TAPHONOMY OF THE TERRESTRIAL MAMMALS OF LEISEY SHELL PIT 1A, HILLSBOROUGH COUNTY, FLORIDA

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ABSTRACT

The terrestrial mammal fraction of the Leisey Shell Pit 1A bone assemblage (early Pleistocene) is numerically dominated by medium-sized herbivores, with camelids and equids accounting for 45% and 22% of the individuals, respectively. Some taphonomic modifications to the bone assemblage took place at the site of deposition (scratchmarks, breakage, hydrodynamic sorting, and a limited amount of scattering); others occurred elsewhere, either in a nearby terrestrial setting (carnivore/scavenger activity, subaerial weathering, both generally to a relatively low degree) or during fluvial transport to the site. There is no preferred orientation of the long bones at the site, suggesting the lack of a strong, directional current. However, multidirectional tidal currents probably aided in carcass disassociation and winnowing of smaller, lighter elements. A significantly greater proportion of equid and proboscidean skeletal elements were weathered and damaged by mammalian carnivores than those of the camelids. Elements of the latter more frequently entered the site in an unmodified state as parts of carcasses (later disassociated) while those of the former were more often brought to the site individually in a modified condition. Population dynamics of *Palaeolama mirifica* and *Equus "leidyi"* (the two most common mammals) also conform to a mixture of catastrophic and attritional mortality. The principal mammalian carnivores responsible for modifying the Leisey bone assemblage were *Canis armbrusteri* and *Arctodus pristinus*. The former caused the bite marks and chewed surfaces on the bones of medium-sized herbivores, while the latter scavenged on the carcasses of ground sloths and proboscideans.

RESUMEN

La fracción de mamíferos terrestres del ensamblaje de huesos del depósito de conchuelas de Leisey 1A, es dominada numéricamente por herbívoros de tamaño medio, con camélidos y équidos representando respectivamente un 45% y 22% de los individuos. El ensamblaje de huesos sufrió algunas modificaciones tafonómicas en: el sitio de deposición (rasguñaduras, rompimiento, reordenamiento

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modificaciones tafonómicas en: el sitio de deposición (rasguñaduras, rompimiento, reordenamiento hidrodinámico y cierto grado de esparcimiento); en otras areas, tanto cerca como lejos del ambiente terrestre (actividad de carnívoros/carroñeros, efectos climáticos subaereos, ambos en un grado relativamente bajo); o durante transporte fluvial hacia el el sitio de deposición. El hecho de que los huesos largos no muestran una orientación preferida en el sitio sugiere la ausencia de una corriente direccional fuerte en el sitio. Sin embargo, corrientes multidireccionales de mareas probablemente ayudaron en la disociación de carcasas y la dispersión de los elementos mas pequeños y livianos. Una proporción significativamente mayor de elementos del esqueleto de équidos y proboscídeos fue afectada por el clima y dañada por mamíferos carnívoros en comparación con elementos del esqueleto de camélidos. Estos últimos entraron mas frecuntemente al sitio como carcasas completas no modificadas (mas tarde disociadas), mientras que los elementos del esqueleto de équidos y proboscídeos fueron mas frecuentemente llevados individualmente al sitio, habiendo ya sido modificados. La dinámica de las poblaciones de *Paleolama mirifica* y *Equus "leidy"* (los dos mamíferos mas comunes) estan en conformidad tambien con una mezcla de mortalidades por catástrofe y competencia. Los principales mamíferos carnívoros responsables de la modificación del ensamblaje de huesos de Leisey fueron *Canis armbrusteri* y *Arctodus pristinus*. El primero causó las marcas de mordidas y superficies masticadas en los huesos de herbívoros de tamaño medio, mientras que el último carroñeó las carcasas de perezosos terrestres y proboscídeos.

INTRODUCTION

Leisey Shell Pit 1A is a rich, early Irvingtonian vertebrate fossil assemblage from southwestern Hillsborough County, Florida (Hulbert and Morgan 1989). The bone-producing sediments of Leisey Shell Pit 1A (= Leisey 1A) consist of a 5 to 30 cm thick layer of muddy sand and shells. Analysis of the Leisey invertebrates, as discussed by Portell et al. (this volume), shows that the depositional environment was nearshore marine, perhaps a grass or mud flat. Mean water depth probably did not exceed one meter and deposition occurred in a relatively low-energy environment (Hulbert and Morgan 1989). Invertebrate contributions from nonmarine environments include both freshwater and terrestrial mollusks. The environment of deposition is suggestive of a marine embayment fed by freshwater streams and open to the Gulf Coast.

As is the case with the invertebrate fauna, vertebrate remains were derived from several sources. Contributions to the vertebrate component of the shell bed originated in at least four different environments:

1) The environment of deposition (autochthonous). Well-preserved remains of nearshore and estuarine species of sharks and bony fish (Scudder et al. this volume) and wading birds (Emslie this volume) represent animals that were living in, or close to, the environment of deposition.
2) Offshore marine environments. Contributions from this area include fragmentary remains of sea turtles and cetaceans (Meylan this volume; Morgan and Hulbert this volume).
3) Freshwater environments. Emydid and trionychid turtles and alligator remains form the major component of the freshwater fauna at Leisey 1A (Meylan this volume). Several species of freshwater

fish and water birds have also been recovered (Scudder et al. this volume; Emslie this volume). Freshwater mammals (*Neochoerus*, *Lutra*, *Trichechus*) are uncommon.

4) Terrestrial environments. The vast majority of the large vertebrate fossils found are those of land mammals. Large tortoises are also common.

Based on the interpretation of Leisey as a shallow embayment fed by freshwater streams, it is not difficult to account for the presence of aquatic vertebrates. Therefore, this analysis deals primarily with the terrestrial vertebrates, in particular the mammals, because the reasons for their great abundance in a marine deposit are not readily apparent. Several possible scenarios will be discussed that could account for the presence of bones of terrestrial vertebrates in the shell bed. For example, the animals may have been killed and buried as the result of a single catastrophic event such as a hurricane or storm surge, or the assemblage may have formed attritionally over a number of years. The terrestrial vertebrates may have been living in the immediate vicinity of the deposit, or at some distance from it. We investigate which agents of transport, if any, played a role in forming the bone-bearing layer, and the condition of the remains when they were introduced into the site of deposition. The intent of this paper is to reconstruct the taphonomic histories of the large mammals of Leisey 1A to determine the sequence of events leading to formation of the terrestrial component of the fauna.

ACKNOWLEDGMENTS

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FIELD EXCAVATION METHODS

The large size of the site (approximately 2,000 m^2) and the enormous number of bones and bone fragments (> 50,000) at Leisey 1A, coupled with the relatively short time period allowed to excavate the site, placed numerous constraints on the collecting methods and the amount of taphonomic data that could be taken. To accurately record the exact position and orientation of every bone was impossible. A procedural compromise was struck between this extreme, and its opposite, to not record any positional data at all.

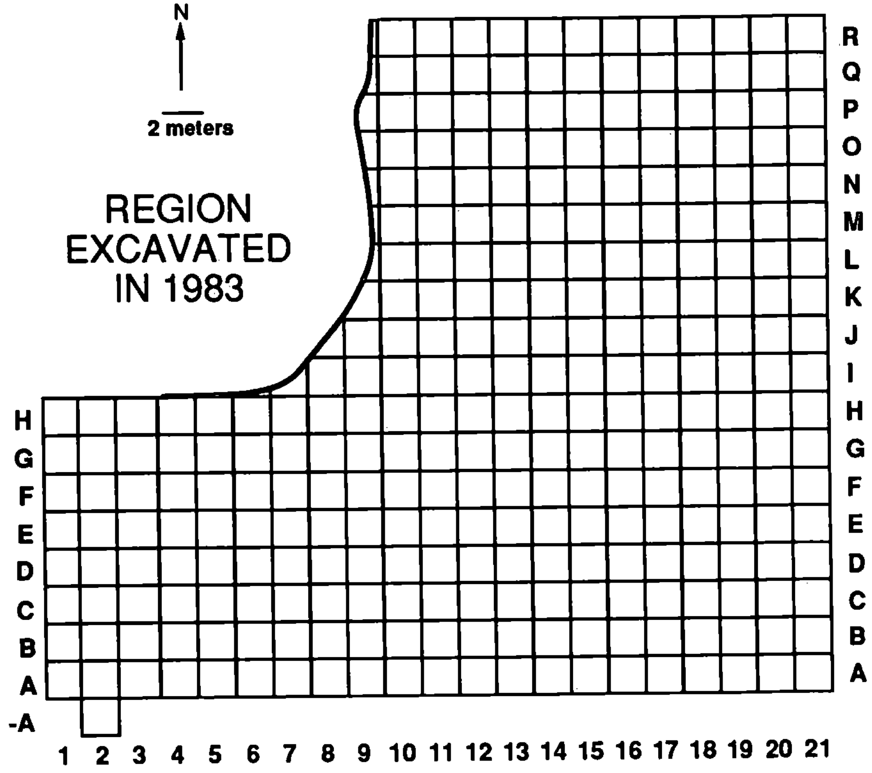

Figure 1. Map of the Leisey Shell Pit 1A fossil site, showing the grid coordinate system that was established in April 1984. Each square is referred to by a letter-numeral combination, for example, B4.

During the 1984 field operations at Leisey 1A, the site was gridded into approximately 2 x 2 meter squares. The east-west running rows of squares were identified by letters, with the southernmost being row A (Fig. 1). Columns were given numerical designations, with the westernmost being column 1. Using this system, individual squares were named by a letter-numeral combination; for example the southwestern-most square was called A1. All bones collected from a particular square were kept together and labelled with its coordinates. When identifiable specimens were eventually cataloged into the FLMNH collection, the square's coordinates were incorporated into the collection's computerized catalog database. This practice proved very useful for retrieving data for sorting and counting analyses.

The bone-bearing unit at Leisey 1A originally lay about 6.5 m below the ground surface (Morgan and Hulbert this volume, fig. 1). Prior to the initial excavation of a portion of the site in 1983, the surficial sand unit and the upper

2 m of the upper shell bed were removed by heavy earth-moving machinery. About a meter of the upper shell bed and 0.5 m of the indurated "hard layer" then remained on top of the bone-bearing horizon. A small bulldozer cleared away most of the upper shell bed before the start of the 1984 field season. The remaining overburden was cleared manually with picks and shovels to expose the bone bed. It was primarily dug with small tools such as awls and screwdrivers, which proved to be more effective in the shelly matrix than standard trowels (Fig. 2). Although many of the bones were crushed, this is thought to be primarily the result of geologic compaction and not from the earth-moving equipment. The color along a freshly broken surface is different (lighter in tone) than along an ancient break. The latter has the same dark color as the surface of the bones. The color of the broken edges of the compacted bones indicated that the crushing was not modern.

Ideally every piece of fossil bone was collected from a square. However, given the thousands of small fragments and gar scales, and the varied patience and experience of the collectors, squares were not collected with equal thoroughness. Undoubtedly almost every identifiable element of the large vertebrates was collected from each excavated square. To ensure completeness, several of the taphonomic analyses were limited to squares excavated by experienced FLMNH personnel. About one metric ton of matrix from the bone-bearing horizon at Leisey 1A was screen-washed for small vertebrates through standard window screen mesh. Although the concentrate contained numerous bones of small fish, recovery of herps, birds, and mammals was rare. Small samples of matrix were saved for geologic and palynologic analysis.

Positional and orientation data were taken on over 1300 bones before their removal from the sediment. We concentrated on obtaining data on mandibles, maxillae, crania, scapulae, innominates, and major limb elements of all the large vertebrates, as well as the elongated cervical vertebrae and proximal phalanges of the camelids. The large sample (N = 1367) is representative and unbiased with regard to distribution of bones within the site. Information taken on each element included location within the square (to the nearest centimeter), bearing, plunge, length, and which side faced "up" in the field. No measurement of (vertical) depth was taken as the bone-bearing unit was quite thin relative to its lateral extent. Bones appeared to be distributed throughout the layer and not concentrated at the top or bottom. The position/orientation data were later sorted and analyzed using the Quattro spreadsheet program.

TAPHONOMIC ANALYSIS

The contribution of various taphonomic processes to the formation of the bone assemblage will be determined by investigation of the following aspects of the

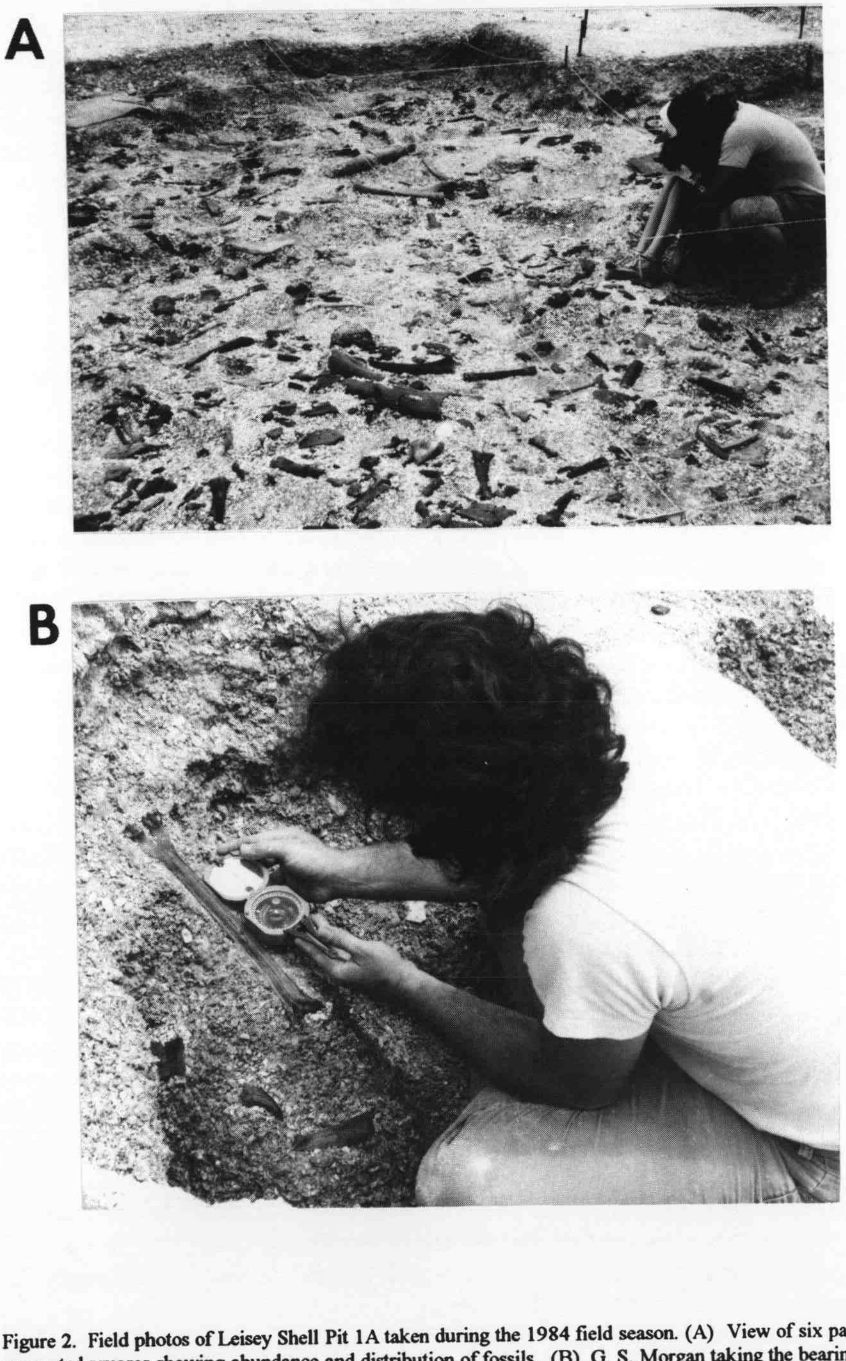

Figure 2. Field photos of Leisey Shell Pit 1A taken during the 1984 field season. (A) View of six partially excavated squares showing abundance and distribution of fossils. (B) G. S. Morgan taking the bearing of a camelid metapodial.

fossil deposit: bone distributions and associations, types and degrees of bone modification, and skeletal part representations. Each of these bone or assemblage features has been shown to provide information concerning the taphonomic pathways leading to formation of a fossil deposit (e.g., Voorhies 1969; Wolff 1973; Behrensmeyer 1975, 1978; Haynes 1980a, 1985, 1988; Badgley 1986a; Blumenschine 1986, 1989; Pratt 1990). Examination of all these lines of taphonomic evidence will be employed to determine the events that culminated in the terrestrial vertebrate assemblage preserved at Leisey 1A.

ARTICULATION AND ASSOCIATION

During excavations at the Leisey 1A locality it quickly became evident that terrestrial vertebrate remains had not been buried as complete, articulated skeletons (Fig. 2). Even though bones were not found in articulation, in a number of instances elements or portions of elements of one individual were found within a few meters of one another. Evidence of association was most obvious for less common taxa, where remains apparently belonging to single individuals were found spread over a distance of a few squares. The large number of individuals of camelids, and to a lesser extent equids, precluded definite identifications of postcranial associations for these taxa; however, many matches were found between cranial elements. The most abundant non-mammalian vertebrates (excluding fish), freshwater turtles and land tortoises, were most frequently represented by individual bones of the plastron and carapace, although contacts could be found with isolated elements from other regions of the site. The total degree of skeletal association may never be known as the number of bones from the site is so large as to make finding all associations a nearly impossible task. Therefore, representative taxa and elements were selected to provide some estimate of association and distribution patterns.

All equid mandibles, symphyseal portions, and lower cheekteeth from the two most common species, *Equus "leidyi"* and *Equus (Hemionus)* sp., were examined for matches. In addition, all cataloged tapir and proboscidean elements were examined for evidence of association. Of a total of 84 equid right or left mandibles, 18 symphyseal regions, and over 300 isolated cheekteeth, matches were found between 20 pairs of right and left mandibles, 11 jaws and symphyses, and 40 mandibles and isolated cheekteeth. Figure 3 illustrates the distribution of these associated elements within the site, and Figure 4 graphically demonstrates the range of distances separating the associated elements. Over 45% of associated cranial elements of equids were located within 2 m of one another, and nearly 75% were separated by a distance of 5 m or less.

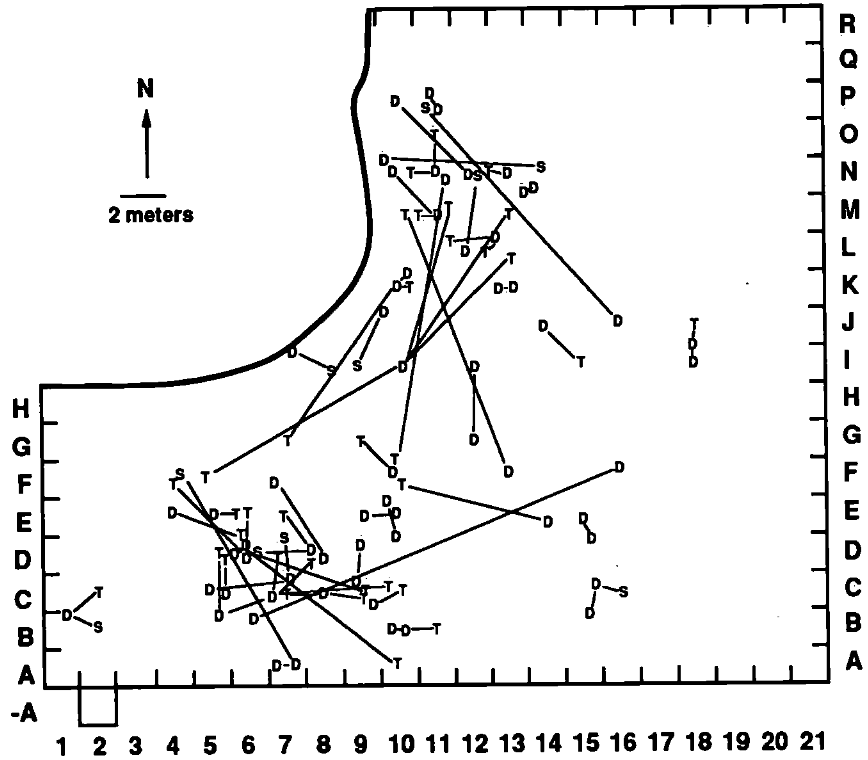

Figure 3. Map of the area of the Leisey Shell Pit 1A excavated in 1984 (see Fig. 1) showing the spatial distribution of associated *Equus* dentaries and lower teeth. Locations of isolated or unmatched specimens are not shown. Lines connect associated remains. D represents a cheektooth-bearing portion of the dentary; S a mandibular symphysis; and T an isolated lower tooth.

Compared to camelids and equids, tapir (*Tapirus haysii*) elements are relatively uncommon, but matches were found between right and left mandibles and lower cheekteeth, as well as between mandibles and maxillae. Four individuals are represented by associated cranial and postcranial material. The majority of associated right and left mandibles were found within 2 m of one another, while maxillae and mandibles were separated by distances of up to 20 m. Definitely associated postcrania were spread over distances from 0.5 to 15 m.

Based on femora, it is estimated that at least 5 proboscidean individuals are preserved at the Leisey 1A locality (analysis of mandibles produced an MNI of 8, see Table 11). However, no evidence of association of proboscidean postcrania was evident with the exception of a pair of juvenile tibiae and humeri, separated by approximately 12 m and 25 m, respectively. Presence of unassociated proboscidean remains raises the question as to the state in which terrestrial vertebrates reached the environment of deposition: primarily as carcasses; as isolated skeletal elements; or as a mixture of the two. It is possible that proboscidean carcasses decomposed and were scattered at the site in a subaqueous environment. However, the fact that proboscidean elements show signs of weathering (see section on weathering modification) indicates that they were exposed in a terrestrial setting. This finding, and the lack of skeletal association suggests that these large elements were transported separately to the environment of deposition, perhaps by moving water. This hypothesis will be dealt with in following sections.

There are numerous matches between isolated shell elements of turtles or tortoises. In a few instances disarticulated but nearly complete carapaces or plastra were spread over an area of 16 m^2 or less. At least 4 *Trachemys scripta* and 3 *Hesperotestudo crassiscutata* shells were found that were over 50% complete when reassembled. These shells must have reached the site as complete units, and subsequently disarticulated. Although it has been suggested that the site formed over a short period of time (Hulbert and Morgan 1989), there was obviously sufficient time for the turtle shells to disarticulate. Based on decomposition studies on Recent marine turtles, plastral and carapace elements may have begun to separate within two weeks of their arrival at the site (Meyer 1991).

