardalis*) [Resident]
- Hartebeeste (*Alcelaphus buselaphus*) [Resident]

- Grant's Gazelle (*Gazella granti*) [Resident]
- Waterbuck (*Kobus ellipsiprymnus*) [Resident]
- Common Warthog (*Phacochoerus africanus*) [Resident]
- Vulture [Resident]
- Crocodile [Resident]

If we picture the animals of the African Serengetti, it is easy to find similarities to the Rancholabrean bestiary that characterized the California Serengetti of late Pleistocene times. With the exception of the crocodile, most of the other African species have direct counterparts in the California Serengetti, which was probably dominated by the mammoth, horse, camel, and bison (cf. Edwards 1996:17).

The Rancholabrean Landscape

Stephen Edwards (1992, 1995, 1996, 1997) has done much to paint the picture of California's Rancholabrean landscape. He points out that Late Pleistocene grazing would have affected the development of California environments including the San Francisco Bay area and the Central Valley.

> Any discussion of grazing ecology in the present must begin in the distant past—at least as far back as the late Pleistocene, 12,000 years ago—though grassland-grazing ecologies extend millions of years back into the Tertiary Period. Twelve thousand years ago, a spectacular grazing-browsing-trampling mammalian megafauna (mammals at least as large as the pronghorn antelope) populated all of California and most of the large herbivores persisted until close to 10,000 years ago (Edwards 1992:3).

The grazing-browsing-trampling (and I would add "pooping") regime that was brought about by the Pleistocene megafauna undoubtedly helped to create the modern California flora (Ibid 1996:27). The plants were affected by the animals' grazing actions and digestive characteristics, as well as the introduction of their waste (both dung and urine) into the soils. Indeed, as seen on the Siberian steppe, the megafauna helped maintain the grasslands:

> What kept the steppe covered in grass instead of mosses, they say, were the big grazers. By churning up the ground with their hooves, the bison and other heavyweights prevented mosses from gaining more than a weak toehold on the landscape. The grazers' dung provided fertilizer for the grasses, that, in turn, nourished the animals (Stone 2001:177).

Closer to home, Edwards has noted a similar botanical effect brought about by the actions of the megafauna:

> Considering all the available evidence, it appears that the Californian Pleistocene megafauna was a complex grazing-browsing-trampling one. We can thus infer

> that California's Pleistocene environments might have included ample open spaces richly endowed with perennial grasses. Even if the Pleistocene vegetation was more of a mosaic, with more limited grasslands, those must have been substantially impacted by large herbivores….Clearly inferences about Pleistocene diets involve considerable speculation. Even when they are supported by detailed evidence, they remain hypotheses. The structural diversity of the California Pleistocene megafauna suggests diversified feeding niches, and grazing would have been a major activity. The California flora evolved for millions of years in that milieu (Ibid 1992:4).

The California Floristic Province measures about 324,000 km², and has approximately 794 genera and 4452 species of native vascular plants. This is more than in the entire central and northeastern United States and adjacent Canada, a region that is ten times larger! California clearly contains the largest and most diverse assemblage of native plant species in all of temperate and northern North America (Raven and Axelrod 1995:4). To some degree, this may be a result of the interaction of Pleistocene plants and megafauna.

In many ways, the Bay Area's Rancholabrean landscape would have been remarkably different from what we see today. For example, San Francisco Bay would have been a large green valley and 30-mile long Pleistocene Lake Benito would have covered much of the lower Santa Clara Valley (Jenkins 1973). The Pacific Ocean was 128 m lower at the time of the last maximum Wisconsinan Glaciation (i.e., ca. 20,000-15,000 yrbp), so the Sonoma Coast would have been about 21 km further west than it is today providing the present gradient of 6 m per km held true at that time (Minard 1971:143). And off San Francisco, the coastal plain would have extended all the way to the Farallon Islands, a distance of about 35 km. As the ocean fell, and the littoral zone moved further west, the newly emergent beaches may have been quickly stabilized in part by the rapid growth of aggressive vegetation, as was the case during low stands of sea water on the Northwest Coast (Minard 1971:144, citing Cooper 1958:130). The coastal hills would have been covered with stands of closed coniferous forest (Parkman 2005). However, the grazing patterns of the megaherbivores, especially the mammoth and bison, would have selected for lush and extensive stands of grass and sedge while preventing the spread of forests onto the plains and valley floors (cf. Owen 1981:48). If the mammoth was anywhere similar to the modern elephant, it would have had a dramatic effect on the landscape:

> Wild elephants are migratory animals, and herd leaders choose their routes in accordance with their remembered knowledge of the terrain, of the change of seasons, of the places where succulent forage may be found after the rains, and of the locations of the best water holes along the way. Most herbivores pull up grass to eat, or pull the leaves off bushes. But elephants grind up leaves, twigs, even small branches with those massive molars. This can have a beneficent effect on wild plants similar to what pruning does for a garden shrub: the remaining plant growth thickens and fills in. But if a herd of elephants is really hungry, if the rains are late in coming, or if other factors intervene, they may destroy everything in their path, yanking out young trees and second-growth shrubbery by the roots (Alexander 2000:47-48).

The mammoth was not the only factor that shaped the Pleistocene landscape. During that time, the Sonoma Coast shoreline and similar areas up and down the Farallon Plain were characterized by "receptive shores" which resulted in the creation of scattered areas of sand dunes (Minard 1971:141). Freshwater ponds, tree-lined streams, and large rockstacks also characterized these areas. Some of the rockstacks (and certain isolated tree trunks) would have had heavily-polished surfaces, the result of mammoth and bison rubbing activities (Parkman 2002a, 2002b, 2004).

In the Sierra Nevada, it is possible to see bright polish on the granitic outcrops that are found there. This is glacial polish, which is produced on rock by the abrasion of mud under high pressure at the base of a glacier (Guyton 1998:28). As Alt and Hyndman (2000:23) have noted, "Looking at glacially polished and striated surfaces is sobering if you consider that those surfaces have been there since the last ice melted, about 10,000 years ago." On the Sonoma Coast, we can view rock polish that is considerably older than 10,000 years old and produced not by the action of glaciers but rather by the grooming behavior of the Ice Age megafauna (Parkman 2002a, 2002b).

In addition to the rubbing rocks, the Rancholabrean landscape would have included numerous other signs of the megafauna presence. The valleys and plains would have been laced by ancient game trails. Most of the migratory trails were probably aligned east to west with secondary trails aligned north to south. Also present were associated features such as broad muddy wallows, enlarged waterholes, dung heaps, debarked trees, scent marks, and kill sites (i.e., areas marked by the sun-bleached bones of prey animals killed by predators).

Mammoth Wallows and Vernal Pools

It is likely that many vernal pools dotted these same plains and valleys during the late Pleistocene. Whereas the brightly-polished rubbing rocks are modern-day reminders of the ancient megafauna, perhaps so, too, are some of the vernal pools.

In western North America, vernal pools are a unique specialized form of wetlands that occur from southern Oregon through California and into northern Baja California, Mexico. "Soils, topography, and the Mediterranean climate are dominant factors determining whether ephemeral pools or lakes will form at all" (Bauder et al. 1997:15). When a vernal pool is filled to capacity, its surface area may be as small as a few square meters or as large as a small lake. Typically, the pool remains filled for 3-5 months. In years of low precipitation, however, it may fail to pond at all.

Vernal pools are specialized habitats that are inundated long enough into the growing season to prevent colonization by grassland plants but are usually too dry in summer to allow for the establishment of marsh species (Holland and Jain 1977). The vast majority of vernal pool plants are annuals (Stone 1990:92). The vernal pool flora is thought to have, "evolved primarily in the Great Valley and from there dispersed to the south and

west as soil-forming processes and increasing aridity created new areas of pool habitat" (Zedler 1987). There are eleven vernal pool taxa that are endemic to the North Coast Ranges. Some of these are found in low-lying areas that include the Santa Rosa Plain, while others are associated with volcanic bedrock pools in the mountains (Stone 1990:99).

Vernal pools are formed after sufficient rainfall, when pools of water form in depressions above an impervious soil layer or layers. Typically, the depressions are part of an undulating landscape, where soil mounds are interspersed with basins, swales, and drainages. This landscape is frequently called "mima-mound" topography, after the Mima Prairie in Washington where the soil mounds were first described (Cox 1984). Occasionally vernal pools or the soils they are located on are degraded (e.g., tire ruts, ditches). These areas often have the ability to function as habitat and may also support vernal pool species (Bauder *et al.* 1997:15).

Evaporation and transpiration through plants are the main causes of pool drying (Hanes *et al*. 1990:56). For Sacramento Valley vernal pools, evapotranspiration rates are lowest in late December. As precipitation decreases in April, and almost disappears in May, evapotranspiration increases. This causes the pools to normally dry sometime between April and July depending on the site and year. Pools with thick adjacent soils tend to be slower in filling, but retain their water longer (Ibid:58).