The fact that the terrestrial vertebrate remains show no degree of articulation suggests that they entered the site of deposition as individual elements. Although the agent of transport has not been identified, it is reasonable to speculate that bones from carcasses that decomposed and were scavenged further inland were carried into the embayment when heavy rains flooded freshwater creeks and surrounding low-lying areas. The presence of freshwater vertebrates and invertebrates, terrestrial gastropods, and transported grains of terrestrial pollen (Rich and Newsom this volume) support this suggestion. However, the occurrence of some associated skeletal remains (e.g., equid crania, tapir and sloth crania and postcrania, turtle carapaces) indicates that a significant fraction of the elements were introduced to the site of deposition as components of larger units, in some cases as complete or partial carcasses. The possible mechanisms by which complete remains may have been added to the assemblage will be discussed further in following sections. The large number of associated elements that were recovered in close proximity to one another essentially rules out the possibility that these bones had been disarticulated or broken prior their arrival at the site of deposition. Therefore, disarticulation, breakage, and scattering of the elements in question took place at the location where final deposition and formation of the bone bed occurred. The relatively limited range of distances between associated elements, as illustrated by the equid jaws and isolated teeth (Fig. 4) and the associated turtle shells, indicates that any transport mechanisms operating within the final depositional environment itself apparently were not highly effective.

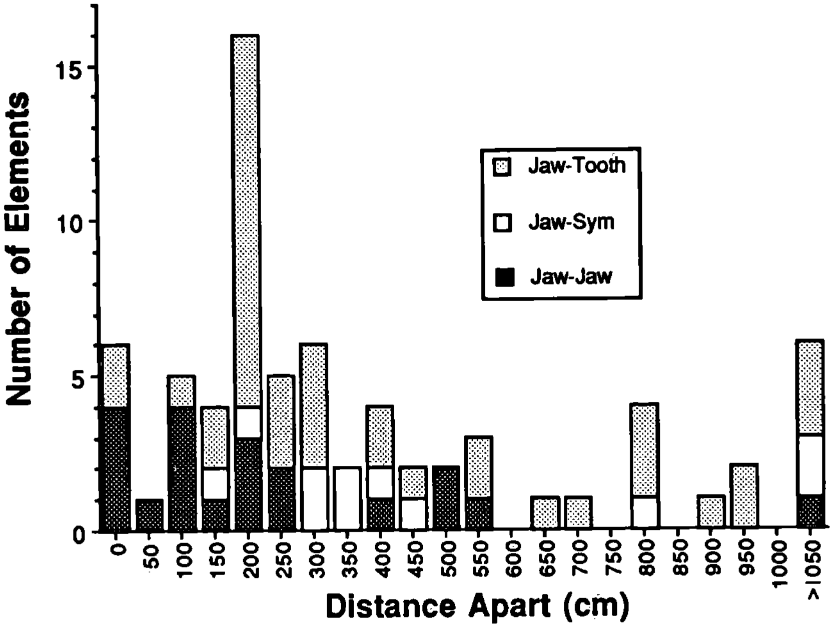

Figure 4. Histogram of distances separating the associated *Equus* dentaries and lower teeth from Leisey 1A shown in Figure 3. The final column includes all associated elements separated by more than 1025 cm. Note that while all but one pair of dentaries was separated by less than 6 m, it was not uncommon for teeth and symphyses to be separated from their corresponding dentary by more than 6 m.

Disarticulation and scattering of remains within the site may be attributed to several factors. Predators and scavengers have been reported to scatter elements of prey carcasses (Haynes 1980a, 1982; Blumenschine 1986). Given the marine nature of the site, scattering of this type in situ could only have taken place during periods of extreme low tide if terrestrial predators and scavengers were involved. It is also possible that aquatic scavengers such as sharks or crabs may have been responsible for some disarticulation and scattering of associated remains. Trampling by large herbivores has also been demonstrated to cause breakage and scattering of elements (Andrews and Cook 1985; Olsen and Shipman 1988; Fiorillo 1989), and Recent elephants are known to actually pick up, move, and carry remains of other elephants (Coe 1980; Conybeare and Haynes 1984; Haynes 1991). While bones in aquatic habitats may be trampled (Behrensmeyer and Boaz 1980; Haynes 1991), water depth at the site of trampling must be relatively shallow to allow the agents of trampling to wade rather than swim. This condition evidently was met at the Leisey 1A site (Hulbert and Morgan 1989). The third factor that could account for scattering of associated remains is the action of moving water (Voorhies 1969; Behrensmeyer 1975; Hanson 1980). It is fairly certain that tidal currents were features of the site of deposition, but it is not clear whether the current strengths were sufficient to cause movement of large, dense elements of large mammals. The possible role of moving water as well as other taphonomic factors will be considered more fully in the following sections.

Bone Orientation

In the case of disarticulated remains, orientations and positions of skeletal elements within a fossil site can provide information concerning agents responsible for bone concentration and dispersion. Presence of a preferred or dominant direction of bone orientation is often considered evidence that moving water was a feature of the depositional environment (Voorhies 1969; Hunt 1978, 1990; Shipman 1981; Pratt 1990), as water currents have the capacity to cause alignment of skeletal elements. There are several interpretations that may be made if a significant orientation pattern is lacking, including the absence of a current of sufficient duration and velocity to cause alignment. It is also possible that other factors that resulted in random patterns of bone dispersion were acting in opposition to the effects of moving water.

During the field collection phase of this study, bearing and plunge data were obtained on 1447 fossil bones. However, as a number of elements do not routinely show predictable preferred axes of orientation in running water (Voorhies 1969; Pratt 1990), directional analysis was restricted to a total of 995 limb bones, mandibles, and rib fragments. These elements possess elongate axes that show predictable alignments relative to current direction and therefore are considered the most informative indicators of the presence and direction of paleocurrent (Voorhies 1969; Pratt 1990). Figure 5 is a mirror-image rose diagram of long axis orientations of these elements, and Figure 6 a stereographic projection of the bearing and plunge of 650 long bones. A χ^2 test for significance shows that there is no preferred directionality of long bone orientations (Table 1).

As some types of long bones are more reliable indicators of current direction than others (Voorhies 1969; Pratt 1990), bearings of various types of elements were also examined for presence of any orientation pattern. For example, long axes of tibiae consistently align in the direction of a prevailing current, provided that water depth is sufficient to completely cover the bone (Voorhies 1969) and that current velocity is greater than the minimum speed necessary to move the bone into this position (Pratt 1990). At current velocities below those required to cause tibial

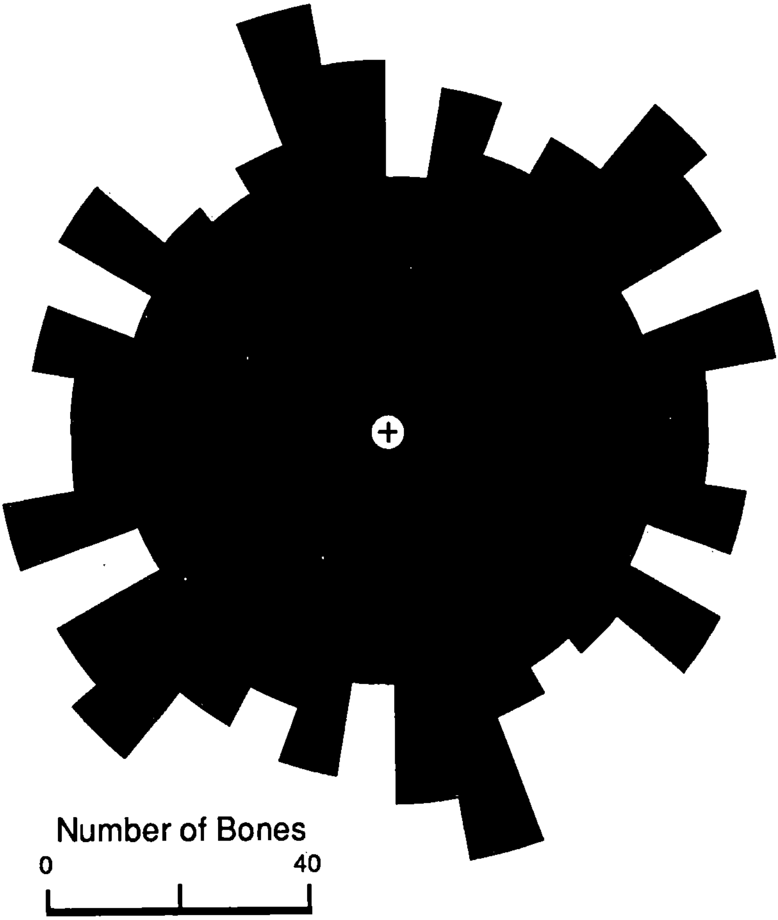

Figure 5. Mirror-image rose diagram showing the directional bearing of 995 long bones collected from Leisey Shell Pit 1A in 1984. Each interval represents 10°.

alignment, proximal ungulate phalanges may show a bimodal distributional pattern (Pratt 1990). Although over 25% of the tibiae (23) were aligned from 160(340) to 180(360) degrees east of north, the overall pattern of orientation was not significantly different from that of a uniform, non-preferred pattern (Table 1). Proximal phalanges also showed no preferred axis of orientation (Table 1).

Within the total area excavated, bones were primarily concentrated in two regions. One area was in the southwestern portion of the site, a roughly rectangular region bounded by squares B5 and B10 on the south and F5 and F10 at the north. The second area was located north of the first, from L10 to L14, and O10 to O14 (Fig. 3). Long bone orientations from each of these two regions of the site were analyzed to determine if elements within these separate concentrations were aligned to any extent. Although some elements from the more northern bone concentration show alignment in a northeasterly to southwesterly direction, in neither of the regions were orientations significantly different from a uniform, non-preferred pattern (Table 1).

The relative positions of associated elements to one another also provides information concerning mechanisms responsible for dispersion of skeletal remains within the site. If separation of two associated elements occurred as a result of the lighter portion being removed from its counterpart by the action of water flowing in one predominant direction, then the direction in which this element moved from its original location would be indicative of current direction. Analysis of the directions in which associated jaws and teeth moved apart (Table 1), indicates that the dispersion pattern of these elements is not significantly different from a random pattern.

The lack of a preferred orientation pattern does not necessarily imply that elements at the site were unaffected by moving water. Coastal marine environments, such as that represented at Leisey 1A, are characterized by tidal currents. In a narrow channel, flow completely changes direction as tide goes in and out, although a 180° change in direction of flow could conceivably cause alignment of bones similar to that of a unidirectional current. However, in a large embayment, tidal currents are often extremely complex; direction of flow not only changes with different stages of the tidal cycle, but may also vary spatially and chronologically. Under such conditions, no preferred alignment of long bones

Table 1. Chi-squared values for bone orientations compared to those expected in a uniform, non-preferred orientation. All samples have 17 degrees of freedom (d.f.) except for phalanges and orientations between associated jaw elements. Data were combined in the latter two tests to accommodate for low numbers of bones per treatment (d.f. = 5). N = number of elements, p = probability, considered significant at 0.05.

Element	N	χ^2	p
Long bones	995	23.43	0.11
Humeri	76	16.37	0.50
Radii	91	16.40	0.50
Femora	70	12.82	0.75
Tibiae	81	22.78	0.15
Metapodia (Camelidae)	89	14.76	0.65
Mandibles	216	15.33	0.60
Long bones, L10-O14	203	25.50	0.07
Long bones, B5-F10	332	14.99	0.65
Proboscidea, Long Bones	87	12.93	0.75
Phalanges	48	4.25	0.51
Orientations between Associated Jaw Elements	39	0.85	0.97

would be evident. It is also possible that a current of one predominant direction was present, but was not of sufficient velocity to cause alignment of the majority of large vertebrate limb elements, most of which belong to Voorhies transport groups III and II (Voorhies 1969; Korth 1979; Pratt 1990). Sediment (Hulbert and Morgan 1989; Hulbert and Morgan this volume) and pollen (Rich and Newsom this volume) analysis indicate that the environment of deposition at Leisey 1A was generally low-energy.

The low angles of plunge of the majority of the elements (Fig. 6) suggest that most bones came to rest on relatively level surfaces and were buried in those positions. There is no directional component to bones that plunged at angles of greater than 10 degrees (Table 1). Voorhies (1969) suggested that groups of bones exhibiting dips in a predominant direction may have been imbricating upstream and dipping against the direction of a prevailing current. The lack of a preferred axis of plunge of bones at Leisey substantiates previous observations that a unidirectional or strong current was not a typical feature of the deposit.

The only feature of the bone positions that indicates the presence of moving water is the side of the bone found facing upward in the field. When exposed to flowing water, some elements routinely assume a predictable, stable position (Voorhies 1969; Pratt 1990). One of the most reliable elements in this regard is the innominate (isolated) which often comes to rest with the lateral (acetabular) side up when exposed to running water (Pratt 1990). Of 47 camel and equid innominates from Leisey for which positional data were obtained, significantly more (36) were recovered with the acetabular surface facing upward as opposed to facing downward ($\chi^2 = 6.65$, $p < 0.01$ at 1 d.f.). This suggests that flowing water moved these elements into their fluvially-stable resting positions.

The absence of a preferred orientation for long bones lends credence to a hypothesis that some of the scattering of bones within the site may have been caused by scavengers or by large herbivores. Recent experimental studies have shown that a random pattern of orientation results when large herbivores trample and kick bones (Fiorillo 1989). However, steeply plunging bones have also been described as a characteristic of trampled assemblages (Hill and Walker 1972; Behrensmeyer and Boaz 1980; Fiorillo 1989); some elements may end up in vertical orientations if they are driven lengthwise into soft sediment. No bones were found that plunged at angles of greater than 53° at Leisey 1A (Fig. 6), suggesting either that trampling did not affect bone orientations and distributions, or that the sediment was relatively hard. Trampling will be considered further in the section on scratchmarks on bones. Small, light elements may have been

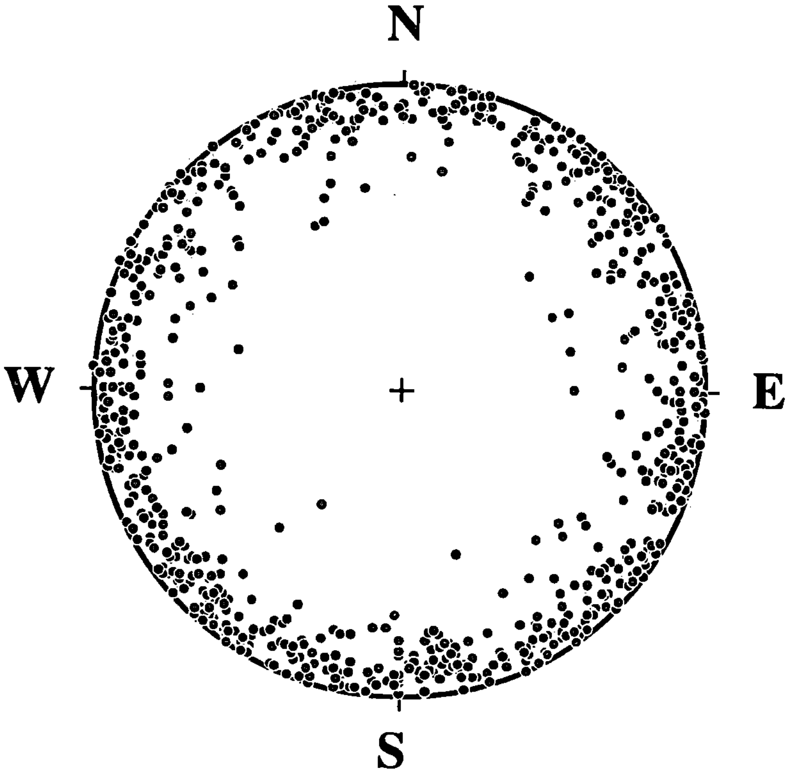

Figure 6. Stereonet projection of the bearing and plunge of 650 long bones collected from Leisey Shell Pit 1A in 1984. The vast majority of the fossils had plunges of less than 15°.

transported in various directions, or removed from the site entirely as the tide ebbed and flowed, while larger, denser elements were periodically scattered by the effects of trampling.

Bone Modification

Bone modification results from any activity that alters the original appearance of bone. The causative agents of bone modification may be instrumental in causing the animal's death (predators), or can cause alteration at any point between death of the animal and recovery of the fossils (e.g., scavenging, weathering, trampling, transport, abrasion by sediments, epibiont activities, post-depositional breakage, reworking).

Identifiable bones of large mammalian taxa (Edentata, Proboscidea, Artiodactyla, Perissodactyla, and Carnivora) were examined for modification, as were shell elements of the freshwater turtle *Trachemys scripta* and the large tortoise *Hesperotestudo crassiscutata*. The majority of identifiable elements examined in this phase of the study were collected from squares B4-B7, C5-C7, C9, D6, D7, D9, D10, and E6. The equid sample was supplemented with bones from squares A1-C4. The comparison of identifiable versus fragmentary bone was tabulated using material collected from B4, a square from which all fossil specimens were collected. Two hundred ninety-two unidentifiable fragments from both this square and from square D9 (another totally sampled square) were randomly selected for analysis of types of bone modification on fragmentary remains.

Bone Completeness.– As a number of taphonomic processes are known to result in bone breakage, analysis of degrees and types of breakage may provide valuable insight into events that may have influenced the formation of a fossil assemblage. One very obvious feature of the Leisey 1A site is that the majority of bone is composed of unidentifiable fragments. Table 2 compares the numbers and proportions of complete (more than 90% of the element preserved) and partial (less than 90% of the element preserved) identifiable terrestrial mammalian elements with those of unidentifiable bone shards found in square B4. Unidentifiable fragments comprise over 90% of the bone sample from this region, although this value is probably inflated due to post-depositional compaction breakage and the presence of non-mammalian fragments. Carnivores and scavengers are known to cause bone splintering in Recent bone assemblages. Binford (1981) reported that over 90% of the specimens at wolf kill sites were unidentifiable fragments and splinters. Felids also cause splintering of bone (Brain 1981). In addition, other activities such as trampling of bones by large ungulates (Haynes 1983b; Fiorillo 1989) and to a lesser extent, transport by running water (Behrensmeyer et al. 1989) may also cause breakage and presumably, splintering of bones. Therefore the presence of high percentages of bone splinters is not informative except in the context of sedimentary particles, as will be discussed later.

The majority of identifiable elements (not including shards) both from B4 and from the site as a whole are complete rather than broken (Table 2). The presence of numerous complete podials, phalanges, and teeth is not surprising, as these compact, dense elements are not generally modified by taphonomic events (Behrensmeyer et al. 1989). Of the identifiable limb elements, vertebrae and mandibles, approximately two-thirds are incomplete, a situation similar to that reported by Behrensmeyer et al. (1989) at Miocene vertebrate fossil localities in Pakistan, in which 75% of the limb elements were incomplete. As pointed out by Behrensmeyer et al. (1989), the high incidence of breakage denotes activities of taphonomic agents and processes.

Table 2. Bone completeness of Leisey 1A mammals. Category A includes cranial elements, girdles, limb elements, and vertebrae. Category B includes podials, phalanges, and teeth.

A. Elements from B4. N = 656.

	Identifiable elements				Unidentifiable fragments			
	Complete A	Complete B	Partial (all A)	Grand Total Identifiable	>10 cm	5-10 cm	<5cm	total
N	14	15	26	55	4	41	556	601
%	2.1	2.3	4.0	8.4	0.6	6.3	84.8	91.6

B. Elements from entire Leisey sample of identifiable bone examined (not including fragments).
N = 566.

	Complete A	Complete B	Grand Total	Partial (all A)
N	142	164	306	260
%	25.1	29.0	54.1	45.9

C. Breakage types on partial limb elements of mammals.

Breakage type	N	% of total
Spiral	8	5.5
Step	14	9.7
Combination Spiral/Step	30	20.7
Gnaw	17	11.7
Recent	76	52.4
Total	145	

In this study, partial limb bones were categorized according to the type of breakage each possessed. The categories used are as follows:

1) Recent breakage: any type of post-fossilization (or prefossilization compression) breakage, including compaction breaks and collection-related breaks.
2) Spiral fractures: prefossilization breaks on the bone shaft that run oblique to the bone's long axis, as described by Binford (1981), Haynes (1983b), and Oliver (1989).
3) Step, or longitudinal fractures: prefossilization breakage that occurs as series of alternating longitudinal and transverse fractures to produce a step-like appearance on the broken edge of the bone (Hill 1979; Haynes 1983b). Breaks tend to follow the line of drying cracks that develop in the bone in the course of weathering.
4) Combination spiral/step fractures (interrupted spiral fractures): the line of the spiral fracture is broken or interrupted by step fractures (Hill 1979; Haynes 1983b).
5) Gnaw breakage: the broken edge of the bone has a scalloped or irregular outline caused by gnawing (Binford 1981; Haynes 1983a, 1983b).

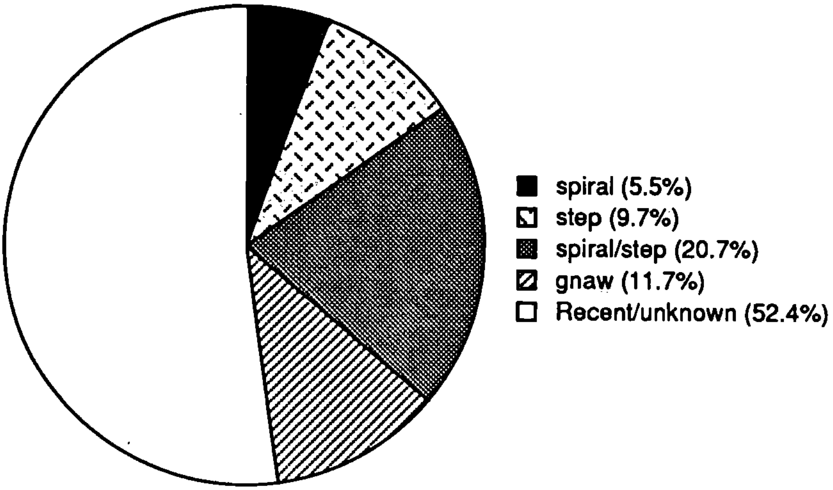

Figure 7. Pie diagram depicting relative frequency of different bone breakage types from a sample of 145 randomly selected, partial limb bones of large mammals from Leisey Shell Pit 1A.

The proportions of bones assigned to each category are listed in Table 2 and Figure 7. The most common type of breakage seen on partial limb elements is post-depositional. The breaks appear to have been caused primarily by naturally-occurring sediment compaction, although it is also possible that heavy mining equipment and large trucks transversing the area contributed to bone breakage prior to the site's discovery. Unfortunately, if the bone was partially fragmented in this manner, in many instances the fragments were not collected with the element and therefore could not be reattached to it. The result is that over half the partial mammal limbs in the collection have post-fossilization breaks, and the original type of pre-fossilization breakage cannot be discerned (Table 2, Fig. 7).