Hoover (1937) referred to vernal pool habitats as the "hog-wallow endemism area." Elsewhere, vernal pools have often been referred to as "buffalo wallows" (Anonymous 1998:15; Keeley 1996:1). In the past, actual buffalo wallows on the Great Plains provided extensive surface water for amphibians (frogs). It is clear that large and heavy animals have an impact on soils and plants, including those associated with vernal pools:

> Hooved animals compact soils. Depending on the number of animals and their size, otherwise permeable soils may become so compacted as to prevent the percolation of water. Most vegetation suffers in such a regime, as does the soil itself. Barren, eroding soils are commonplace around waterholes or salt licks frequented by grazing animals. These conditions are localized, however, and generally do not represent normal soil conditions for unconfined wildlife populations. Most herds of grazing species are more or less nomadic, so that soil compaction and trampling are minimal as the animals move about (Bolen and Robinson 1995:250).

Many of California's vernal pools are associated with late Pleistocene soils and landforms. It is likely that some of them began as megaherbivore wallows, or perhaps they were pools that were enlarged by mammoths (Parkman 2004, 2006d). At the end of summer, vernal pools are often dry and bare of vegetation. It seems likely that Rancholabrean mammals would have used the vernal pools as watering holes and for mud baths during the late winter to early summer months when they held water, and as dirt wallows in late summer when the pools were dry. Given that the Rancholabrean megaherbivores, such as the bison and mammoth, co-existed with the vernal pools, it is

absurd to think that they never came in contact. Based on what is known of modern elephant behavior, we can assume that a herd of mammoths, using vernal pools as watering holes, would occasionally have enlarged the pool to allow for easier access. Wallowing in the mud at the pool's edge would have enlarged the depression and caused an increase in compaction. As a megamammal attraction, waterholes would have benefited from the enhanced chemical properties brought about by the concentration of animal urine and dung. The properties of animal urine and dung would have benefited the local plants around the pools just as bison urine and dung are known to have benefited the grasses around prairie dog towns on the Great Plains. In truth, some of California's vernal pools may have been created, maintained, and enhanced by Rancholabrean megaherbivores.

Certain vernal pools may have begun as mineral licks excavated by mammoths and other Rancholabrean megafauna (cf. Haynes 2006: Fig. 9). All ruminant species in North America have been reported to use licks (Jones and Hanson 1985:22). In temperate regions, animals seek out salt licks in late spring and early summer. Calcium, magnesium, sodium, and potassium are mineral elements found in lick earths. Calcareous outcrops, such as metamorphosed sedimentary rocks, are sometimes used as licks. Sedimentary rocks (shale, claystone, limestone, sandstone, or siltstone) are often licks. Jones and Hanson (Ibid:83) note a lick in located in San Bernardino County, California, associated with a fault that has controlled groundwaters and from which calcium and magnesium carbonates have precipitated. In Virginia, they note a schist outcrop used as a lick for calcium chloride. Licks often occur at certain springs and sometimes at springs located along faults. Sometimes, these waters carry salt, but usually they are of the calcium and magnesium bicarbonate type that precipitate calcium carbonate upon exposure to the ground surface, leaving magnesium in solution from which it can exchange onto clay particles.

While many vernal pools are characterized by sizeable amounts of watershed runoff and impermeable layers such as claypans, duripans (silica-cemented horizons), or bedrock immediately beneath the pool bottom soil, they are not the only conditions leading to vernal pools. It is also possible that vernal pools could form simply as "depressions where the ground water table is locally exposed" (Hanes *et al.* 1990:51). In some cases, the megafauna may have created dry summer wallows leaving a landscape marked with shallow depressions. In winter, when the ground water table rose, some of these depressions may have become pools, thus constituting vernal pools.

California's vernal pools appear associated with Pleistocene landforms, and are thus recent on the scale of geologic time (Stone 1990:91). Geomorphologists have determined the ages of vernal pool-bearing landforms. As an example, the highest alluvial terraces in the Sacramento area are estimated to be early Pleistocene (Shlemon 1967). The older terrace soils in eastern Stanislaus County have been isotopically dated to 600 kyr ago (Arkley 1964). The pool-bearing coastal terraces in the San Diego area are between 1 myr and 100 kyr old (Kern 1977).

The Mediterranean-type climate (wet winters and dry summers) of California began during the late Pliocene, just before the beginning of the Pleistocene. Thus, California's vernal pools are essentially Pleistocene features. Interestingly, the bison did not come to California until well into the Pleistocene, about 500 kyr ago. The mammoth arrived near the beginning of the Pleistocene about 2 myr ago.