The majority of pre-fossilization limb bone breaks are of the combination spiral/step fracture variety (Table 2). This type of breakage, as well as spiral fracturing, is primarily caused either by carnivore/scavenger activity or by trampling. However, in the absence of other types of bone modification, breakage patterns alone cannot identify the causative agent of modification. The percentage of bones in an assemblage that are broken in spiral or combination fractures has been shown to vary with the size and condition of the bone, and the size and type of predator, or trampler. Fractures caused by carnivores in recent studies range from 8% of the total limb number to 100% (Haynes 1983b; Haynes and Stanford 1984). Up to 50% of long bones in an assemblage may be fractured by trampling (Haynes 1983b; Haynes and Stanford 1984; Agenbroad 1989). At Leisey, about 25% of the total mammalian limb elements examined were broken in this way, but this number is probably low as undoubtedly some elements in the Recent breakage category originally possessed prefossilization fractures. In addition, the majority of the elements examined (camelid and equid) are relatively large in size and were not as subject to breakage as smaller elements from deer and peccaries (Haynes 1983b).

Regardless of whether bone breakage is caused by a carnivore or by trampling, in either case the exact breakage type is related to the amount of weathering the bone has experienced. "Fresh," or green bone tends to fracture in a spiral pattern (Behrensmeyer et al. 1989). Although bones broken in this manner are most often attributed to carnivores (Haynes 1980b, 1983b; Hill 1980; Binford 1981) it can also occur when "fresh" or even slightly weathered bones are trampled (Myers et al. 1980; Haynes 1983b; Haynes and Stanford 1984; Fiorillo 1989). In addition, bones deposited in moist or aquatic habitats retain characteristics of "fresh" bones for long periods of time and may fracture in a spiral fashion as long as they remain moist (Haynes and Stanford 1984). Bone that is slightly to moderately weathered most often breaks along combination spiral/step fractures when scavenged or trampled (Haynes 1980b, 1982, 1983b; Olsen and Shipman 1988). If a bone is broken after prolonged exposure to the forces of weathering, then a step fracture commonly results (Conybeare and Haynes 1984). Figure 8 shows that the type of breakage on mammal limb elements from Leisey 1A is

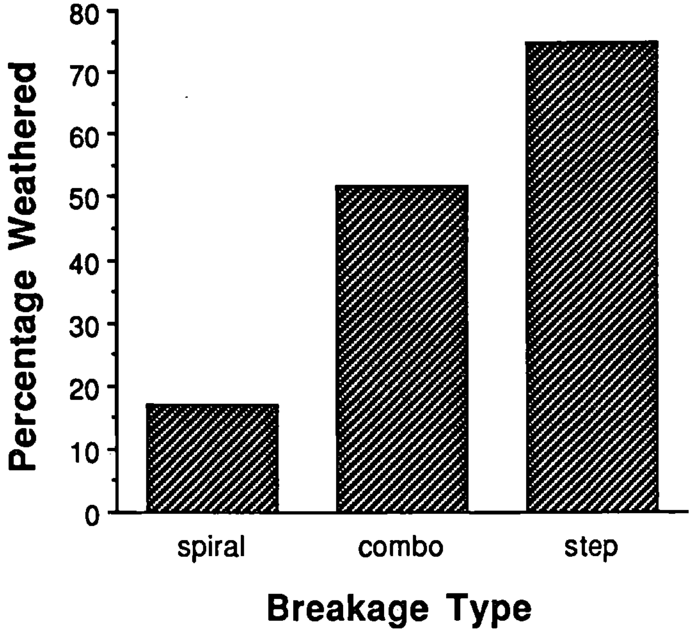

Figure 8. Percentage of broken mammalian limb bones subdivided by breakage type, showing features evident of slight to moderate weathering at Leisey Shell Pit 1A.

related to extent of weathering. Only one spirally fractured bone is even slightly weathered, while over half of the elements with combination spiral/step fractures are discernibly weathered, and 75% of the bones possessing step fractures are weathered to some degree.

Investigation of surface features is required in order to ascertain if broken bones were primarily modified by carnivores or by trampling; however a few observations may be made concerning bone breakage. Based on breakage type and percentage of bones broken, it is not possible to determine the agent(s) of modification; however, the low percentage of "green" spiral breaks indicates that most bones were not broken by carnivores or trampling immediately following the death of the animal. It also indicates that any fresh bones immediately deposited in an aquatic habitat were probably not broken while wet. The presence of combination and step fractures indicates that most bones that were broken were probably modified after they had been exposed to some extent to drying and weathering, either by scavenging or by trampling. However, based solely on the breakage pattern, it is not possible to determine if these partial elements were broken prior to, or following their arrival at the site of deposition. It has been suggested in the section on articulation and association, and will be shown in following sections, that while some breakage did occur at the site of deposition, many elements were broken before they were deposited at the site of fossilization.

Bone Surface Features.– Bones were examined for evidence of modification caused by predation and/or scavenging, exposure to subaerial weathering, water-borne sediments or other abrasive factors, and trampling by large herbivores. Degrees of modification were assessed using the following scales:

1) Evidence of predation was determined by characteristic breakage patterns, puncture marks, and depressed fractures (Haynes 1980a, 1983a; Hill 1980; Binford 1981). Light modification includes at least one of the following; one set of puncture marks, one chewed or gnawed edge, or obvious scoring marks: moderate modification is indicated by at least one of the following; two to five sets of puncture marks, two gnawed or chewed edges, and numerous scoring marks: heavily damaged bone has completely gnawed ends, epiphyses, or numerous tooth marks. These stages are roughly comparable to the utilization stages described by Haynes (1983a). Elements for which definite assignments to modification categories could not be made were scored as "possibly modified or unknown."
2) Weathering stages were assessed using the scale proposed by Behrensmeyer (1978) ranging from stage 0, or unmodified bone, to stage 5, completely weathered bone near final stages of destruction.
3) Evidence of water-wear, polishing or erosion was determined using a scale proposed by Pratt (1990) ranging from unmodified bone (stage 0) through a series of progressively more severely stages categorized as minimal (stage 1), moderate (stage 2), and finally extreme water-wear (stage 3) characterized by rounding and loss of diagnostic processes (comparable to "bone pebbles" of Andrews and Ersoy 1990).
4) Scratch marks were quantified by estimating the percentage of the bone surface covered by scratches, as described by Fiorillo (1989).

Features Caused by Predation/Scavenging.– Bone damage caused by predation or scavenging is one of the most difficult types of modification to identify. Unless the type of damage is clearly recognizable, it is often not possible to definitely attribute it to a carnivore (Haynes 1983b). In addition, some carnivores, even in the process of breaking bone, may not leave identifiable marks on either the shaft or fragments (Haynes 1980b, 1982, 1983a, 1985, 1988; Haynes and Stanford 1984). For these reasons, a large number of elements (in particular partial bones with post-depositional breaks) from Leisey 1A could not be definitely categorized with regard to carnivore modification, and therefore are listed as "possibly modified." Figures 9-10 and Table 3 compare the extent of carnivore-

Table 3. Extent of carnivore damage to Leisey elements. Man = mandibles; L/G = limbs/girdles; Ver = vertebrae; Pod = podials; GT = grand total; P = possible.

A. Complete elements from entire Leisey sample examined.

Modification Stage	Man N	L/G N	Ver N	Pod N	Total	% of GT
None	5	48	41	164	258	84.3
Light	0	20	5	0	25	8.2
Moderate	0	0	0	0	0	0.0
Heav;y	0	0	0	0	0	0.0
P	14	9	0	0	23	7.5
GT					306	

B. Partial elements from entire Leisey sample examined.

Modification Stage	Man N	L/G N	Ver N	Pod N	Total	% of GT
None	3	22	11	0	36	14.3
Light	0	24	16	0	40	15.9
Moderate	0	4	1	0	5	1.9
Heavy	0	0	0	0	0	0.0
P	21	101	49	0	171	67.9
GT					252	

C. Unidentifiable fragments from B4 and D9.

Modification Stage	N	% of GT
None	0	0.0
Light	4	1.4
Moderate	0	0.0
Heavy	0	0.0
P	288	98.6
Total	292	

D. Carnivore damage to complete long bone and girdle elements of selected taxa.

	Camelidae		Equidae		Proboscidea	
Modification Stage	N	%	N	%	N	%
None	15	51.7	15	65.2	17	70.8
Light	6	20.7	7	30.4	7	29.2
Moderate	0	0	0	0	0	0
Heavy	0	0	0	0	0	0
P	8	27.6	1	4.3	0	0
Total	29		23		24	

Table 3 Continued.

E. Carnivore damage to partial long bone and girdle elements of selected taxa.

	Camelidae		Equidae		Proboscidea	
Modification Stage	N	%	N	%	N	%
None	6	7.6	10	24.4	6	24.0
Light	14	17.7	5	12.2	4	16.0
Moderate	3	3.8	1	2.4	0	0.0
Heavy	0	0.0	0	0.0	0	0.0
P	56	70.9	25	61.0	15	60.0
Total	79		41		25	

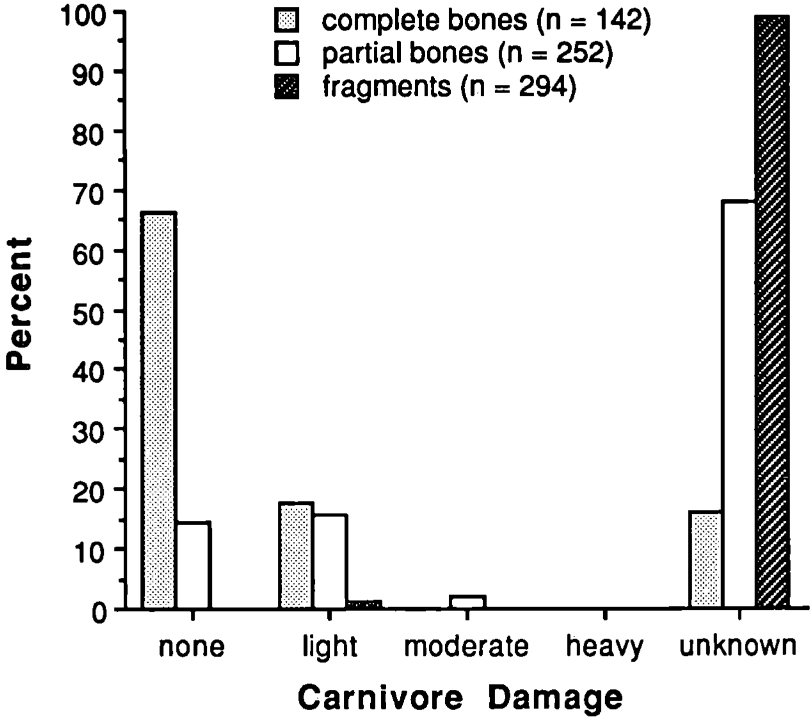

Figure 9. Comparison of the degree of bone modification by carnivores/scavengers on complete, partial, and fragmentary bones from Leisey Shell Pit 1A. Elements included in this analysis were dentaries, limb bones, girdle elements, and vertebrae of large herbivores (Table 3).

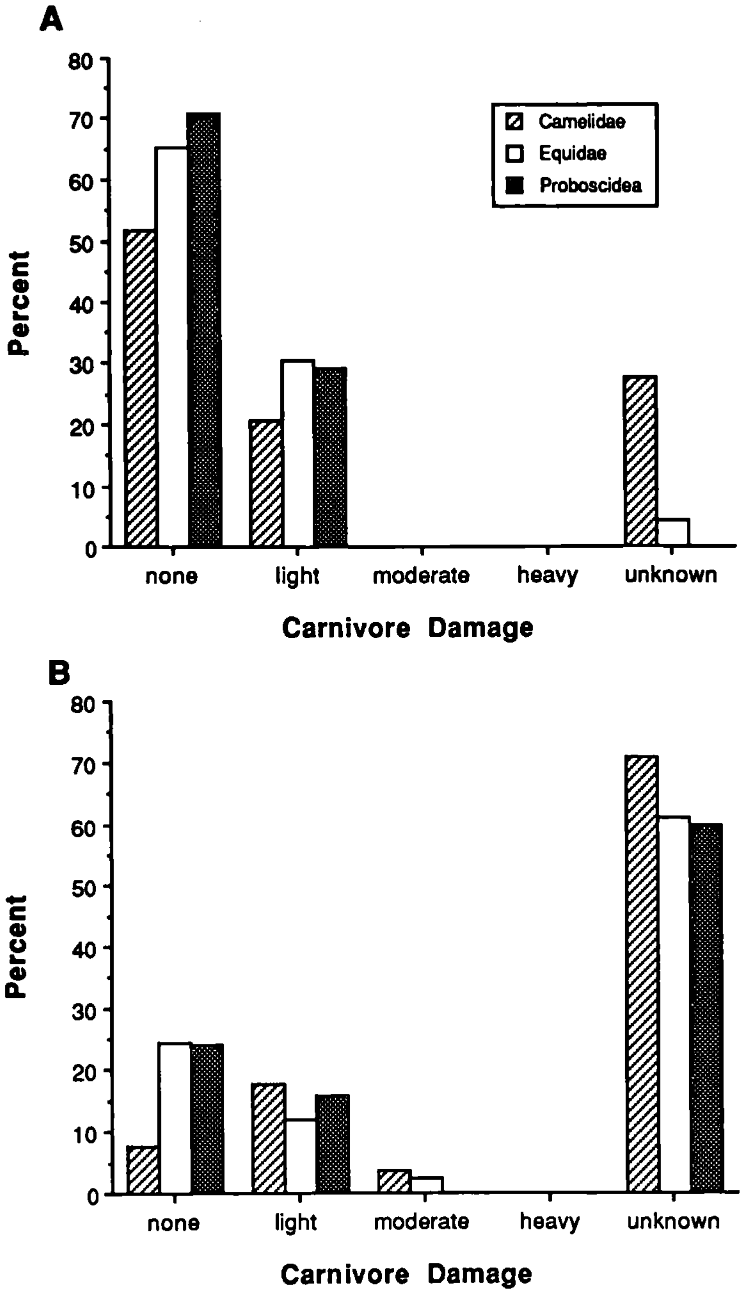

Figure 10. Comparison of the degree of bone modification by carnivores/scavengers on complete (A) and partial (B) bones from Leisey Shell Pit 1A, sorted by taxa.

inflicted damage on complete, partial, and fragmentary skeletal elements. Many of the identifiable bones of the most abundant large herbivores (proboscidean, camel, horse) show no evidence of being modified to any extent by carnivores. Over 83% of complete elements (including podials) are unmodified. Complete podials are least damaged (Table 3) which is not surprising considering that unless they are ingested (Haynes 1985; Behrensmeyer and Boaz 1980), they are not significantly modified by carnivores (Haynes 1980b; Behrensmeyer et al. 1989). Most complete mandibles and isolated dentaries are broken into numerous pieces by post-depositional compaction, and it is difficult to assess modification, particularly breakage patterns, on those that have been repaired. In the case of equids, many mandibles have breaks at the diastema just posterior to the symphysis on either one or both sides. Camelid mandibles are more fragmentary, and separation of right and left dentaries may be either at the symphysis, or just posterior to it. Breakage of a herbivore jaw in the diastema region is a feature often attributed to carnivores, which pull off the upward-facing dentary of their prey in order to feed on its tongue (Behrensmeyer and Boaz 1980; Haynes 1980b, 1982; Hill 1980). However, there are several features of Leisey mandibles that suggest that much of the jaw breakage was caused by other means. First of all, there is no clear evidence of carnivore-inflicted damage on jaws as described by Haynes (1980a). Many of the horse jaws are complete, with no pieces missing from the ascending ramus. Second, some mandibles possess pre-depositional breaks on both left and right mandibles, rather than on just one side. Third, in many cases, the break is a longitudinal fracture rather than the spiral fracture or v-shaped lever fracture that would result as the upward-facing jaw was forced open (see Haynes 1983b: fig. 4). In many instances, the breakage pattern indicates that the break occurred as a result of downward pressure, rather than upward tension. Finally, the close proximity of associated right and left mandibles to one another would mandate that these elements separated from one another at the site of deposition. Given the marine nature of the site, there are very few explanations that could account for mammalian predation within the actual environment of deposition. It is possible that carcasses that accumulated in the site were scavenged during low tide, or live animals trapped in quicksand or mud were attacked by predators. The latter explanation is not supported by the geology of the site (Morgan and Hulbert this volume).

Approximately 17% of the vertebrae (including sacra) examined possess canine and cheektooth impressions on the centra, or gnawed processes. Unfortunately, the majority of vertebral remains are too fragmentary to allow positive identification of surface modification features. The clearest examples of carnivore modification are seen on girdle elements and long bones (Figs. 10-11; Tables 3-4). Approximately 25% of complete and nearly complete limb and girdle elements examined are modified (Fig. 10A), with damage consisting primarily of gnawed or bitten-off epiphyses and processes, depressed fractures and crenulated

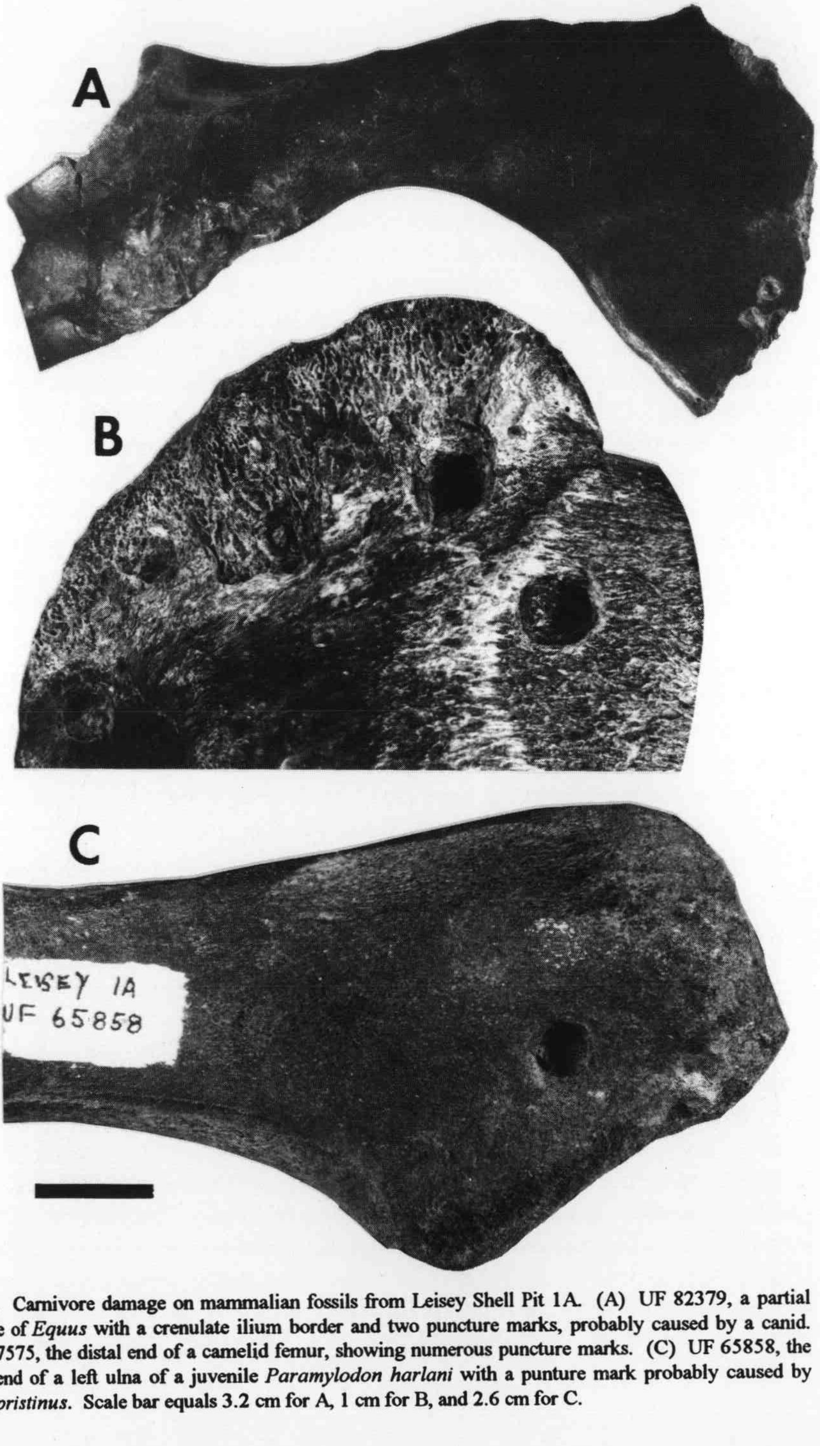

Figure 11. Carnivore damage on mammalian fossils from Leisey Shell Pit 1A. (A) UF 82379, a partial innominate of *Equus* with a crenulate ilium border and two puncture marks, probably caused by a canid. (B) UF 67575, the distal end of a camelid femur, showing numerous puncture marks. (C) UF 65858, the proximal end of a left ulna of a juvenile *Paramylodon harlani* with a punture mark probably caused by *Arctodus pristinus*. Scale bar equals 3.2 cm for A, 1 cm for B, and 2.6 cm for C.

Table 4. Carnivore damage to mammalian elements. Categories: 1 = minimal punctures, gnawing, 2 = more extreme, 3 = bone cylinders.

Bone type	Modification in sample	# of bones in category	Modification description	Example (UF #)
Scapula	1	5	blade and cranial border chewed	83374
	2	1	crenulated, scalloped edges	
Humerus	1	4	head and trochlear ridge gnawed furrows, tooth impressions	82327
Radio-ulna and ulna	1	6	olecranon chewed, moon-shaped bite	82485
Radius	1	2	distal epiphysis gnawed	
Innominate	1	16	ilium blade chewed, punctured crenulated, scalloped edges tooth furrows on ischial crest	82379
Femur	1	5	head, trochanter, or condyle ridge gnawed, canine impressions on condyles	82261
	3	2	epiphyses removed--bone cylinders	
Tibia	1	4	cnemial crest chewed, removed	81572
	2	2	proximal epiphysis removed	
Vertebrae				
Axis	1	2	canine puncture holes	85240
Cervical	1	5	puncture holes, processes chewed	83483
Thoracic	1	7	puncture holes, processes chewed	84217
Lumbar	1	4	puncture holes, processes chewed	82271
Sacral	1	3	puncture holes, processes chewed	83368
	2	1	partially gnawed	

edges, and occasional tooth impression marks (punctures and furrows). Due to the lack of recognizable surface features on many of the partial elements, the percentage (17%) of incomplete girdles and limb bones possessing obvious carnivore damage is somewhat lower than that of more complete long bones. Most modification consists of gnawed ends, tooth punctures and scoring marks. Several bone cylinders (sensu Binford 1981) were recovered, but not from the completely sampled squares that form the basis of the taphonomic analysis. If prefossilization breakage of partial elements was caused primarily by carnivores or scavengers, it seems reasonable to suggest that many fractured elements would possess features indicative of carnivore modification. About 20% of limb elements with prefossilization fractures (recent breaks not included) possess surface features interpreted as carnivore-caused. This value is much lower than the value reported by Haynes (1983b) in which 70% of broken limb elements at a bison kill site were visibly modified by wolves. While the Leisey value might be greater if a number of the unidentifiable bones belong in this category, the value would probably not approach the 70% level.

The relationship of carnivore modification to breakage may also be examined by comparing the ratio of carnivore-modified to unmodified complete elements with the ratio of carnivore modified to non-modified partial elements. The "possibly modified" bones are not included in these calculations. The ratio of modified to unmodified complete elements is 0.42, while the ratio for partial elements is 1.27. The differences between these ratios for complete and partial elements suggests that bone breakage was in some way related to carnivore modification, either directly or indirectly. Some elements possessing evidence of carnivore modification may have actually been broken by other means, such as trampling, after being initially weakened by chewing and gnawing (Haynes 1983b).

Bones were also analyzed to determine the relationship between stage of weathering and presence of carnivore-inflicted damage. Although reports in the literature suggest that most scavenging and accompanying breakage of limb bones generally occurs before the bones have begun to weather extensively (e.g., Haynes 1982), some scavenging may take place as much as 6 months after death of the prey, when elements have entered visible stages of weathering (Haynes 1982: fig. 3). Fossils showing evidence of exposure to weathering were accessible to scavengers for the period of time that these elements retained some nutritive value. In contrast, some, if not all, of the unweathered elements may have been made unavailable to terrestrial scavengers, either by immediate entry into the subaqueous environment of deposition, or by initially coming to rest in a moist habitat with dense ground cover (see following section on bone weathering). The ratio of modified to non-modified bone increases with weathering stage for both complete and partial elements (Fig. 12), showing that remains exposed to weathering also

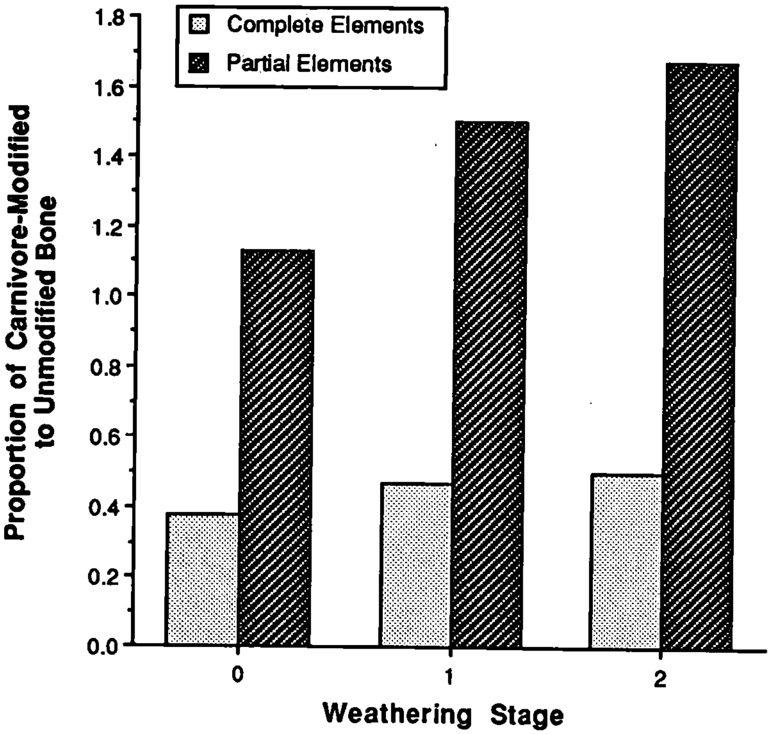

Figure 12. The relationship between weathering stage and carnivore modification on complete and partial bones from Leisey Shell Pit 1A.

experienced more damage due to scavenging than bones that were not obviously weathered. This is indicative of different taphonomic histories for the unweathered, unchewed elements and the modified bones.

The relative rarity of highly utilized or modified elements at Leisey may also be in part explained by the lack of bone-crushing specialists at the site. Among the mammalian carnivores at Leisey, there are only a few that were large enough to have to preyed upon large herbivores and have caused bone modification; two felids, *Smilodon gracilis* and *Homotherium* sp., one canid, *Canis armbrusteri*, and an ursid, *Arctodus pristinus*. One problem in assessing the amount of destruction that these carnivores may have caused is that they are all extinct species, and in three cases extinct genera. Therefore, direct comparisons with living analogs cannot be made. However, some basic inferences can be drawn based on the predator's dental morphology and types of modification seen on bones of prey.

In terms of relative numbers, the most abundant carnivore at Leisey 1A was the saber-toothed felid *Smilodon gracilis* (Table 11). While it has been shown that this cat was probably an active predator (Gonyea 1976), capable of killing camelids and equids, it is very unlikely that this species, or any other saber-toothed predator, was able to modifying bone to any great degree (Brain 1981). Van Valkenburgh et al. (1990) showed that *Smilodon* and other saber-cats avoided bone contact in order to protect their sabers from breakage. Although some of the types of bone modification at Leisey 1A, such as bitten-off epiphyses, are similar to types of damage caused by Recent felids such as lions (Haynes 1983a; 1985), it is also possible that modification was caused by another predator such as a bear, which, as pointed out by Haynes (1985) may cause bone damage indistinguishable from felid damage. *Homotherium* sp. is also known from the site, although remains of this felid are rare. *Homotherium* was probably capable of killing large mammalian prey, but it is doubtful that this saber-toothed felid caused extensive bone modification.

The majority of carnivore-inflicted bone damage appears similar to that caused by canids, in particular wolves (Haynes 1980a; 1980b; 1983a; Binford

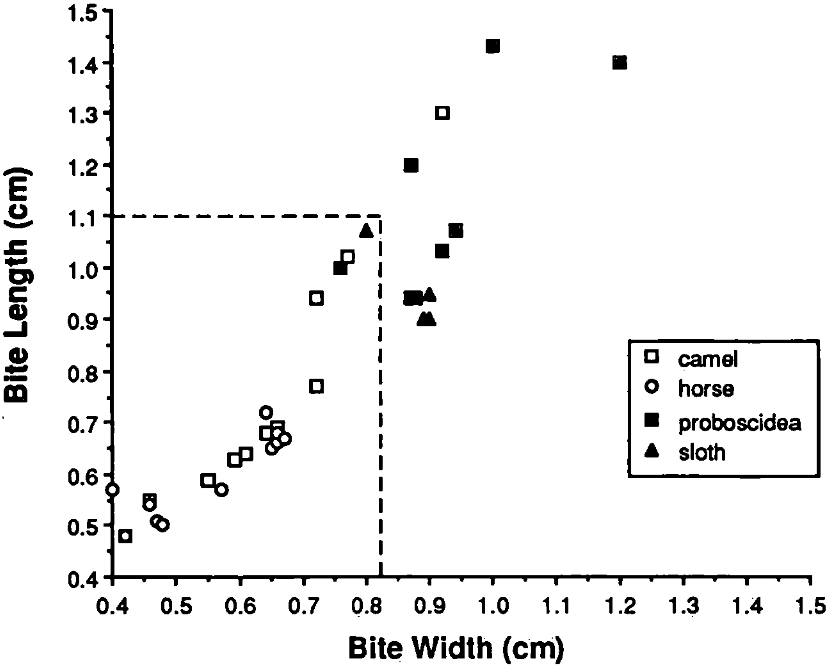

Figure 13. Size distribution of the length and width of puncture impressions ("bite marks") on large mammalian herbivores from Leisey Shell Pit 1A caused by the canine teeth of predators or scavengers. Dashed lines indicate the maximum (basal) canine dimensions of *Canis armbrusteri*. Larger marks fall within the range of size of the canines of *Arctodus pristinus*. The larger bite marks (presumably caused by *A. pristinus*) were found predominantly on prey species with greater body size (ground sloths and proboscideans), while *C. armbrusteri* apparently preyed or scavenged primarily on equids and camelids.

1981). The only canid at the site of sufficient size to have caused significant bone modification was *Canis armbrusteri*. This canid was slightly larger in size than *C. lupus*, the extant gray wolf, and had an extremely wolf-like dental morphology (Van Valkenburgh 1991). It was probably able to kill large herbivores, particularly if it was a pack hunter. In addition, *C. armbrusteri* may have scavenged carcasses, including those abandoned by *Smilodon gracilis*, although it also had limited bone-crushing or bone-breaking abilities (Van Valkenburgh 1991). Much of the recognizable carnivore damage on camelid and equid remains includes canine and cheektooth impressions and furrows, the size and spacing of which match the dentition of *C. armbrusteri* (Figs. 11, 13). The semi-lunar shaped bites on olecranon processes (such as UF 82485) correspond well with the size and shape of the anterior toothrow in this species.

The final large mammalian carnivore represented at the Leisey 1A locality is the ursid *Arctodus pristinus*. The diet of the better-known late Pleistocene *Arctodus simus* has been discussed at length by several workers. Kurtén (1967) and Van Valkenburgh (1988) suggested that it was a specialized carnivore or scavenger. Emslie and Czaplewski (1985) noted similarities of the dental morphology and jaw structure of this ursid to more herbivorous forms, but suggested that it may have been primarily omnivorous with scavenging tendencies. Agenbroad and Mead (1986) and Gillette and Madsen (1992) provided evidence that *A. simus* was scavenging mammoth carcasses. Kurtén (1967) suggested that the older, smaller *A. pristinus* may have been more omnivorous and less predaceous than *A. simus*. However, carnivore-damaged elements of proboscideans and sloths from Leisey indicate that *A. pristinus*, while perhaps not capable of killing adult proboscideans, was definitely feeding on their carcasses and in some instances damaging bones. Canine and cheektooth impressions of large size are perfect matches for the dentition measurements of *A. pristinus* from the site (Figs. 11, 13). The majority of damage to sloth bones is seen on specimens of *Nothrotheriops texanus*, a small ground sloth. Nearly all of the identifiable tooth marks identified on *N. texanus* elements were apparently caused by *Arctodus*. However, at this point it cannot be determined if *A. pristinus* was an active predator, or only a scavenger.

It is interesting to note that no true bone-crushing specialists are present at Leisey. This is the only gap of this "niche" in Florida over the last 12 million years. At earlier Irvingtonian sites in Florida, such as Inglis 1A, the hyaenid *Chasmaporthetes ossifragus* is present (Berta 1981). Miocene and Pliocene sites almost always contain borophagine canids (e.g., Webb et al. 1981; Van Valkenburgh 1991), widely regarded as ecological analogs of modern hyenas. Recent hyenas are known to cause extensive damage to bones from both fresh-caught and scavenged carcasses (Brain 1980; Haynes 1983a; Blumenschine 1989). Later Pleistocene faunas contain the dire wolf, *Canis dirus*, which may also have had bone-crushing capabilities (Haynes 1983b, 1985; Van Valkenburgh et al.

1990). The absence of a bone-crushing specialist from the Leisey 1A fauna may account in part for the low degree of modification seen on prey elements.

Results of the preceding analysis indicate that predation and scavenging were taphonomic events that to some extent influenced and contributed to the Leisey 1A terrestrial mammal portion of the bone assemblage. The relative importance of these factors in forming the bone accumulation can be assessed as follows. At Leisey, innominate bones are the most abundant elements of equid and camel (see following section on bone representation). As evidence of predation is relatively easy to discern on this element, the ratio of carnivore-modified to intact innominates can be used to indicate the percentage of individuals of these taxa either killed by carnivores or scavenged after death. Based on the innominates examined (N = 20 camelid, 15 equid), an estimated 25% of the camels and 36% of the equids found in the deposit were either killed by carnivores and/or fed upon by scavengers. Based on femora (the most common element of proboscideans [N =10] and sloths [N = 7]), about 33% of the proboscideans, and 43% of the small ground sloth *Nothrotheriops* were modified to some extent by carnivores.

While these percentages may seem high, it is important to stress that this is the percentage of dead animals, not the percentage of the total living population. Given that the overall death rate for Recent zebra is about 22% per annum (Western 1980), and that the predation-caused death rate is approximately 8 to 10% per annum, or in some cases as high as 16% (Foster and Coe 1968; Haynes 1988), then the remaining deaths (normally, 12-14% of the total population per annum) are not caused by predators. Therefore, in an ideal attritional death assemblage it is expected that from 36 to 45% of prey individuals would show evidence of predation. Scavenging of carcasses of individuals that died of natural causes would lead to a greater than predicted percentage of carnivore-modified bone, but in an attritional assemblage this increase would probably be offset by two factors: a greater tendency for bone damaged by carnivores to be subsequently completely destroyed, and by periodic occurrences of increased mortality due to drought or other catastrophic events (Coe 1980; Conybeare and Haynes 1984; Haynes 1988). The likelihood that minor catastrophic events may have contributed to the Leisey 1A bone accumulation is supported by several lines of evidence, including the types and levels of bone modification (Table 4) which are generally consistent with "light to moderate" utilization of carcasses (Behrensmeyer and Boaz 1980; Haynes 1980a, 1980b; Conybeare and Haynes 1984; Blumenschine 1989). In Recent environments, low utilization is seen during periods of high prey-to-predator densities, when prey species are weakened and die in large numbers as a result of drought or other environmental factors, and thus provide more food than carnivores can exploit (Behrensmeyer and Boaz 1980; Coe 1980; Haynes 1980b). This appears to have been the case for the Leisey camelids, for which the proportion of modified individuals is lower than expected, and lower than the other large herbivore taxa. The percentages of other prey species that were either killed by carnivores or scavenged following death fall within the ranges expected in a typical population. An abnormally high amount of carnivore activity is not indicated for any of the taxa examined. Therefore it is unlikely that the deposit represents primarily a carnivore-formed accumulation. It is also unlikely that the site was a mammal trap, such as a mudhole or quicksand, that attracted a high number of predators to the region. This finding is in agreement with the results of the population dynamics analysis. Bones of terrestrial mammals accumulated attritionally as a result of both natural deaths and predation, with perhaps some input from catastrophic events.

Weathering.— Figure 14 and Table 5 illustrate the extent of weathering on mammalian elements from Leisey 1A. There is a significantly greater incidence of weathering on partial, identifiable bones as opposed to complete elements (Table 8). This result agrees with the observation made by Haynes (1991) that breakage increases with the amount of time a bone is exposed to the effects of weathering. The majority of bones possessing weathering features are only slightly modified, suggesting that conditions favoring extensive weathering (extremely dry climate, long periods of subaerial exposure) were not in operation. The extent of weathering overall is consistent with that of bone that has weathered for a period of four years or less (Behrensmeyer 1978; Andrews and Cook 1985; Fiorillo 1989), or bone that has weathered in relatively protected environments, including damp habitats, or regions with ground cover. It has been shown that the amount of ground cover as well as microclimatic conditions influence the degree of bone modification caused by exposure to climatic factors (Behrensmeyer 1978; Brain 1980; Conybeare and Haynes 1984; Haynes 1991).

If bone modification due to weathering is considered for each of the major large herbivore taxa, a more informative pattern emerges (Fig. 15, Table 8). For all three taxa examined, a greater but non-significant proportion of partial limb and girdle elements are weathered compared to complete bones. In between-taxa comparisons, a significantly greater proportion of equid and elephant remains, both complete and partial, possess exposure-related modification than do camelid bones. The difference in extent of weathering between equids and proboscideans is not significant (Table 8). The greater incidence of weathering on equid and proboscidean remains as opposed to camels suggests different taphonomic histories for these groups. A larger proportion of camelid remains as opposed to both equids and proboscideans were either deposited immediately as carcasses into the aquatic depositional environment, or decomposed in terrestrial areas where rates of weathering were retarded for various reasons. The former explanation seems more acceptable, and it is supported by other data, as discussed previously (see section on carnivore modification).

As bones of all taxa were found in close proximity to one another (Fig. 2), similar patterns of weathering for all taxa would be expected if weathering exposure had occurred at the site of deposition. The differences in degrees of weathering between taxa indicate that weathering did not occur at the location

Table 5. Weathering modification on Leisey mammalian elements. Stages described in the text. Man = mandibles; L/G = limbs and girdles; Ver = vertebrae; Pod = podials; T = total; GT = grand total.

A. Weathering stages on complete elements from entire Leisey sample examined.

Stage	Man N	L/G N	Ver N	Pod N	Total	% of GT
0	6	47	33	155	241	78.7
1	8	24	12	9	53	17.3
2	5	6	1	0	12	4.0
3	0	0	0	0	0	0.0
GT					306	

B. Weathering stages on partial elements from entire Leisey sample examined.

Stage	Man N	L/G N	Ver N	Pod N	Total	% of GT
0	6	76	40	0	122	48.4
1	14	54	34	0	102	40.5
2	2	19	3	0	24	9.5
3	2	2	0	0	4	1.6
GT					252	

C. Weathering stages on unidentifiable fragments from squares B4 and D9.

Stage	N	% of GT
0	176	60.2
1	84	28.8
2	32	11.0
3	0	0.0
T		292

D. Weathering stages on complete long bones and girdle elements of selected taxa.

Weathering Stage	Camel N	Camel %	Horse N	Horse %	Proboscidea N	Proboscidea %
0	23	79.3	12	52.2	11	45.8
1	5	17.2	9	39.1	10	41.7
2	1	3.4	2	8.7	3	12.5
3		0.0	0	0.0	0	0.0
T	29		23		24	

Table 5 Continued.

E. Weathering stages on partial long bones and girdle elements of selected taxa.

Weathering	Camel		Horse		Proboscidea	
Stage	N	%	N	%	N	%
0	49	62.0	16	39.0	7	28.0
1	22	27.8	19	46.3	11	44.0
2	8	10.1	6	8.7	5	20.0
3	0	0.0	0	0.0	2	8.0
T	79		41		25	

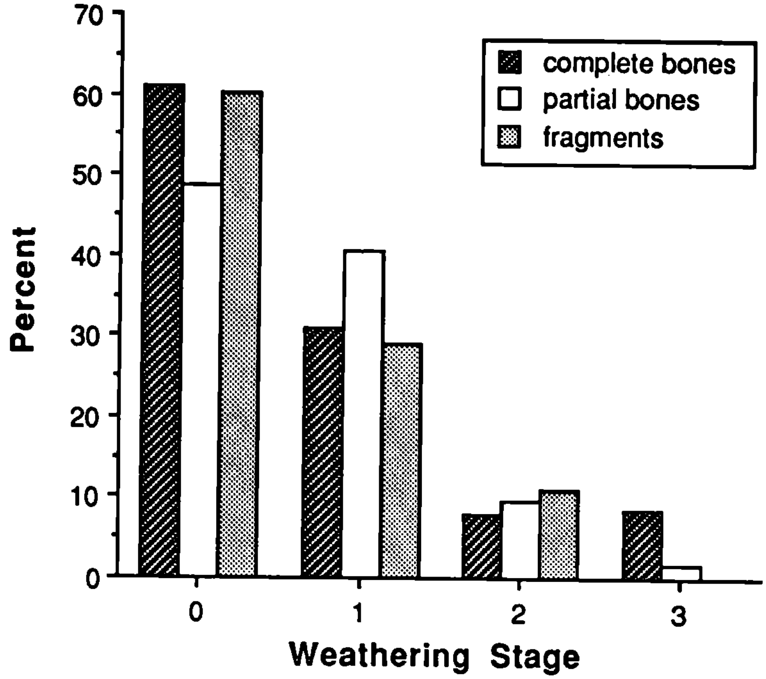

Figure 14. Percentage of complete, partial, and fragmentary mammalian bones from Leisey Shell Pit 1A showing different weathering stages.

where the bones were finally deposited. The more weathered elements undoubtedly represent carcasses that were skeletonized and weathered elsewhere before the bones were introduced into the site (see previous sections on disarticulation and orientation).

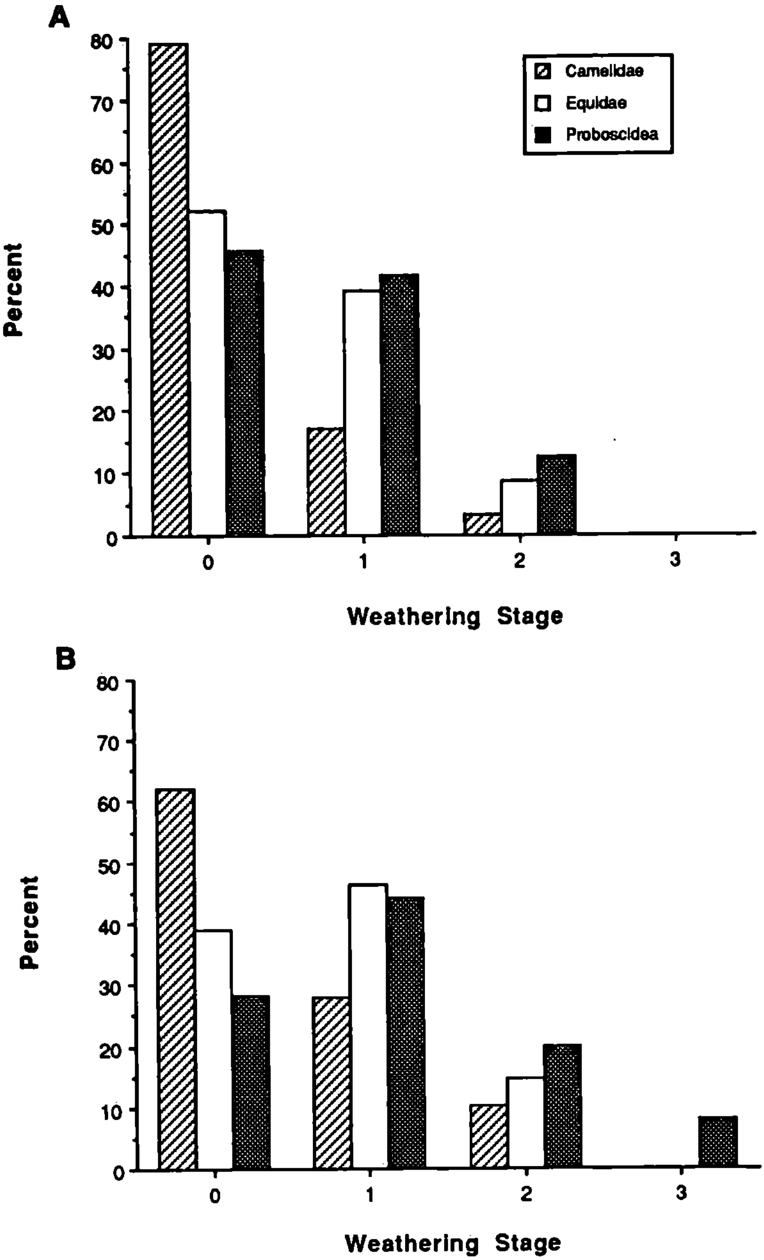

Figure 15. Percentage of complete (A) and partial (B) limb bones and girdle elements from Leisey Shell Pit 1A, sorted by taxa, showing different weathering stages (Table 5).