Modern humans arrived in this late Pleistocene environment sometime prior to 13,000 yrbp, just before the mass extinctions eliminated so many of the Rancholabrean species.[10] It is possible that humans were initially prevented from crossing the Land Bridge into the New World by the many large predators that occupied Beringia (Pielou 1991:260). This is reminiscent of the "Grizzly Bear Hypothesis" put forward by archaeologist Paul Chace (personal communication 1982), which states that California Indians only settled the Peninsular Range of San Diego County in late times due to settlement pressure finally overriding their concerns about the many grizzly bears that resided there. The "Beringian Predator Hypothesis" probably holds true. It is very likely that early Paleoindians were killed and eaten by fierce Arctic predators such as American lions and short-faced bears (Ibid:260-261). A similar situation may have challenged the first Paleoindians upon their arrival in the San Francisco Bay area, regardless whether they came by foot across the Land Bridge and on to California, or were transported to the California coast by small boats that had traveled along the northernmost Pacific Rim (Parkman 2004).

Conclusions

In this paper, I have proposed that the San Francisco Bay area during the late Pleistocene was essentially a California Serengetti, a place where an abundance and variety of animal species interacted with the landscape to create one of the world's great natural wonders. Today, little remains of that landscape that can be seen by the untrained eye. However, to the careful observer, elements remains that attest to the grandeur of the past. The polished rubbing rocks on the Sonoma Coast, perhaps the vernal pools of the Santa Rosa Plain, and even the local California flora are all testimonials to the past influence of the Rancholabrean megafauna. The bones of these animals remain, too, to help map their distribution on the Ice Age landscape. Remarkably, the California Serengetti of the late Pleistocene was much grander than even the fabled African Serengetti of historic times.

I have also proposed that a seasonal round characterized the Bay Area's Rancholabrean megafauna and that there was both a North and South round on either side of the Golden Gate. The megafauna and their seasonal rounds helped to shape the landscape we know today. Future research is needed in order to better define the influences that the Rancholabrean megafauna had on the Bay Area landscape. There are three key areas where future research might prove especially useful:

(1) Megafauna and the alteration of the rocks
(2) Megafauna and the creation of vernal pools
(3) Megafauna and the development of the flora

I hope that this report will inspire others to further explore some of these same topics. It is my intent to bring more attention to the interaction of wildlife and wild lands. One is not complete without the other. We must not forget the magnificent natural landscape that was once the San Francisco Bay area, complete with its rich Rancholabrean bestiary. Furthermore, it is essential that we strive to protect the wildlife species and landscape features that still exist today. Otherwise, all will be gone like the mammoth and saber-tooth cat.

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[1] Even though it was an "Ice Age," coastal California during the late Pleistocene represented a refugium thanks to a milder climate than was found elsewhere on the continent (Johnson 1977). As a result, summer days would have been warm enough to encourage coastal visits by the megafauna.
[2] This was not a true "migration" in the purest sense of the term.
[3] In this and all other cases, only Rancholabrean fossils (late Pleistocene) are considered. Some of the areas referenced in this report may contain paleontological sites of an earlier origin.
[4] It is quite possible that California's Great Central Valley was part of the Bay Area's Rancholabrean landscape. Mammoths and other large megaherbivores may have migrated from the Central Valley through the Franciscan Valley via the California River on their way to the coast. If so, then the total acreage of this California Serengetti was considerably larger than attested to in my figures, as was its carrying capacity for sustaining wildlife populations.
[5] Note that Areas 1-23 do not represent all of the Bay Area but just those areas that I have calculated to have been interior valleys, the coastal plain, and the migration routes that connected them. Areas 1-23 do not include what I calculate to have been highlands and woodlands.
[6] The black bear that is found at Rancho La Brea is related to the modern-day black bear, but it is not exactly like it. For one thing, the older bear had large grinding teeth, unlike its modern relative.
[7] While some of these zoofacts may have disappeared, many of them probably still exist to confuse archaeologists and geologists alike.
[8] Note that I have not calculated the carrying capacity of the highlands for camels. My figures only concern Areas 1-23. As a result, the actual number of camels living in the Bay Area may have been slightly larger than I have stated.
[9] The ratio of mastodons to saber-tooth cats may be off in my calculations. If the saber-tooth specialized in hunting the mastodon (and infant mammoth), then there would have been less saber-tooths than my ratio accounts for. My calculations are based on the saber-tooth also predating other species of large megaherbivores (such as bison and horse). Additionally, my ratio of dire wolf to American lion may also be off and should perhaps be reversed.
[10] The Rancholabrean extinctions are thought to have been a result of one or more of three factors: 1) the environmental changes that resulted from the changing climate at the conclusion of the Ice Age; 2) over-hunting by early Paleoindians; and 3) the spread of a super-deadly virus.