Surface Erosion.– Figure 16 and Table 6 show the proportions of mammalian elements and podials possessing some degree of polishing or rounding. This type of modification is referred to by Olsen and Shipman (1988) as surface erosion, and on mammalian elements from Leisey 1A consists primarily of slight rounding and smoothing of processes and polishing of broken edges. As is the case with other types of modification discussed previously, the majority of limb and girdle elements (62%) are unmodified (Fig. 17). A significantly greater proportion of complete bones show this type of modification than partial elements and unidentifiable fragments (Table 8). The large percentage of fragments lacking any evidence of polishing is due mainly to the fact that a number of these pieces resulted from post-depositional breakage, however, even polished broken edges of fragments do not show any appreciable degree of rounding of sharp edges. If fragments are eliminated from the comparison, the percentage of abraded partial elements is significantly greater compared to complete elements. This difference indicates that partial elements were more frequently exposed to agents of erosion. It is also possible that this finding reflects the fact that it is easier to discern polishing on a broken edge than on a complete element.

Surface erosion is most often attributed to polishing caused by water-borne particles in a fluvial environment, however, polishing and rounding of bones may also occur as a result of trampling (Behrensmeyer 1978; Brain 1981; Haynes and Stanford 1984; Oliver 1989; Haynes 1991) or licking and manipulation by carnivores (Binford 1981; Haynes and Stanford 1984; Haynes 1991). In the case of the skeletal elements from Leisey 1A, there is evidence that the primary agent of polishing was sediment entrained in running water. Examination of podial elements shows that almost half (significantly more than the percentage of abraded complete limb elements) are rounded to some degree (Table 8). This modification most likely occurred as these small elements were rolled from place to place within the site by the action of moving water. In addition, among the limb elements, there is no significant difference in levels of abrasive wear between taxa (Table 8). Within taxa, although in all cases a greater proportion of partial as opposed to complete elements are abraded (Fig. 17), the difference is significant only in the Equidae, and is due to the large number of complete elements that do not show evidence of any abrasion. The general similarities in extent of bone erosion between taxa suggests that the agent or agents responsible for the modification were acting at the site of deposition and affecting limb bones of all mammalian taxa more or less equally. Given the aquatic nature of the site, it is reasonable to assume that water-related polishing occurred. Although some polishing of bones may be attributed to trampling of skeletal remains in the depositional environment, there is no apparent correlation between the amount of carnivore damage and amount of abrasion. It therefore is unlikely that carnivores or scavengers were main agents of surface abrasion and polishing.

Table 6. Surface erosion or waterwear on Leisey mammalian elements. Abbreviations as in Table 5.

A. Erosion or waterwear on complete elements from entire Leisey sample examined.

Stage	Man N	L/G N	Ver N	Pod N	Total	% of GT
None	12	55	31	87	185	60.5
Minimal	7	21	14	68	110	35.9
Moderate	0	1	1	9	11	3.6
Extreme	0	0	0	0	0	0.0
GT					306	

B. Erosion or waterwear on partial elements from entire Leisey sample examined.

Stage	Man N	L/G N	Ver N	Pod N	Total	% of GT
None	10	74	47	0	131	52.0
Minimal	14	61	28	0	103	40.8
Moderate	0	15	2	0	17	6.8
Extreme	0	1	0	0	1	0.4
GT					252	

C. Erosion or waterwear on unidentifiable fragments from squares B4 and D9.

Stage	N	% of GT
None	208	71.2
Minimal	84	28.8
Moderate	0	0.0
Extreme	0	0.0
T	292	

D. Erosion or waterwear on complete long bones and girdle elements of selected taxa.

Weathering Stage	N	Camel %	N	Horse %	N	Proboscidea %
None	18	62.1	18	78.3	18	75.0
Minimal	11	37.9	5	21.7	5	20.8
Moderate	0	0.0	0	0.0	1	4.2
Extreme	0	0.0	0	0.0	0	0.0
T	29		23		24	

Table 6 Continued

E. Erosion or waterwear on partial long bones and girdle elements of selected taxa.

Weathering		Camel		Horse		Proboscidea
Stage	N	%	N	%	N	%
None	34	43.0	21	51.2	15	60.0
Minimal	15	44.3	17	41.5	7	28.0
Moderate	10	12.7	3	7.3	2	8.0
Extreme	0	0.0	0	0.0	1	4.0
T	79		41		25	

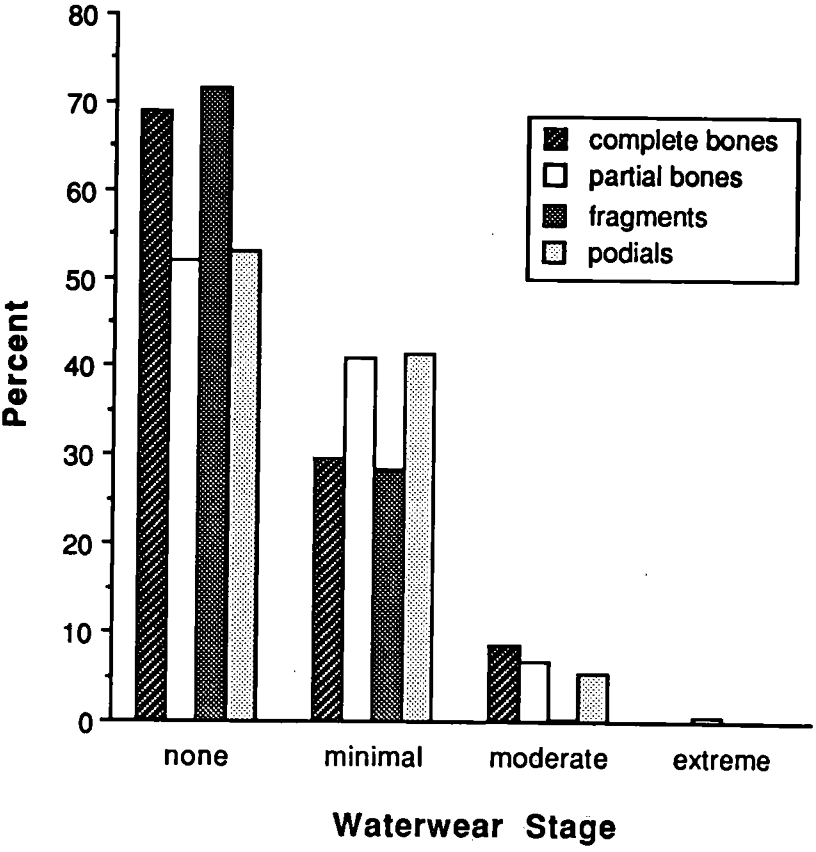

Figure 16. Percentage of mammalian fossils from Leisey Shell Pit 1A, sorted by completeness, showing evidence of different degrees of waterwear (surface erosion; Table 6).

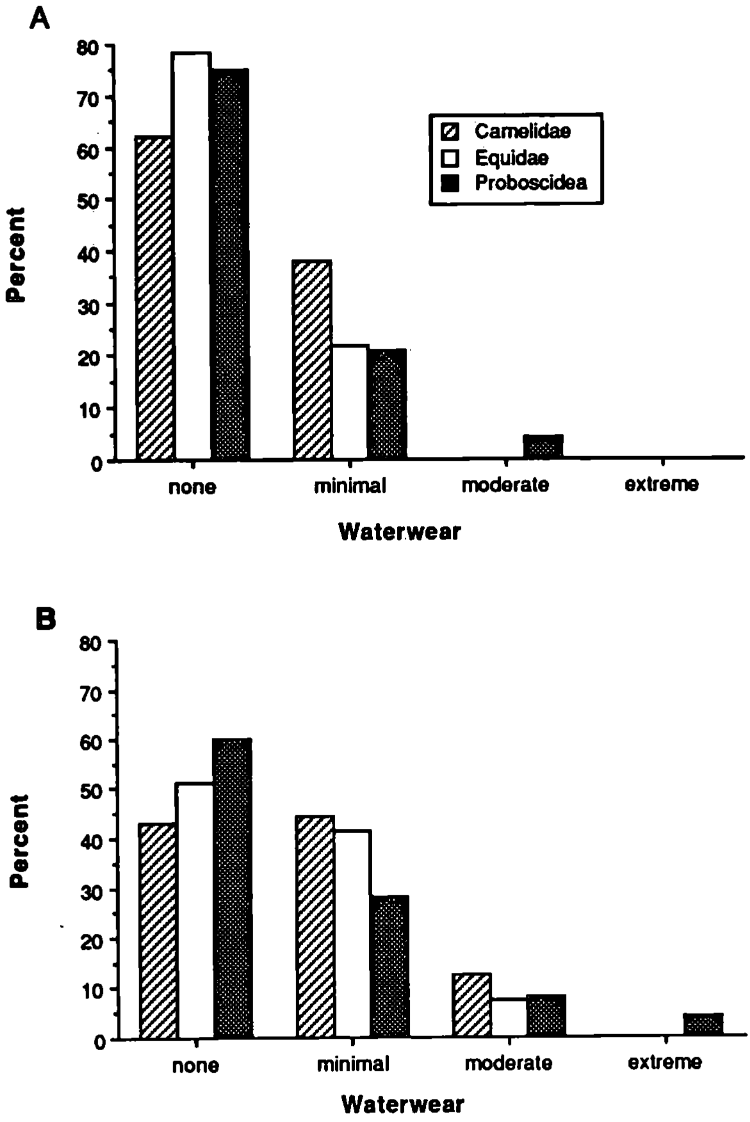

Figure 17. Percentage of complete (A) and partial (B) limb bones and girdle elements from Leisey Shell Pit 1A, sorted by taxa, showing different waterwear stages (Table 6).

Based on the levels of surface erosion seen on terrestrial elements from Leisey 1A, a number of conclusions may be drawn concerning bone transport into the depositional environment, and the length of time bones were exposed before burial. The absence of highly polished or rounded bones typically recovered from fluvial sites such as the Verdigree quarry (Voorhies 1969), the Love site (Webb et al. 1981) and the Pasalar, Turkey, bone assemblage (Andrews and Ersoy 1990), indicate that elements were not carried long distances by a high energy fluvial system. Bones may have been transported into the site by the action of running water, but many came from regions near to the site of deposition, perhaps during brief periods when current velocities of feeder streams were greatly augmented by floods or storms.

Once the bones reached the depositional environment, they evidently were not exposed to strong current action for long periods of time. It is likely that moderate currents caused the majority of polishing before the bones were buried in the sediment, an event that occurred not long after the bones were initially introduced into the site. These conclusions are supported by features of the site geology, palynology, and invertebrate fauna (Morgan and Hulbert; Portell et al.; and Rich and Newsom, this volume).

Scratch Marks.-- The most obvious type of physical damage to the elements from Leisey 1A is fairly extensive scratching on the surface of many bones (Fig. 18; Table 7). The scratches appear as relatively shallow fine striations, from less than a centimeter to several centimeters in length. Commonly, a series of scratch marks of similar size, depth and direction are present on a portion of the bone. On extensively scratched bone, much of the surface is criss-crossed by numerous, multidirectional series of scratches. The marks are most evident on flat, shiny surfaces, and on limb bones the extent of surface covered ranges from 0 to 80%, with an average scratched surface area of about 35% (Fig. 19). Podials, bodies of vertebrae, and articular surfaces of limb elements are not noticeably scratched. The marks are very similar to scratches produced by sedimentary abrasion (Olsen and Shipman 1988: fig. 5), which occurs as abrasive sediment either moves across a bone surface, or as a bone is dragged across sediment. The matrix must be scraped against the bone surface with some degree of force in order to produce scratches. Sedimentary abrasion is generally ascribed to three types of agents; trampling by large herbivores (Andrews and Cook 1985: fig. 3a; Haynes and Stanford 1984: fig. 6; Behrensmeyer et al. 1986; Fiorillo 1989; Haynes 1991: figs. 4.36-4.40), moving water (Behrensmeyer et al. 1989, Olsen and Shipman 1988), and post-depositional, post-fossilizational shifting of bones and sediment (Olsen and Shipman 1988; Behrensmeyer et al. 1989). The fossil matrix surrounding the bones at Leisey 1A consists primarily of sharp fragments of mollusk shells and angular quartz sand which both would have been abrasive enough to cause the scratchmarks in question. In order to determine if this was in fact the case, it is necessary to ascertain whether scratchmarks were applied before or after the remains reached the site of deposition. This aspect of the study is restricted to long bones, as other elements seldom show evidence of scratching.

Table 7. Scratchmarks on Leisey mammalian elements. Man = mandibles; L/G = limbs and girdles; Ver = vertebrae; Pod = podials; T = total; GT = grand total.

A. Scratchmarks on complete elements from entire Leisey sample

Surface Coverage	Man N	L/G N	Ver N	Pod N	Total	% of GT
<5%	2	24	40	139	205	66.9
>5%	17	53	6	25	101	33.1
GT					306	

B. Scratchmarks on partial elements from entire Leisey sample examined.

Surface Coverage	Man N	L/G N	Ver N	Pod N	Total	% of GT
<5%	7	72	68	0	147	58.3
>5%	17	79	9	0	105	41.7
GT					252	

C. Scratchmarks on complete long bones and girdle elements of selected taxa.

Surface Coverage	Camel N	Camel %	Horse N	Horse %	Proboscidea N	Proboscidea %
<5%	8	27.6	11	47.8	4	16.7
>5%	21	72.4	12	52.2	20	83.3
T	29		23		24	

D. Scratchmarks on partial long bones and girdle elements of selected taxa.

Surface Coverage	Camel N	Camel %	Horse N	Horse %	Proboscidea N	Proboscidea %
<5%	38	48.1	22	53.7	9	36.0
>5%	41	51.9	19	46.3	16	64.0
T	79		41	25.0		

Figure 18. Ventral view of a portion of the plastron of the turtle *Trachemys scripta* from Leisey Shell Pit 1A, showing the size and extent of scratch marks found on many of the bones. The arrow indicates the suture between the hyoplastron, found in square F5, and the hypoplastron which was found in F6. The scratch marks do not cross this suture, indicating that they were produced at the site of deposition, and not in some other environment and subsequently transported to the Leisey site. Scale bar is 0.5 cm.

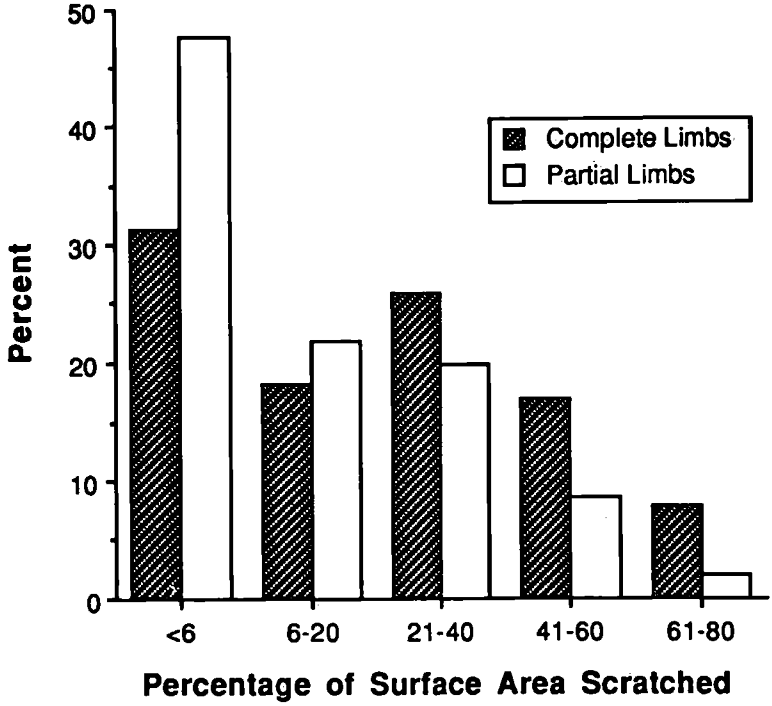

Figure 19. Percentage of complete and partial mammalian limb bones and girdle elements from Leisey Shell Pit 1A showing proportion of their surface area covered by scratch marks. Samples consisted of 77 complete and 151 partial specimens.

Several lines of evidence suggest that bones were scratched after reaching the fossil site. First, if scratches had been applied in a terrestrial setting, bones exposed for the longest periods of time to the causative agents should be the most scratched. It has been shown previously that an increase in terrestrial scavenger damage is correlated with increased bone weathering, however, such is not the case for scratchmarks (Table 8). In fact, a greater percentage of complete bones in weathering stages 1 or 2 are unmarked when compared with complete, unweathered elements, although these differences are not significant according to a χ^2 test (Table 8). Fiorillo (1989) noted that scratches on bone surfaces may be obscured or obliterated in late stages of weathering, but weathering damage to bones in this study is so slight that scratches are still clearly visible. Second, in most cases, there is no significant difference in presence or absence of scratchmarks on bones of different herbivore taxa (Table 8). A notable exception is seen for complete proboscidean elements, a significantly greater proportion of which are scratched when compared to complete elements of camelids or equids.

A significantly greater proportion of complete elements are scratched compared to partial elements for all taxa combined (Table 8; Fig. 20). This may be due to the fact that flat, easily scratched surfaces are more common on complete elements than partial elements. The overall similarities between taxa and between whole and partial bones in terms of presence or absence of scratchmarks suggests that most of the bones were subjected to scratching under similar conditions, after they had reached a similar environment (i.e. the environment of deposition). Complete proboscidean limbs may be more scratched than limb elements of smaller herbivores particularly if the latter were not buried quickly due to their large size, and thus were subjected to this type of modification in the aquatic environment for a longer period of time than smaller elements.

Further support along these lines is provided by an investigation of elements of organisms that lived in completely different environments than the terrestrial herbivores. Isolated plastron and carapace elements of the freshwater turtle *Trachemys* were examined for scratches. Although scratchmarks could not be discerned on the majority of the elements examined, in part due to the rugose surface of the carapace elements, nearly 30% (primarily smooth-surfaced plastral elements) were scratched to some degree, and some were scratched extensively (45% of surface covered). This issue is complicated somewhat by the fact that a number of turtle shells undoubtedly were introduced into the depositional environment in a complete state, and therefore all surfaces of the shell were not equally exposed to agents of scratching. Nevertheless, the presence of scratches on nearly a third of turtle elements examined suggests that they were scratched in the same environment where large terrestrial herbivore bones were scratched, that is, the site of bone accumulation.

Third, if bones were scratched in a terrestrial environment and then transported to the environment of deposition, no correlation should be seen between the side facing up in the field and the most scratched surface, given that final resting position of an isolated bone after transport is not related to its position in a decaying, articulated carcass prior to transport. Such is not case for Leisey 1A limb elements and mandibles examined; of bones having unequal surface scratch distributions, a significantly greater number (65 of 71 elements) were recovered with the more scratched side facing upward, according to a χ^2 test for significance ($p < 0.001$). This finding suggests that the upward-facing surface of the bone was most prone to scratching, and that many bones did not move appreciably after they were scratched. Therefore it is unlikely that bones were transported any great distance from the location where they were scratched.

A final, convincing line of evidence for in situ scratching is provided by examination of those elements that reached the final depositional environment as complete bones and were broken at a later point in time (see preceding section on articulation and association). When contacts between the broken pieces are

Table 8. Chi-squared test results for differences in bone surface modification factors. Statistically significant differences are signified by: * - significant at $p \leq 0.05$, ** = significant at $p \leq 0.01$. χ^2 values not so indicated have $p > 0.05$. There is 1 degree of freedom in all cases.

A. Weathering

Complete Bones vs. Identifiable Partial/ Bones/ all taxa combined

	Podials Included	Podials Excluded
χ^2	55.98**	5.38*

Complete Limb and Girdle Bones vs. Partial Limb and Girdle Bones/ all taxon

	Camel	Horse	Proboscidean
χ^2	2.99	1.15	2.59

Comparisons between Taxa--Complete Limbs and Girdles

	Camel vs. Horse	Camel vs. Proboscidea	Horse vs. Proboscidea
χ^2	4.16*	6.34*	0.25

Comparisons between Taxa--Partial Limbs and Girdles

	Camel vs. Horse	Camel vs. Proboscidea	Horse vs. Proboscidea
χ^2	5.03*	10.15**	1.87

B. Surface erosion or waterwear

Complete Bones vs. Identifiable Partial Bones and Fragments/ all taxa combined

χ^2	6.32*

Complete Bones vs. Identifiable Partial/ Bones/ all taxa combined

	Podials Included	Podials Excluded
χ^2	4.04*	10.82**

Complete Bones vs. Podials/ all taxa combined

χ^2	7.31**

Complete Bones vs. Partial Identifiable Bones/ all taxon

	Camel	Horse	Proboscidean
χ^2	0.89	4.08*	1.44

Comparisons between Taxa--Complete Bones

	Camel vs. Horse	Camel vs. Proboscidea	Horse vs. Proboscidea
χ^2	1.55	0.76	0.74

Comparisons between Taxa--Partial Bones

	Camel vs. Horse	Camel vs. Proboscidea	Horse vs. Proboscidea
χ^2	0.01	0.08	0.18

Table 8 Continued.

C. Scratchmarks

	Complete Bones vs. Partial Identifiable Bones/ all taxa		
	Podials Included	**Podials Excluded**	
χ^2	4.45*	5.14*	
	Complete Bones vs. Partial Identifiable Bones/ by taxon		
	Camel	**Horse**	**Proboscidean**
χ^2	3.08	0.20	2.30
	Comparisons between Taxa--Complete Bones		
	Camel vs. Horse	**Camel vs. Proboscidea**	**Horse vs. Proboscidea**
χ^2	2.23	5.14*	5.91*
	Comparisons between Taxa--Partial Bones		
	Camel vs. Horse	**Camel vs. Proboscidea**	**Horse vs. Proboscidea**
χ^2	0.58	0.824	1.92

D. Weathering vs. Scratches

	Complete Bones	**Partial Identifiable Bones**
χ^2	1.33	0.11

rejoined, in most instances (90% of associated elements examined), scratchmarks do not cross the break (Fig. 18). This finding demonstrates that most scratches were applied following breakage of these elements, which almost certainly occurred at the site of deposition.

Based on the results discussed above, it is highly likely that the shell-sand matrix of the Leisey 1A locality was involved in producing the numerous striations on bone surfaces. The question remains as to whether the agent responsible for exerting the force required to cause abrasive damage to the bone surface can be determined. Post-depositional, post-fossilization scratching by sediment shifting can be ruled out for several reasons. The scratches are found predominantly on the upper bone surfaces. In post-depositional sediment shifting, other surfaces should be scratched as well. Behrensmeyer et al. (1989) suggest that during compaction events, vertically-oriented rather than horizontally-oriented surfaces would be most heavily scratched. There is no predominant directionality to the marks on the Leisey elements (Fig. 18) as might be expected if sediment moved or shifted in one direction. In addition, the marks are darkly colored and obviously were made on

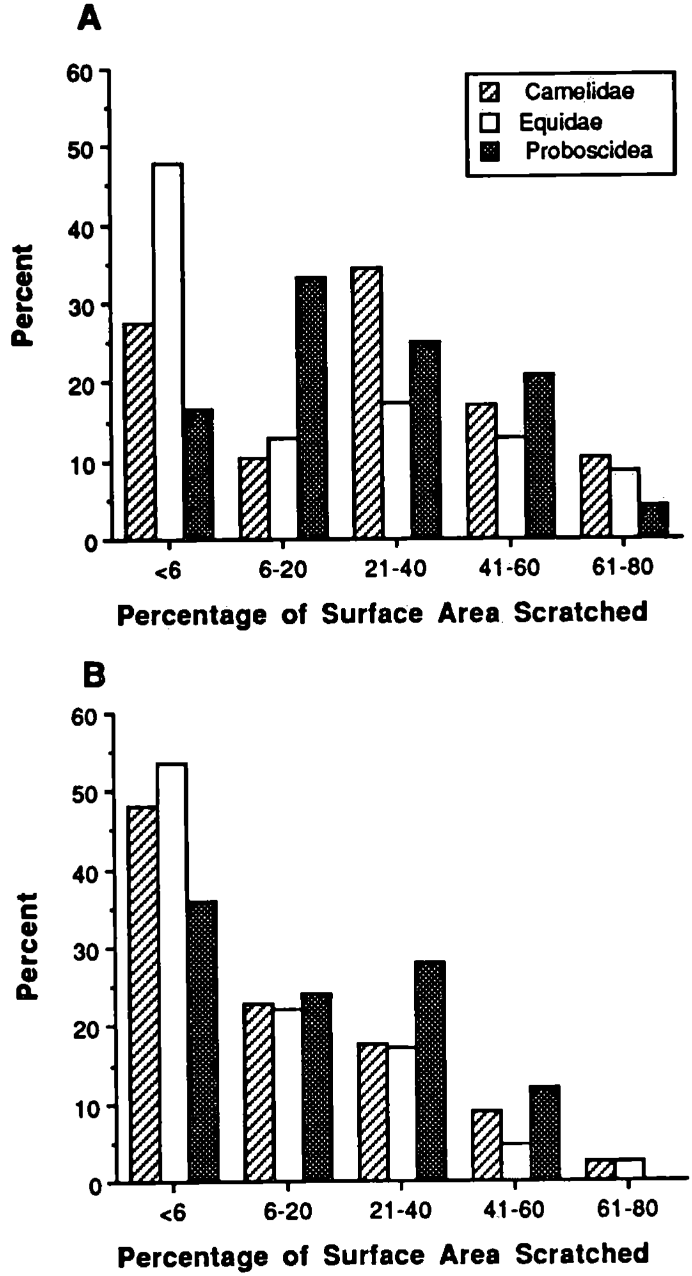

Figure 20. Percentage of complete (A) and partial (B) limb bones and girdle elements from Leisey Shell Pit 1A, sorted by taxa, showing proportion of the surface area covered by scratch marks. Samples consisted of 29 complete and 79 partial camelid specimens, 23 and 41 of equids, and 24 and 25 of proboscideans.

the bones before fossilization occurred. Post-fossilization scratches on Leisey elements are generally light in color and easy to discern from pre-fossilization scratches.

Support for damage by trampling is provided by the great similarity of the marks to those caused by large herbivores (Fiorillo 1989; Haynes 1991). The types and proportions of bones characterized by scratching, and the average degree of scratching are also similar to values reported in studies on trampling of Recent and fossil bones (Olsen and Shipman 1988; Behrensmeyer et al. 1989; Fiorillo 1989; Oliver 1989). As the scratching occurred in a marine environment, a trampling scenario mandates that water depth must have been relatively shallow, at least periodically, so that terrestrial mammals would have had no difficulty crossing the area by walking. The invertebrate fauna of the bone bed indicate that water depth was shallow (Hulbert and Morgan 1989; Morgan and Hulbert, this volume; Portell et al. this volume).

Several other features suggest that attributing scratchmarks to trampling may be erroneous. A major problem is that scratches do not cross breaks on associated partial elements. If these elements were broken by trampling impact, it seems that scratches applied at the time of breakage would transverse the fracture; however more comparative studies on modern bone are needed to substantiate this supposition. In addition, the rarity of steeply plunging long bones within the site argues against the presence of a force sufficient to drive elements into soft or moist sediment (Fig. 6). It has been noted that trampling of bones lying on wet or moist muddy sediments often results in vertically-plunging bones (Hill and Walker 1972; Behrensmeyer and Boaz 1980; Fiorillo 1989), although the amount of plunge may vary with sediment consistency (see Olsen and Shipman 1988). The Leisey 1A sediment, with its high sand and shell content, probably provided a more resistant surface than fine-grained muds.

The locations of scratchmarks on bone surfaces suggests that perhaps water-related abrasion rather than trampling was the major agent of scratching, however, the findings do not conclusively support this hypothesis. In an analysis of location of scratchmarks on mandibles, it was noted that in the majority of cases, a right or left mandible (complete with symphysis and diastema of the opposite side) possessed scratchmarks predominantly on the side found facing up in the field. Its associated mandible, broken posterior to the diastema and often separated from its partner, was equally scratched on both the upper and lower surfaces. Complete limb elements for which these data were recorded also possess the majority of scratches on the side facing up in the field, while incomplete bones tend to be equally scratched on both sides. Only a very small proportion of elements have more scratches on downward-facing surfaces. These findings suggest, as previously noted, that most scratches were applied to the upward-facing surface of the bone. Larger bones did not move or flip over before final burial, unlike smaller or incomplete elements that bear scratches on both upward and downward facing flat surfaces. Behrensmeyer et al. (1986) indicated that the upward-facing surface of the bone is scratched as sediment lying on top of the element or attached to the foot is driven across the bone surface when the foot steps on the bone. Olsen and Shipman (1988) showed that scratches are also applied to the downward-facing surface of the bone if it moves slightly across an abrasive surface when it is stepped on. The large number of elements with scratches predominantly on the upper surface is therefore best explained by the movement of water-driven sand and shells across these surfaces, although there is some question as to whether the pressure applied would have been sufficient to cause scratchmarks. It has been noted previously in this paper that current velocities within the environment of deposition were for the most part relatively slow. Bones with equally-scratched upper and lower surfaces may either have been trampled and kicked on several occasions, or transported by moving water within the site, turning over several times before burial. Based on the information currently available, it is unclear as to which agent, moving water or trampling, was ultimately responsible for causing the scratchmarks.

Summary: Bone Modification.– The findings from the investigation of bone modification may be summarized as follows:

1) The presence of associated elements indicates that some individuals were introduced into the site of deposition as complete or partial carcasses. Breakage and scratching of associated elements took place within the site, and may have been the result of trampling. Isolated and broken elements with no associations were introduced individually after decomposition, disarticulation, breakage, weathering, and scavenging occurred elsewhere, probably in a terrestrial habitat.
2) Bones that were exposed on terrestrial surfaces belong primarily to equids and proboscideans, as evidenced by the extent of weathering and scavenger damage. Camelid bones show lower proportions of these types of modification, suggesting their introduction into the environment of deposition in more complete condition.
3) The main scavengers/carnivores on large mammalian herbivores were *Smilodon gracilis*, *Canis armbrusteri*, and *Arctodus pristinus*. The relatively low percentage of carnivore-damaged bone indicates that the assemblage was not formed primarily by carnivores. It also indicates that prey (or prey carcass) to predator ratios may have been high, perhaps on a seasonal basis. The population dynamics of the equids and camelids resemble those of an attritional assemblage with periodic catastrophic additions. Relatively low degrees of weathering indicate that even weathered bones were not exposed to the effects of climatic deterioration for long periods of time. Periodic floods of feeder streams may have cleansed the banks of remains and carried them to the site of deposition on a regular basis.

4) Relatively little sedimentary erosion or polishing of bones suggests that the site was not characterized by a sustained current of high velocity, that agrees with the lack of a preferred orientation of the long bones.
5) Location and position of scratchmarks shows they were applied in the depositional environment as the bones were scraped against the shelly-sand matrix. The actual agent of scratching may have been either trampling herbivores or moving water.

BONE RELATIVE REPRESENTATION

Relative representation involves the numerical assessment of the types of skeletal elements that comprise the fossil deposit. Generally, taxa are grouped by size in relative representation studies, as bone abundance is often a size-related phenomenon. In most cases small taxa elements are more subject to destruction by transport and various agents than those of larger vertebrates (Dodson 1973; Wolff 1973; Behrensmeyer and Boaz 1980; Andrews 1990). In the case of Leisey mammals, as total bone counts could only be undertaken in those squares that had been completely sorted and curated, abundances of mammals other than camelids and equids were not represented by sufficient numbers of elements to comprise a reliable sample. As these taxa were of similar body size, analysis of different patterns of bone relative representation due to differences in body size cannot be addressed at this time. However, as evidence presented in previous sections suggests different taphonomic histories for the camelids and equids, their bone relative representation patterns were analyzed separately. It was not possible to identify all camelid and equid postcrania to species, so the analysis is limited to the generic level for equids, and the tribal level (Lamini) for the camelids. Based on jaws, it is likely that the majority of the camelids were *Palaeolama mirifica* and the equid, *Equus "leidyi."* Due to the difficulty in assigning ribs and post-cervical vertebrae to family, these were not used in family level assessments.

Bones of camels and equids from squares B4, B5, B6, B7, C5, C6, C7, D6, D7, D9, D10, E6, E7 and F5 were counted. These squares, located in the most fossiliferous region of the site, were primarily or exclusively excavated by FLMNH personnel, insuring maximum bone recovery and minimum collecting bias. In addition, a large number of these squares were contiguous, so the likelihood of counting possibly associated remains was high.

There are two generally accepted methods of assessing bone abundance: relative representation or percentage skeletal preservation (Voorhies 1969; Wolff 1973; Korth 1979; Pratt 1990), which is determined by dividing the number of one type of bone found by the number expected based on the minimum number of individuals (MNI) represented; and relative skeletal part frequencies (SPF)

(Behrensmeyer and Boaz 1980; Badgley 1986a), a value obtained by dividing the number of elements of one type by the total number of all elements recovered. Although the latter method was used in order to compare Leisey 1A bone abundances with Recent assemblages analyzed in this fashion, relative representation is deemed the most useful, reliable, and informative method, for the following reasons:

1. It is based on MNI (minimum number of individuals), which provides a reliable indication of the actual number of individuals of a taxon preserved in the fossil site, especially in cases where there is evidence of skeletal articulation or association. In these instances, the relative representation values can be used to determine the numbers of each element type that have been lost from the complete skeleton. The proportion missing of each bone is equal to one minus the relative representation of that element.
2. Each bone relative representation value is calculated independently of those of other elements. In contrast, SPF calculations have no clear meaning unless they are compared with the percentage representation of that element in a complete skeleton. SPF also does not provide an independent assessment of the bone's abundance, because each value is a percentage of the total. A high value for one bone will mean that another bone will have a low percentage value.
3. SPF underemphasises losses of bones that are present in large numbers in a skeleton (ribs, vertebrae, phalanges) and overemphasises losses of elements that are the only element of that type in a skeleton, such as the skull.
4. When the SPF is used in statistical tests, it is less powerful than relative representation in determining differences. In a comparison of two bone assemblages using the Spearman rank-coefficient test, a test frequently used in these types of assessments, SPF's are less likely to indicate actual difference between bones assemblages than are relative representation values. Unless the assemblage has been drastically modified, the bones with the highest SPF values will always be those with the greatest number of elements in the skeleton, and the lowest will be those represented in a skeleton by only one or two elements.

A total of 466 identifiable elements were counted for camelids and 212 for equids. Minimum number of individuals recovered from these squares was based on left innominates for both taxa. Camelids were represented by 20 left innominates, and equids by 11. Relative representations are shown in Table 9 and Figure 21. In the figure, elements are arranged in descending order by quartz grain equivalent values (Behrensmeyer 1975; Korth 1979; Pratt 1986, 1990) and transport groups (Voorhies 1969; Korth 1979; Pratt 1990), which provide a general indication of each element's transportability in running water. In addition, because the grain equivalent value is related to the density and size of the bone, it is also to some extent indicative of the element's resistance to destruction by other taphonomic factors.

In a comparison of Figures 21A and 21B it is immediately evident that skeletal representations for camelid and equid elements are different (Tables 9-10). Representation of camelid elements is relatively high, with mean representation of 33.3%, while mean representation for equid elements is 20.4%. The greatest difference is seen in Group II elements, in particular long bones. On average, approximately 58% of the expected number of camelid limb elements were recovered, as opposed to about 27% for equids. The pattern of skeletal preservation of camelids is similar to that reported for several Recent bone assemblages (Table 10), including caribou remains killed and fed upon by wolves (Binford 1981) and a surface assemblage in Amboseli Park, Kenya (Behrensmeyer and Boaz 1979; 1980). In the case of the former, although the pattern of skeletal preservation is similar, the actual relative abundances of elements are generally greater for the fossil camelids than for the caribou, showing that a lower proportion of the elements in the fossil assemblage were subject to loss or modification than the wolf-modified assemblage. The Leisey camelid assemblage is very similar in overall pattern of abundances to the Amboseli bone assemblage, but less so to accumulations from Ngorongoro Crater and Serengeti National Park, Tanzania (Blumenschine 1989). There are two reasons for this result. First of all, the Amboseli study is based on SPF, which as mentioned above, generally provides a high degree of similarity in bone abundance rankings between assemblages. In addition, there are some basic differences between the Recent bone assemblages. The Amboseli accumulation evidently formed in part as a result of mass deaths, which led to an increase in prey (carcass)-to-predator ratios and resulted in a lower degree of bone destruction than normally occurs (Behrensmeyer and Boaz 1980). The two assemblages in Tanzania were heavily scavenged by hyaenas, which cause high rates of bone loss from carcasses (Blumenschine 1989). The absence of a bone-eating scavenger at Leisey probably contributed to the high representation of elements (see section on carnivore-modified bone) and the greater similarity of the Leisey camelid assemblage to the Amboseli accumulation.

Greater percentages of camelid elements than those reported in Recent "landscape" studies suggests that some of the camelids were introduced into the depositional environment in a complete or nearly complete state. It has been shown previously that only about 18% of the camelid remains (not including podials) were modified by predation and scavenging. Periodic mass deaths occurring close to the site of deposition provided a possible source of more complete remains. The striking similarity of the camelid element representation pattern to that of a hypothetical lag deposit (Hanson 1980: fig. 9.3) suggests that moving water, rather than carnivores or scavengers, may have been the primary agent that removed camelid elements from the environment of deposition. It was previously shown that a constant unidirectional current was not a feature of site,

Table 9. Bone abundances of camelids and equids. Relative representation = number of elements of one type recovered/number expected based on MNI (x 100). In both cases, MNI is based on innominates.

Element	Number found	Number expected based on MNI	% Relative Representation
A. CAMELIDAE (MNI= 20)			
Mandible (R or L)	30	40	75.0
Maxilla	23	40	57.5
Scapula	26	40	65.0
Humerus	26	40	65.0
Radio/ulna	22	40	55.0
Innominate	37	40	92.5
Femur	26	40	65.0
Patella	3	40	7.5
Tibia	16	40	40.0
Cervical Vertebrae	42	140	30.0
Sacrum	12	20	60.0
Metapodials	22	80	27.5
Astragalus/Calcaneum	23	80	28.8
Fibula	11	40	27.5
Other Podials	84	440	19.1
Phalanges (Prox. & Med)	48	320	15.0
Distal Phalanges	4	160	2.5
B. EQUIDAE (MNI = 11)			
Mandible (R or L)	15	22	68.2
Maxilla	3	22	13.6
Scapula	5	22	22.7
Humerus	5	22	22.7
Radius	1	22	4.5
Ulna (proximal end)	5	22	22.7
Innominate	21	22	95.5
Femur	2	22	9.1
Patella	2	22	9.1
Tibia	4	22	18.2
Cervical Vertebrae	26	77	33.7
Sacrum	2	11	18.2
Medial Metapodials	5	44	11.3
Lateral Metapodials	22	88	25.0
Astragalus/Calcaneum	5	44	11.3
Other Podials	45	242	18.6
Phalanges (Prox. & Med)	13	88	14.8
Distal Phalanges (Hooves)	6	44	13.6

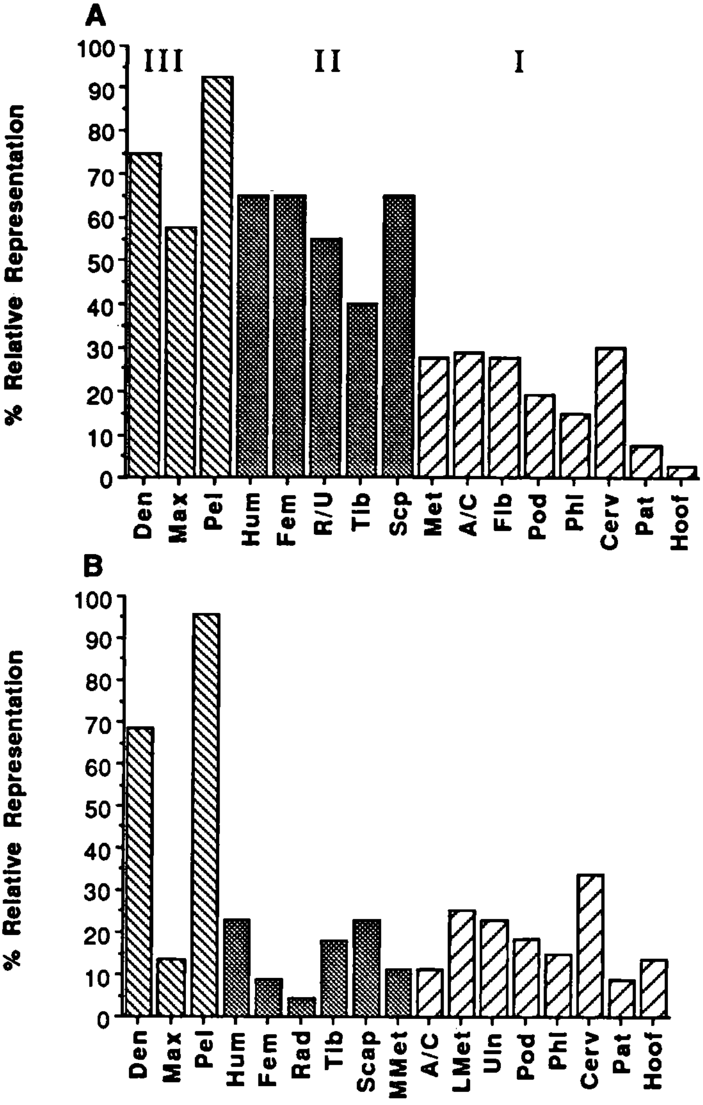

Figure 21. Percentage relative representations of skeletal elements from Leisey Shell Pit 1A, based on MNI (Table 9). A. Camelidae (*Palaeolama* and *Hemiauchenia* combined), with an MNI of 20 based on left innominates. B. *Equus*, with an MNI of 11, also based on left innominates. Roman numerals and different shading patterns separate the elements into the hydraulic transport groups of Voorhies (1969). Element abbreviations: **Den**, dentary; **Max**, maxilla; **Pel**, pelvis (innominate); **Hum**, humerus; **R/U**, radioulna (camelids only); **Rad**, radius; **Tib**, tibia; **Scap**, scapula; **Met**, fused metapodials 3 and 4 (camelids only); **MMet**, medial metapodial (of digit 3, *Equus* only); **A/C**, astragalus and calcaneum; **Fib**, fibula (camelids only); **LMet**, lateral metapodials (*Equus* only); **Uln**, ulna (*Equus* only); **Pod**, podials (carpal and other tarsal elements); **Phl**, proximal and medial phalanges; **Cerv**, cervical vertebrae; **Pat**, patella.

Table 10. Values of *r* for Spearman rank-coefficent test. d.f. = degrees of freedom. * = significant at $p \leq 0.05$, ** = significant at $p \leq 0.01$. RR= relative representation, SPF = skeletal part frequency.

Comparisons	d.f.	Camelidae	Equidae
Leisey Camelidae–RR	15	–	0.477
Wolf Kills of Caribou–RR (Binford 1981: Tab. 5.01)	10	0.990**	0.521
Size 3 Herbivores–RR Ngorongo Crater, Africa (Blumenschine 1989: Tab. 5)	13	0.506	0.207
Size 3 Herbivores–RR Acacia woods, grass plains (Blumenschine 1989: Tab. 5)	12	0.611*	0.201
Size 3 Herbivores–RR Riparian woodlands (Blumenschine 1989: Tab. 5)	13	0.448	0.216
Surface Bone Assemblage–SPF Amboseli Basin, Kenya (Behrensmeyer and Boaz 1980: Tab. 5.6)	6	0.959**	–
Wolf Kills of Caribou–RR (Binford 1981: Tab. 5.01) Corrected for losses due to hydraulic transport	13	–	0.563*
Group III, II elements only	8	–	0.833**

but other factors such as water-abraded bone, low preservation of terrestrial microfaunal species, and the transported aspect of pollen grains (Rich and Newsom, this volume), indicate the presence of flowing water. The current velocity of water flowing through the site may have been sufficient to transport many of the group I and some of the group II elements from the site of deposition.

The relative representation of equid elements is less easily explained. The pattern of bone representation bears no statistically significant resemblance to patterns seen in Recent landscape assemblages (Table 10). Limb elements of Leisey *Equus* are generally not as highly represented as are those in modern assemblages, while podials and phalanges are more abundant. According to most modern bone assemblage studies, small, distal limb elements are lost in a number of ways, including burial (Behrensmeyer and Boaz 1980) and destruction or ingestion by carnivores (Haynes 1980a; Blumenschine 1989). It is also possible that these small elements may be missed in surface bone counts, so that their low representation is in part due to sampling problems. Among the Recent bone samples, the equid assemblage is most similar to that of Blumenschine's description of a "stage 3" carcass (1989: fig. 6) represented primarily by the axial skeleton and the scapula. In this stage, limb elements have been removed from the carcass by predators and scavengers, and the axial skeleton remains articulated with the pelvis. It was previously demonstrated that equid elements were significantly more weathered than camelid elements, indicating that equid carcasses may have been available for modification by carnivores and scavengers while some camelid skeletons were not.

The lack of similarity between the Leise equid bone representation and those of modern assemblages indicates that multiple taphonomic factors determined the final abundances of equid elements. Assuming that we accept the previous hypothesis that the bulk of camelid bone loss was through hydraulic transport from the depositional environment, then it is logical to assume that the equid bone assemblage that reached the site of deposition was also subjected to this type of loss. The major difference in the final bone accumulations for these two taxa would therefore result from differing bone frequencies in the assemblages of each taxon brought to the site (different input). Based on previously discussed data (see section on carnivore modification), the original equid bone assemblage may have initially resembled a modern caribou bone assemblage resulting from wolf predation and scavenging (Binford 1981: Table 5.09 Column 26); the carnivores present and the prey size are both similar to those at the Leisey site. If the same proportion of each element type is removed from this assemblage as was lost from a presumed complete skeletal assemblage of Leisey camelids, the skeletal relative representations shown in Figure 22 result. For example, if relative representation of a certain element type for Leisey camelids is 75%, then it is assumed that 25% of those elements were removed from the assemblage by hydraulic transport. Representation of the same element type is reduced by 25% in Binford's caribou assemblage. The resulting bone abundance ranks are correlated with those of the Leisey equids (Table 10). The similarity between Group III and II elements is the most startling, and the correlation between abundance ranks for these groups is highly significant (Table 10). The greater representation of equid Group I elements may be explained in several ways. First of all, as mentioned previously, it is possible that these elements may have been missed in counts of the modern assemblage. It is also possible that the fossil agents of bone destruction were operating differently and not destroying or removing these bones to the same extent as wolves. Finally, given that horse carcasses may have been decomposing along bodies of water that eventually fed the environment of deposition, during some periods smaller bones may have washed in when larger bones were not affected, thus increasing the number of bones of this type in the deposit.

Results of this portion of the study substantiate other findings. While the possibility that factors causing mass deaths of camelids were also affecting equid population dynamics is certainly likely, apparently camelids were living and dying closer to site of deposition than equids, and a lower proportion of camelid remains were exposed on terrestrial surfaces to agents of bone destruction than equids. The equid remains may have been carried to the depositional environment by moving water, and once there, the entire assemblage of all elements was modified by a relatively low velocity current, most likely less than 50 cm/second in velocity (Behrensmeyer 1975; Pratt 1986, 1990) and capable of transporting primarily Transport Group I elements from the depositional environment.

RELATIVE ABUNDANCES OF MAMMALIAN TAXA

Relative abundances of the Leisey 1A terrestrial mammals (i.e., Mammalia exclusive of Sirenia and Cetacea) were calculated using the MNI method (Table 11; Shipman 1981). Only specimens collected in 1984 were used in the analysis, as they represent the least biased sample for the entire site. Badgley (1986b) discussed the relative merits of various measures of relative abundance, and concluded that MNI was the most appropriate for sites containing disassociated skeletons. As shown on pages 190-193, there are numerous examples of these from Leisey 1A. Fossils of large mammals (body mass > 1 kg) were observed and collected in the field, while those of smaller mammals were most often recovered by screen-washing matrix. Since only a small percentage of the entire volume of the bone-bearing horizon was screen-washed, the overall relative abundances of small versus large mammals can not be directly compared. The most valid comparison is to use the contents of square D9, from which all of the matrix was collected and screen-washed (about 120 kg, dry weight). As shown in Table 12, the remains of large mammals from D9 far outnumber those of small mammals.

The large terrestrial mammalian fauna of Leisey 1A is dominated by herbivores with body masses ranging between 40 and 250 kg (Table 11): notably camelids, equids, tayassuids, and tapirids. Two families, comprising five species, the Camelidae and Equidae, together account for about two-thirds (68%) of the individuals. All artiodactyls and perissodactyls combined make up 81% of the individuals. Megaherbivores (body mass > 1000 kg) account for only about 7%. This group includes the three proboscideans and the larger of the two ground sloths, *Paramylodon harlani*. Despite the richness of the Leisey mammalian fauna, it is not especially diverse, as the five most abundant species account for over 75% of the individuals, and the ten most abundant, over 90%.

Altogether, the relative abundance of the nine members of the Carnivora is about 6% of the total (Table 11). Five of these taxa, *Lutra canadensis*, *Procyon* sp., *Urocyon* sp., *Homotherium* sp., and *Lynx rufus*, are represented by only one or two elements each and an MNI of 1. Although the MNI of the canids *Canis*

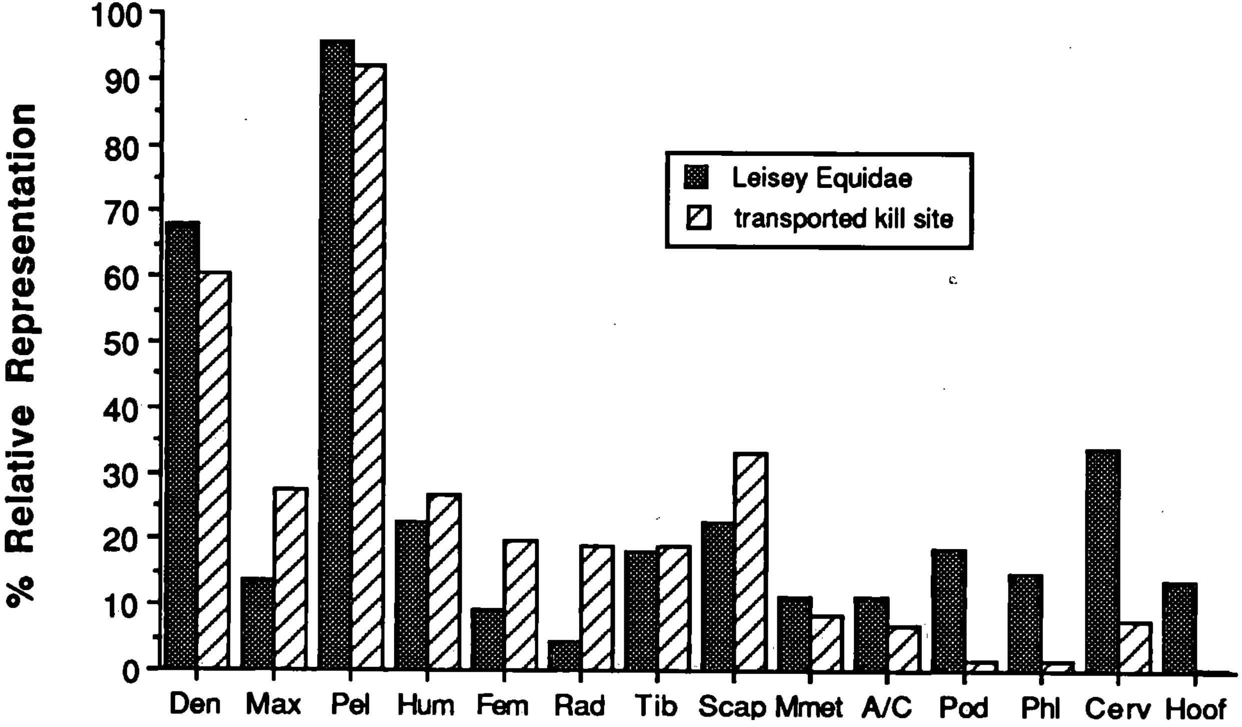

Figure 22. Comparison between the percent relative representation of skeletal elements of the Leisey Shell Pit 1A *Equus* compared with that of caribou from a wolf kill site (Binford 1981) adjusted for hypothetical losses during hydraulic transport. See text for discussion. Abbreviations as in Figure 21.

Table 11. Relative abundances of large terrestrial mammals at Leisey Shell Pit 1A. Minimum numbers of individuals (MNI) were tabulated from mandibles collected during the 1984 field season. Note that the MNI reported here do not necessarily reflect the maximum values from the site, as isolated teeth and postcrania were not considered. Mandibles were selected because they are all cataloged and can be identified to species. Eleven species (indicated by asterisks) were not represented by a mandible from the 1984 collection and were arbitrarily given an MNI of 1. Also reported is the percentage of the total MNI (N = 242) for each taxon and the percentage of the total number of herbivores (N = 226) for the appropriate taxa.

	MNI	Overall relative abundance (%)	Herbivore relative abundance (%)
**Dasypus bellus*	1	0.4	
*Dasypodidae, n. gen. and sp.[1]	1	0.4	
Holmesina floridanus	1	0.4	0.4
Nothrotheriops texanus	8	3.3	3.5
Paramylodon harlani	8	3.3	3.5
**Castoroides* n. sp.	1	0.4	0.4
**Neochoerus* sp.	1	0.4	0.4
Lepus sp.	1	0.4	0.4
**Urocyon* sp.	1	0.4	
Canis armbrusteri	1	0.4	
Canis edwardii	1	0.4	
**Procyon lotor*	1	0.4	
**Lutra canadensis*	1	0.4	
Arctodus pristinus	2	0.8	
Smilodon gracilis	5	2.1	
**Homotherium* sp.	1	0.4	
**Lynx rufus*	1	0.4	
Tapirus haysii	3	1.2	1.3
Equus "leidyi"	36	14.9	15.9
Equus (Hemionus) n. sp.	17	7.0	7.5
**Equus "fraternus"*	1	0.4	0.4
Platygonus cf. *P. vetus*	22	9.1	9.7
Mylohyus cf. *M. fossilis*	2	0.8	0.9
Hemiauchenia macrocephala	18	7.4	7.9
Palaeolama mirifica	92	38.0	40.7
Odocoileus virginianus	6	2.5	2.6
**Cuvieronius tropicus*	1	0.4	0.4
Mammut americanum	2	0.8	0.9
Mammuthus hayi	6	2.5	2.6

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[1] See Downing and White (this volume, Pt. II, p. 378) for the description.

armbrusteri and *C. edwardii* is also 1 (based on mandibles), they are more common than the other rare carnivores. Each is represented by a number of specimens of various elements. Of the carnivores, only *Smilodon gracilis* is among the ten most abundant mammals at Leisey 1A. The *Smilodon* sample includes several examples for most skeletal elements. Notably all are from fully adult individuals (indeed the carnassials in many of the jaws exhibit very heavy wear). The lack of juveniles or subadult *Smilodon* individuals contrasts sharply with the herbivores, in which younger age classes predominate (see below). Among the limited number of small mammalian taxa, *Sylvilagus floridanus* and *Geomys pinetis* are most abundant (Morgan and White this volume).

Table 12. Relative abundances of large (> 1 kg) and small (< 1 kg) terrestrial mammals from square D9 of Leisey Shell Pit 1A. Both minimum number of individuals (MNI) and number of identifiable specimens (NISP) are reported. In contrast to the five small mammal specimens, this square produced 712 identifiable fish specimens, with an MNI of 56 representing about 50 taxa (Scudder et al. this vol.).

	MNI	NISP
Large Mammals		
Dasypodidae n. gen. and sp.[1]	1	1
Holmesina floridanus	1	4
Nothrotheriops texanus	1	3
Paramylodon harlani	2	7
Hemiauchenis macrocephala	1	2
Palaeolama mirifica	2	14
Camelidae, gen. indet.	-	23
Platygonus cf. *P. vetus*	1	2
Tayassuidae, gen. indet.	-	4
Tapirus haysii	1	2
Equus spp.	2	24
Proboscidea	1	4
Vertebrae	-	12
Ribs	-	22
Total	14	124
Small Mammals		
Sigmodon libitinus	1	2
Pedomys n. sp.	1	1
Rodent postcrania	-	2
Total	2	5

[1] See Downing and White (this volume, Pt. II, p. 378) for the description.

The relatively very low representation of small species among the terrestrial mammals (Table 12) suggests one or more taphonomic filters acting on body size. Some of these were apparently not acting at the actual site of deposition, as remains of small aquatic birds and fish were abundant (Emslie this volume; Scudder et al. this volume). Apparently the bones of the smaller terrestrial mammals were preferentially destroyed, either by weathering, carnivores, or trampling, far from the site. It is also possible that if small and large bones (or carcasses) were being transported together in a fluvial system, hydrodynamic sorting separated the two (Behrensmeyer 1976). The remains of the proboscideans may also be underrepresented for hydrodynamic reasons, as very large carcasses and bones would require higher than normal current velocities to transport them. This is supported by two types of data. Associated skeletons of proboscideans at Leisey 1A (both *Mammut* and *Mammuthus*) belong to very young juveniles, not adults. Second, adult limb bones are significantly more weathered than those of the camelids (Table 8). This suggests they lay exposed on the ground for long periods of time until a sufficiently severe storm occurred to provide current velocities needed to transported them.

Of the herbivores, grazers (*Hemiauchenia*, *Equus*, and *Mammuthus*) make up 35% of the individuals, while browsers and mixed-feeders the remaining 65%. These numbers do not necessarily reflect the actual areal extent of open versus wooded landscape. However, the pollen and macrobotanical evidence corroborates the presence of at least some mixed hardwood/pine woodlands (Rich and Newsom this volume). In addition to body size, relative abundances of the Leisey 1A mammals were influenced by habitat and behavior of the various taxa. Those that were more likely to die along or in rivers would tend to be more highly represented. However, other factors must have been involved, considering the relative rarity of *Castoroides*, *Neochoerus*, *Lutra*, and *Trichechus*.

POPULATION DYNAMICS AND MORTALITY PROFILES

Analysis of population dynamics and mortality profiles has proven to be a valuable tool in the taphonomic study of large mammals, especially ungulates (Voorhies 1969; Klein 1982). The large samples from Leisey 1A readily allow such an analysis of the two most common species, *Palaeolama mirifica* and *Equus* "*leidyi*." Fossil populations are usually classified into two general categories, attritional or catastrophic. Attritional assemblages are thought to result when the cause of death includes predation, disease, and accidents. The key factor is that mortality rates (the q_x of life tables) are very high for juveniles and old-age adults, low for mature adults, and very low for very young (prime) adults. In catastrophic assemblages, mortality rates are independent of age, resulting in much greater numbers of prime and mature adults, and relatively fewer very old adults. There is often a mistaken one-to-one correlation inferred between whether a fossil population is attritional or catastrophic, and the amount of time (on an ecological time scale) that is represented by the sample. Attritional assemblages are often considered to represent more lengthy accumulations (hundreds to thousands of years), while catastrophic assemblages represent very rapid events (days to months). This may be true in many cases, but certainly there are various combinations of life history strategies and causes of mortality that provide numerous exceptions. For example, a snow-covered dead-fall trap (as described by Oliver 1989) should produce an assemblage in which mortality was independent of age (i.e, catastrophic), but which represents an accumulation of many years. Analysis of population dynamics should take geologic and other taphonomic data into account to reach conclusions on the amount of time represented by a fossil assemblage (e.g., Kurtén 1983).

In many cases fossil ungulate populations closely approximate expected distributions for either attritional (e.g., Van Valen 1964; Hulbert 1982, 1984; Klein 1982) or catastrophic (e.g., Kurtén 1953; Voorhies 1969; Klein 1982) assemblages. The degree of underrepresentation of the juvenile age-class(es) varies depending on the taphonomic history of the individual site. Not all attritional assemblages in modern ungulates have a very high peak among the oldest age-classes (Klein 1982: figs. 3-4); thus the often reproduced example of Dall sheep from Mt. McKinley National Park (Deevey 1947) is an extreme form. Klein (1982) referred to these two types of attritional assemblages as "U-shaped" and "L-shaped." A more reliable indicator of an attritional assemblage is a low frequency of young adults relative to more mature and very old adults.

Methods.— The two most common ungulate species at Leisey 1A, *Palaeolama mirifica* and *Equus "leidyi,"* were chosen for analysis. The age at death was estimated using the methods of Klein (1982; Klein and Cruz-Uribe 1984). This involved measuring the crown height of either a deciduous or permanent cheektooth for each individual. The measurement was then placed in a quadratic equation along with estimates of initial crown height, age of eruption for the particular tooth, and potential longevity (or age when the tooth is shed if it is a deciduous tooth). For *Palaeolama*, the dp4 and m3 were measured at the protoconid (as illustrated by Klein 1982 for many artiodactyls). Using Wheeler's (1982) data on modern llama and alpaca, the dp4 was estimated to have been erupted at birth and shed at 4.5 years, while the m3 erupted at 3.2 years. Potential longevity was estimated as 18 years.

For *Equus*, the dp2 and p2 were measured at the metaconid. Isolated dp4s cannot always be distinguished from dp3s in equids, so they were not used in the analysis. The crown height of the more hypsodont horse teeth usually could not be measured if the tooth remained in its alveolus. However, most of the horse jaws were extensively broken by compaction, so the crown heights were measured before they were repaired. In a few instances the crown height of the p2 in a jaw could not be measured, but other teeth were measurable. In these cases least-squares regression was used to estimate the p2 crown height based on the crown height of another tooth. By using either of these two methods, all but a few of the adult mandibles could be included in the analysis. Following Klein (1982), for *E. burchelli*, the dp2 was assumed to be erupted at birth and shed at 3 years, while the p2 erupted at 3 years. Potential longevity was estimated as 22 years.

Maximum, unworn crown heights were estimated using specimens in the samples that had little or no wear. For *Palaeolama*, these were 16.0 mm for the dp4 and 24.5 mm for the m3. For *Equus*, these were 23.0 mm for the dp2 and 63.3 for the p2. After age determination, specimens were grouped into one of ten age-classes (each representing 10% of the potential longevity) to produce mortality profiles such as those used by Klein (1982). Comparisons between mortality profiles used the Kolmogorov-Smirnov test as illustrated by Klein and Cruz-Uribe (1984: 59-60). Life tables were constructed as described by Voorhies (1969) using dynamic analysis, primarily to estimate mortality rates and juvenile underrepresentation using the methods of Hulbert (1982).

This method uses assumptions of birthrate, sex ratio, stable population size, and litter size to estimate the number of offspring produced by the analyzed population per year (Hulbert 1982). Usually this value far exceeds the number of observed individuals that comprise the first year age-class. Under the assumption that the population is stable (neither increasing nor decreasing in size), this discrepancy is accounted for by juvenile underrepresentation. That this is indeed the case is shown by unrealistically low first year mortality rates. Juvenile underrepresentation is common because the bones and teeth of young juveniles are more easily destroyed than older individuals. To estimate first-year juvenile underrepresentation in a life table, the number of individuals of the first age class in the d_x column is increased so that the number in the corresponding l_x column matches the number of expected offspring (the sum of the $l_x m_x$ column). The juvenile underrepresentation factor is the number of individuals added to the first year d_x column divided by the unadjusted value. For example, suppose in an attritional sample of 100 individuals, 20 are first year individuals, and (based on modern analogues) such a population would annually produce 160 offspring. In this case, the first number in the d_x column is changed from 20 to 80, which increases the first value in the l_x column to 160. The sample would then have a juvenile underrepresentation factor of 60/20 or 3.0.

Results.— The analysis of the Leisey 1A samples of *Palaeolama mirifica* and *Equus "leidyi"* produced two important results (Fig. 23; Tables 13-14): (1) both samples are dominated by juvenile individuals, especially by those that died within three months after birth; and (2) neither sample produced a mortality profile that unambiguously matches either a "classic" catastrophic or attritional population. As expected in both models (but not usually observed due to juvenile underrepresentation), the first age-class contains the most individuals, about 40%

in both cases. The *Palaeolama* sample has successively increasing numbers of individuals in age-class 2 through 4 (Fig. 23A), that differs from catastrophic populations in which the numbers should progressively decline. However, unlike hypothetical attritional populations, the combined percentage of mature and old-age adults (age-classes 5 to 10) is less than those of prime adults (age-classes 2 to 4), 26% vs. 33%. The progressive decline in numbers in age-classes 6 to 10 is also unlike attritional assemblages, especially those with "U-shaped" mortality profiles (Klein 1982). Leisey *Equus* does have successively declining numbers in the prime adult age-classes, and the second age-class has the second highest number of individuals (Fig. 23B), both of which are characteristic of catastrophic assemblages. However, there are secondary peaks in the sixth and ninth age-classes, that is atypical of catastrophic samples. These are more characteristic of attritional assemblages, but, as was the case with the *Palaeolama* sample, the combined percentage of prime adults (37%) is greater than older adults (24%).

Table 13. Life tables for the Leisey 1A population of *Palaeolama mirifica* calculated in the manner of Voorhies (1969) and Hulbert (1982, 1984). The following are reported for each annual age class: the number of deaths in age class x (d_x); the number living at the beginning of the year (l_x); the percent annual mortality rate ($q_x = 100d_x/l_x$); the estimated annual birth rate (m_x); and the estimated number of newborns produced by members of age class x (l_xm_x).

Age class	d_x	l_x	q_x	m_x	l_xm_x
1	95[1]	177	53.7	0.00	0
2	13	82	15.9	0.00	0
3	3	69	4.4	0.23	16
4	7	66	10.6	0.45	30
5	6	59	10.2	0.45	27
6	11	53	20.8	0.45	24
7	7	42	16.7	0.45	19
8	8	35	22.9	0.45	16
9	3	27	11.1	0.45	12
10	7	24	29.2	0.45	11
11	5	17	29.4	0.45	8
12	2	12	16.7	0.45	5
13	3	10	30.0	0.45	5
14	3	7	42.9	0.45	3
15	3	4	75.0	0.45	2
16	0	1	0.0	0.45	
17	0	1	0.0	0.23	1
18	1	1	–	0.11	

[1] This value includes 55 individuals added to the original 40 to account for juvenile underrepresentation (see text). This corresponds to a juvenile underrepresentation factor of 1.375.

Table 14. Life table for the Leisey 1A population of *Equus* "*leidyi*". Format as in Table 13.

Age class	d_x	l_x	q_x	m_x	l_xm_x
1	57[1]	97	58.8	0.0	0
2	7	40	17.5	0.0	0
3	2	33	6.1	0.23	7
4	4	31	12.9	0.45	14
5	6	27	22.2	0.45	12
6	1	21	4.8	0.45	9
7	4	20	20.0	0.45	9
8	3	16	18.8	0.45	7
9	1	13	7.7	0.45	6
10	1	12	8.3	0.45	5
11	0	11	0.0	0.45	5
12	1	11	9.1	0.45	5
13	3	10	30.0	0.45	3
14	2	7	28.6	0.45	2
15	0	5	0.0	0.45	2
16	1	5	20.0	0.45	2
17	0	4	0.0	0.45	2
18	0	4	0.0	0.45	2
19	1	4	25.0	0.23	
20	3	3	–	0.11	1

[1] this value includes 43 individuals added to the original 14 to account for juvenile underrepresentation (see text). This corresponds to a juvenile underrepresentation factor of 3.07.

The Kolmogorov-Smirnov test (Klein and Cruz-Uribe 1984) was used to compare the Leisey samples with each other and with hypothetical samples (Table 15). The two Leisey samples are clearly most similar to each other than they are to any of the models, no doubt reflecting some shared aspects in their taphonomic history. Neither is significantly different from pure attritional or catastrophic assemblages, emphasizing the ambiguity discussed above. If the Kolmogorov-Smirnov statistic is used as a measure of similarity, then the *Equus* sample is closer to a catastrophic population than is the Leisey *Palaeolama* (Table 15). However, both samples are instead more similar to a hypothetical population whose source is half attritional, half catastrophic than they are to either pure attritional or catastrophic populations.

Life tables for Leisey 1A *Palaeolama mirifica* (Table 13) and *Equus* "*leidyi*" (Table 14) indicate that first year juveniles are underrepresented at the site for both taxa, even though this age group has the greatest number of individuals. Estimated juvenile underrepresentation factors are 1.375 for *Palaeolama* and 3.07 for *Equus*.

Without using this factor first year mortality rates are 26% for *Equus* and 33% for *Palaeolama*. The adjusted values are 59 and 54%, respectively (Tables 13-14). Data on first year mortality rates in modern ungulates vary considerably, but indicate that values in the range of 45 to 65% are typical (Klingel 1969; Spinage 1972; Dagg and Foster 1976; Sinclair 1977). Previously computed juvenile underrepresentation factors are 8.4 for a late Miocene horse from a fluvial deposit (Hulbert 1982) and 12.0 for an early Miocene horse from a sinkhole deposit (Hulbert 1984). The much lower values for the two Leisey 1A samples indicate they have a distinctly different taphonomic history, with much less destruction of bone. That the juvenile underrepresentation factor of *Palaeolama* is less than half that of *E.* "*leidyi*" is consistent with other taphonomic factors (less carnivore modification, less weathering; Table 8). They all indicate there was relatively less bone destruction to the camelid bones prior to their arrival at the site.

To further investigate the possibility of mass catastrophic mortality as a source of the Leisey terrestrial mammals, the juvenile individuals of *Palaeolama* and *Equus* were grouped into age-classes of three month intervals (Table 16). As indicated earlier, the largest age-class is the youngest for both samples. Although predation is a significant component to mortality in this age group in modern ungulates, it usually results in complete destruction of the relatively fragile skeleton. It is likely that many of the "missing" juveniles discussed above are those that were killed and/or scavenged by mammalian carnivores. Other possible sources of mortality of very young juveniles include disease, malnutrition, loss or abandonment of mothers (Sinclair 1977: plate 36), and being mired in mud (Berger 1983). If the Leisey 1A sample resulted from a single catastrophic event (e.g., a major flood or drought), then discreet annual age-classes should be observed in seasonally breeding ungulates (Kurtén 1953; Voorhies 1969). The distribution of juvenile age-classes from Leisey 1A do not show such a pattern. Instead, after the high peak in the first age-class, there is not a second peak one year later (Table 16). Rather there is a distinct, second peak about 1.25 to 1.8 years after birth. If this peak represented a catastrophic, mass-mortality event, then there should be corresponding peaks at 0.25-0.8 and 2.25-2.8 years. These are not present. The peak at 1.25 to 1.8 years could have resulted from summer and early fall environmental stress and drought on weaned yearlings.

Discussion.-- The Leisey 1A samples of *Palaeolama mirifica* and *Equus* "*leidyi*" do not comfortably fit either of the classic models of attritional or catastrophic mortality. There are several possible reasons for this. First, the samples may not be representative of the once-living populations because of chance. Although this can never be discounted entirely, it is unlikely to be a major factor, especially in the case of *Palaeolama* when the sample size exceeds 100. Second, a skewed picture of the structure of an entire population can result if either the mode of death is unusual or acts preferentially on certain segments of a

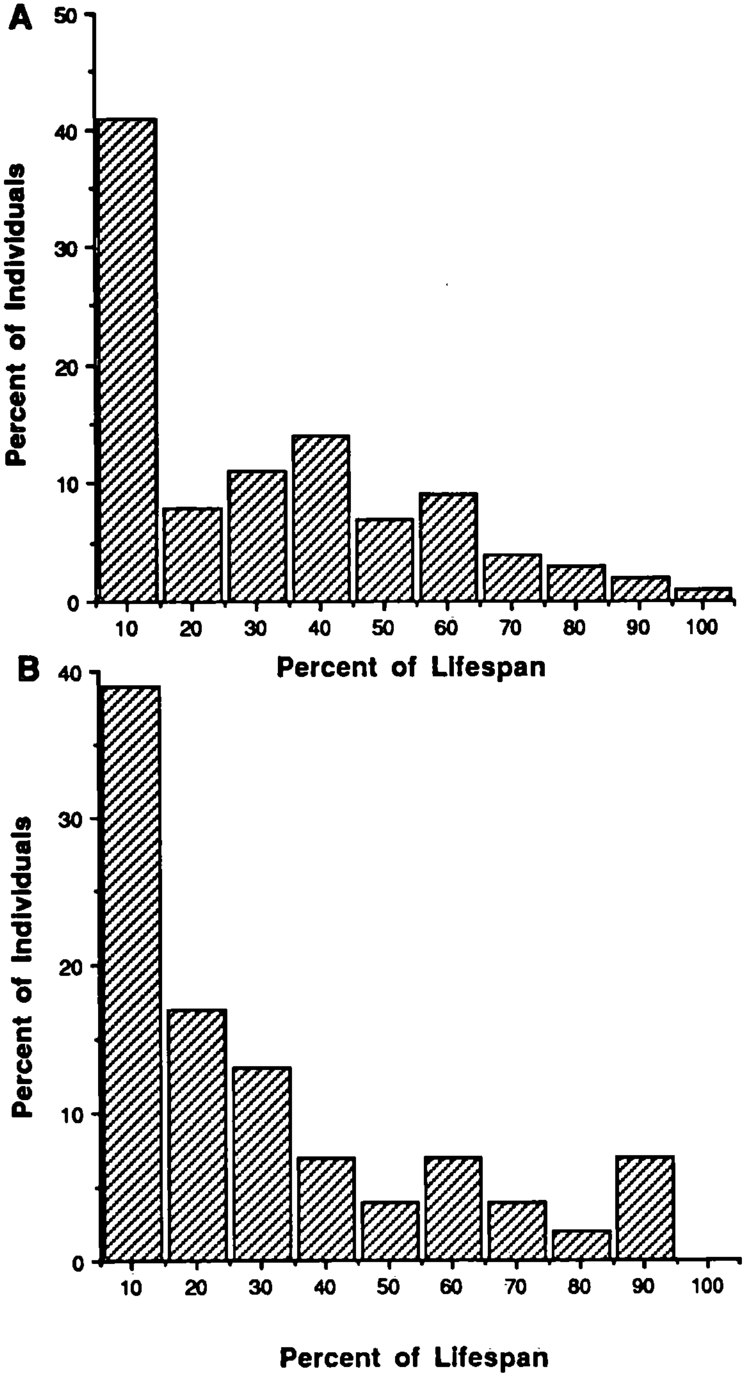

Figure 23. Mortality profiles of Leisey Shell Pit 1A samples of *Palaeolama mirifica* (A) with an MNI of 122, and *Equus* "*leidyi*" (B) with an MNI of 54. Profiles calculated following the methods of Klein (1982).

Table 15. Comparison of the Leisey 1A *Palaeolama mirifica* and *Equus* "*leidyi*" mortality profiles with those of hypothetical attritional, catastrophic, and mixed assemblages using the Kolmogorov-Smirnov statistic (Klein and Cruz-Uribe 1984). Smaller values indicate greater similarity. The hypothetical populations were taken from Klein (1982). Neither of the Leisey 1A samples are significantly different from any of the hypothetical assemblages, but each (especially the camelid) is closest to a mixed attritional-catastrophic sample.

	Palaeolama mirifica	*Equus* "*leidyi*"
Leisey 1A *E.* "*leidyi*"	0.53	–
Pure Attritional (A)	1.03	0.87
Pure Catastrophic (C)	1.13	0.78
1:1 Ratio, A:C	0.72	0.76
2:1 Ratio, A:C	0.86	0.75
4:1 Ratio, A:C	0.82	0.95

Table 16. Age distribution of Leisey 1A *Palaeolama mirifica* and *Equus* "*leidyi*" juveniles. Values represent MNI in each age class.

Age class (in years)	*Palaeolama mirifica*	*Equus* "*leidyi*"
0.00 - 0.25	32	11
0.25 - 0.50	6	2
0.50 - 0.75	1	2
0.75 - 1.00	2	0
1.00 - 1.25	1	2
1.25 - 1.50	3	3
1.50 - 1.75	6	2
1.75 - 2.00	3	1
2.00 - 2.25	3	1
2.25 - 2.50	1	1
2.50 - 2.75	0	1

population (Berger 1983). For example, a catastrophic sample of a bachelor herd of young and very old males would not give a complete picture of the population as a whole. Again the Leisey 1A samples are large, include both sexes, and all ages are represented. Thus this is at most a contributing factor, but not the overall cause.

Third, if predation is a major cause of mortality, and the dominant predators are readily able to kill healthy, adult individuals (usually by working in groups), then there can be little difference in numbers of prime, mature, and old-age adults killed. This is the case for lion predation on zebra, Cape buffalo, and wildebeest (Schaller 1972; Sinclair 1977; Klein 1982: fig. 6). The Leisey mortality profiles are similar to those figured by Klein, except for the high numbers of first age-class juveniles, so this could be a factor. The most common carnivore at Leisey, *Smilodon gracilis*, is relatively small (leopard-size) and thought to be a solitary hunter. However, the enlarged canines allowed it to kill relatively large prey, and *Smilodon* had a very limited capacity to damage and consume bone (Van Valkenburgh et al. 1990). Packs of the wolf-sized *Canis armbrusteri* would also have been able to kill adult *Equus* and *Palaeolama*, while the smaller but more common *C. edwardii* would have only been a threat to unprotected juveniles (see previous discussion on bone modification by carnivores). Leisey chronologically falls in a gap of bone-crushing specialists in North America, postdating the last appearances of borophagine canids and the hyaenid *Chasmaporthetes* and predating the first appearance of *Canis dirus*. Thus while the relatively limited severity of bone modification caused by carnivores, the relative representation of the skeletal elements, and the high representation of young juveniles all argue against predation as a dominant component of ungulate mortality at Leisey 1A, the makeup of the carnivore fauna suggests that it would be hard to detect.

CONCLUSIONS

Results of both paleobotanical analysis (Rich and Newsom this volume) and vertebrate taphonomy indicate that the site was not a mangrove swamp as originally suggested (Hulbert and Morgan 1989), but a shallow, perhaps grassy embayment. While all the vertebrates represented at the locality were living not far from the depositional site, the camelids were living in the immediate vicinity and many may have been introduced into the environment of deposition in a complete state. Equid and proboscidean remains were more modified than camelids by taphonomic factors that operated in terrestrial environments, and may have been transported to the site by streams that became engorged and flooded their banks during rainy periods. Carnivores and scavengers modified some elements, but lack of excessive carnivore damage argues against the presence of a trap situation or a den.

While in the depositional environment, breakage, scratching and movement of skeletal elements occurred, either due to trampling by large herbivores, by moving water, or by a combination of the two factors. Although a strong unidirectional current is not indicated, moving water may have caused bone movement and also is thought to have transported small, light elements from the depositional environment.

Several lines of evidence argue against a single depositional event producing the Leisey 1A biota (e.g., a catastrophic hurricane). Some elements are encrusted with marine epibionts such as barnacles and oysters (Portell et al., this volume). The separation of associated elements and the multidirectional aspect of scratches on bones also indicate that elements spent some time in the depositional environment before being buried. The distribution of age classes of the Leisey 1A horse and llama samples is compatible with other taphonomic indicators of varied sources for the bones, with different taphonomic histories. The samples of at least these two taxa are best interpreted as a mixture of attritional and catastrophic mortality. The attritional component represents the more weathered, more broken, isolated elements, while the catastrophic component is the source of the unweathered, complete, associated elements. The latter could include corpses of drowned animals that floated downstream to the bay, and/or animals that tried to cross the bay during low tide and became mired in the mud. When herds are weakened by drought, disease, or overgrazing, the latter method is a known cause of mass mortality (Sinclair 1977: plate 41). Together, all these sources could produce the types of ungulate samples observed at Leisey 1A. Klein (1982) suggested a similar scenario of mixed attritional/catastrophic mortality for the bovid *Mesembriportax acrae* from bed 3aN at Langebaanweg (South Africa), although other species in the same deposit had pure catastrophic mortality profiles.

LITERATURE CITED

Agenbroad, L. D. 1989. Spiral fractured mammoth bone from nonhuman taphonomic processes at Hot Springs Mammth Site. Pp. 139-147 *in* R. Bonnichsen and M. A. Sorg, eds. Bone Modification. Inst. for Quaternary Studies, Univ. Maine, Orono.

_____, and J. I. Mead. 1986. Large carnivores from Hot Springs Mammoth Site, South Dakota. Natl. Geogr. Res. 2(4):508-516.

Andrews, P. 1990. Owls, Caves, and Fossils. Univ. Chicago Press, Chicago, 231 p.

_____, and J. Cook 1985. Natural modifications to bones in a temperate setting. Man (N. S.) 20:675-691.

_____, and A. Ersoy. 1990. Taphonomy of the Miocene bone accumulations at Pasalar, Turkey. J. Human Evol. 19:379-396.

Badgley, C. 1986a. Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan. Paleobiology 12(2):119-142.

_____. 1986b. Counting individuals in mammalian fossil assemblages from fluvial environments. Palaios 1:328-338.

Behrensmeyer, A. K. 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolph, Kenya. Bull. Mus. Comp. Zool. 146(10):473-578.

_____. 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4(2):150-162.

_____, and D. E. Dechant Boaz. 1980. The Recent bones of Amboseli National Park, Kenya, in relation to East African paleoecology. Pp 72-92 *in* A. K. Behrensmeyer and A. P. Hill, eds. Fossils in the Making. Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press, Chicago.

_____, D. Western, and D. E. Dechant Boaz. 1979. New perspectives in vertebrate paleoecology from a Recent bone assemblage. Paleobiology 5(1):12-21.

_____, K. D. Gordon, and G. T. Yanagi. 1986. Trampling as a cause of bone surface damage and pseudo-cutmarks. Nature 319(6056):768-771.

_____, _____, and _____. 1989. Nonhuman bone modification in Miocene fossils from Pakistan. Pp. 99-120 *in* R. Bonnichsen and M. A. Sorg, eds. Bone Modification. Inst. for Quaternary Studies, Univ. Maine, Orono.

Berger, J. 1983. Ecology and catastrophic mortality in wild horses: Implications for interpreting fossil assemblages. Science 220:1403-1404.

Berta, A. 1981. The Plio-Pleistocene hyaena *Chasmaporthetes ossifragus* from Florida. J. Vert. Paleon. 1(3-4):341-356.

Binford, L. R. 1981. Bones, Ancient Men and Modern Myths. Academic Press, New York, 320 p.

Blumenschine, R. J. 1986. Carcass consumption sequences and the archaeological distinction of scavenging and hunting. J. Human Evol. 15:639-659.

_____. 1989. A landscape taphonomic model of the scale of prehistoric scavenging opportunities. J. Human Evol. 18:345-371.

Brain, C. K. 1980. Some criteria for the recognition of bone-collecting agencies in African caves. Pp. 108-130 *in* A. K. Behrensmeyer and A. P. Hill, eds. Fossils in the Making, Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press, Chicago.

_____. 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. Univ. Chicago Press, Chicago, 365 p.

Coe, M. 1980. The role of modern ecological studies in the reconstruction of paleoenvironments in Sub-Saharan Africa. Pp. 55-71 *in* A. K. Behrensmeyer and A. P. Hill, eds. Fossils in the Making, Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press, Chicago.

Conybeare, A., and G. Haynes. 1984. Observations on elephant mortality and bones in water holes. Quat. Res. 22:189-200.

Dagg, A. I., and J. B. Foster. 1976. The Giraffe: Its Biology, Behavior, and Ecology. Van Nostrand Reinhold Co., New York, 210 p.

Deevey, E. S. 1947. Life tables for natural populations of animals. Q. Rev. Biol. 22:283-314.

Dodson, P. 1973. The significance of small bones in paleoecological interpretation. Univ. Wyoming Contrib. Geol. 12(1):15-19.

Emslie, S. D., and N. Czaplewski. 1985. A new record of giant short-faced bear *Arctodus simus* from western North America, with a re-evalution of its paleobiology. Contrib. Sci. Los Angeles Co. Mus. Nat. Hist. 371:1-12.

Fiorillo, A. R. 1989. Experimental study of trampling: implications for the fossil record. Pp. 61-71 *in* R. Bonnichsen and M. A. Sorg, eds. Bone Modification. Inst. for Quaternary Studies, Univ. Maine, Orono.

Foster, J. B., and M. J. Coe. 1968. The biomass of game animals in Nairobi National Park, 1960-1966. J. Zool. (London) 155:413-425.

Gillette, D. D., and D. B. Madsen. 1992. The short-faced bear *Arctodus simus* from the late Quaternary in the Wasatch Mountains of central Utah. J. Vert. Paleon. 12(1):107-112.

Gonyea, W. J. 1976. Behavioral implications of saber-toothed felid morphology. Paleobiology 2(4):332-342.

Hanson, C. B. 1980. Fluvial taphonomic processes: models and experiments. Pp 156-181 *in* A. K. Behrensmeyer and A. P. Hill, eds. Fossils in the Making, Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press, Chicago.

Haynes, G. 1980a. Prey bones and predators: Potential ecologic information from analysis of bone sites. Ossa 7:75-97.

_____. 1980b. Evidence of carnivore gnawing of Pleistocene and Recent mammalian bones. Paleobiology 6(3):341-351.

_____. 1982. Utilization and skeletal disturbances of North American prey carcasses. Arctic 35(2):266-281.

_____. 1983a. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. Paleobiology 9(2):164-172.

_____. 1983b. Frequencies of spiral and green-bone fractures on ungulate limb bones in modern surface assemblages. Amer. Antiq. 48(1):102-114.

_____. 1985. On watering holes, mineral licks, death, and predation. Pp. 53-71 *in* J. I. Mead and D. J. Meltzer, eds. Environments and Extinction: Man in Late Glacial North America. Center for the Study of Early Man, Univ. Maine, Orono.

_____. 1988. Mass deaths and serial predation: comparative taphonomic studies of modern large mammal death sites. J. Archaeol. Sci. 15:219-235.

_____. 1991. Mammoths, Mastodonts, and Elephants: Biology, Behavior, and the Fossil Record. Cambridge Univ. Press, Cambridge, U.K.

_____, and D. Stanford. 1984. On possible utilization of *Camelops* by early man in North America. Quat. Res. 22:216-230.

Hill, A. P. 1979. Disarticulation and scattering of mammal skeletons. Paleobiology 5(3):261-274.

_____. 1980. Early postmortem damage to the remains of some contemporary East African mammals. Pp. 131-152 *in* A. K. Behrensmeyer and A. P. Hill, eds. Fossils in the Making, Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press, Chicago.

_____, and A. Walker. 1972. Procedures in vertebrate taphonomy. J. Geol. Soc. London 128:399-406.

Hulbert, R. C. 1982. Population dynamics of the three-toed horse *Neohipparion* from the late Miocene of Florida. Paleobiology 8(2):159-167.

_____. 1984. Paleoecology and population dynamics of the early Miocene (Hemingfordian) horse *Parahippus leonensis* from the Thomas Farm site, Florida. J. Vert. Paleon. 4:547-558.

_____, and G. S. Morgan. 1989. Stratigraphy, paleoecology, and vertebrate fauna of the Leisey Shell Pit local fauna, early Pleistocene (Irvingtonian) of southwestern Florida. Pap. Florida Paleon. 2:1-19.

Hunt, R. M. 1978. Depositional setting of a Miocene mammal assemblage, Sioux County, Nebraska (U.S.A.). Palaeogeog., Palaeoclim., Palaeoecol., 24:1-52.

_____. 1990. Taphonomy and sedimentology of Arikaree (lower Miocene) fluvial, eolian, and lacustrine paleoenvironments, Nebraska and Wyoming; a paleobiota entombed in fine-grained volcaniclastic rocks. Pp. 69-111 *in* M. G. Lockley and A. Rice, eds. Volcanism and Fossil Biotas. Geol. Soc. Amer. Spec. Pap. 244, Boulder, Colorado.

Klein, R. G. 1982. Patterns of ungulate mortality and ungulate mortality profiles from Langebaanweg (early Pliocene) and Elandsfontein (middle Pleistocene), south-western Cape Province, South Africa. Ann. South Afr. Mus. 90(2):49-94.

_____, and K. Cruz-Uribe. 1984. The Analysis of Animal Bones from Archeological Sites. Univ. Chicago Press, Chicago, 266 p.

Klingel, H. 1969. The social organisation and population ecology of the plains zebra (*Equus quagga*). Zool. Africana 4:249-263.

Korth, W. W. 1979. Taphonomy of microvertebrate fossil assemblages. Ann. Carnegie Mus. Nat. Hist. 48(15):235-285.

Kurtén, B. 1953. On the variation and population dynamics of fossil and Recent mammal populations. Acta Zool. Fenn. 76:1-122.

_____. 1967. Pleistocene bears of North America. 2. Genus *Arctodus*, short-faced bears. Acta Zool. Fenn. 117:1-66.

_____. 1983. Variation and dynamics of a fossil antelope population. Paleobiology 9(1):62-69.

Meyer, C. 1991. Burial experiments with marine turtle carcasses and their paleoecological significance. Palaios 6(1):89-96.

Myers, T. P., M. R. Voorhies, and R. G. Corner. 1980. Spiral fractures and bone pseudotools at paleontological sites. Amer. Antiq. 45(3):483-490.

Oliver, J. S. 1989. Analogues and site context: bone damage from Shield Trap Cave (24CB91), Carbon County, Montana, U.S.A. Pp. 73-98 *in* R. Bonnichsen and M. A. Sorg, eds. Bone Modification. Inst. for Quaternary Studies, Univ. Maine, Orono.

Olsen, S. L., and P. Shipman. 1988. Surface modification on bones: Trampling versus butchery. J. Archaeol. Sci. 15:535-553.

Pratt, A. E. 1986. The taphonomy and paleoecology of the Thomas Farm local fauna (Miocene, Hemingfordian), Gilchrist County, Florida. Ph.D. dissertation, Univ. Florida, 487 p.

_____. 1990. Taphonomy of the large vertebrate fauna from the Thomas Farm locality (Miocene, Hemingfordian), Gilchrist County, Florida. Bull. Florida Mus. Nat. Hist. 35(2):35-130.

Schaller, G. B. 1972. The Serengeti Lion: A Study of Predator-Prey Relations. Univ. Chicago Press, Chicago, 480 p.

Shipman, P. 1981. Life History of a Fossil: An Introduction to Taphonomy and Paleoecology. Harvard Univ. Press, Cambridge, 222 p.

Sinclair, A. R. E. 1977. The African Buffalo: A Study of Resource Limitation of Populations. Univ. Chicago Press, Chicago, 355 p.

Spinage, C. A. 1972. African ungulate life tables. Ecology 53(4):645-652.

Van Valen 1964. Age in two fossil horse populations. Acta Zool. 45:93-106.

Van Valkenburgh, B. 1988. Trophic diversity within past and present guilds of large predatory mammals. Paleobiology 14(2):155-173.

_____. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. Paleobiology 17(4):340-362.

_____, M. F. Teaford, and A. Walker. 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabertooth cat, *Smilodon fatalis*. J. Zool. (London) 222:319-340.

Voorhies, M. R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. Univ. Wyoming Contrib. Geol., Spec. Pap. 1:1-69.

Webb, S. D., B. J. MacFadden, and J. A. Baskin. 1981. Geology and paleontology of the Love Bone Bed from the late Miocene of Florida. Amer. J. Sci. 281:513-544.

Western, D. 1980. Linking the ecology of past and present mammal communities. Pp 41-54 *in* A. K. Behrensmeyer and A. P. Hill, eds. Fossils in the Making, Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press, Chicago.

Wheeler, J. C. 1982. Aging llamas and alpacas by their teeth. Llama World 1(2):12-17.

Wolff, R. G. 1973. Hydrodynamic sorting and ecology of a Pleistocene mammalian assemblage from California. Palaeogeog., Palaeoclim., Palaeoecol. 13:91-101.