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An owl-pellet accumulation of small Pliocene vertebrates from the Verde Formation, Arizona, USA

Nicholas J. Czaplewski

ABSTRACT

A small quarry in Pliocene lacustrine deposits at House Mountain in the Verde Formation of central Arizona produced a high concentration of microvertebrate fossils of early Blancan (early Pliocene) age. Within a single bedding plane on excavated blocks, a miniature (0.25 m$^{2)}$ bone bed was exposed piecemeal under a microscope and mapped. The deposit contained about 300 recognizable skeletal elements representing a small finch and several kinds of rodents. Concomitant screenwashing of the site produced 1085 more rodent and bird bone fragments plus shrew, bat, and salamander remains. The House Mountain assemblage clearly exhibits the characteristics of nocturnal raptor (owl) pellet accumulations. Comparison with modern owl pellet accumulations in Arizona, including a quantitative consideration of bones from an area equal to that quarried for fossils showed similar partial association of the elements of individual skeletons. Weathering of bones prior to burial probably was limited to brief subaerial exposure to rainfall and insect activity or deposition in calm, shallow water sufficient to disintegrate owl pellets but not sufficient to completely dissociate some skeletal elements of individual prey animals. A medium-sized owl (100 to 400 g) probably accumulated the House Mountain microvertebrates. Contrary to other evidence, the age-frequency profile of extinct kangaroo rats, *Prodipodomys*, does not indicate attritional mortality. Had screenwashing been used as the only method of recovery of fossils, much taphonomic information would have been lost. However, unless the taphonomic information for a given site is crucial or equivocal, the additional time spent on quarrying and mapping may be unwarranted.

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INTRODUCTION

The Verde Formation of central Arizona, USA, is a Miocene-Pliocene sequence of predominantly lacustrine limestones and mudstones, with occasional interbedded volcanics, evaporites, fluvial sediments, and spring deposits (Twenter and Metzger 1963; Nations et al. 1981; Figure 1). Ancient Lake Verde is interpreted by these authors as having been a spring- and river-fed, shallow, algae-filled lake with marshy edges surrounded by terrestrial habitats including open oak-juniper

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FIGURE 1. Outline map of the southwestern U.S. state of Arizona showing major rivers, cities, and the limits of the Verde Formation (stippled area).

FIGURE 2. View westward across the Verde Formation and Beaverhead Flat as seen from the rest area on Interstate highway 17 north of McGuireville, Arizona. The summit of House Mountain is on the horizon to the right of center.

savanna and grasslands with broadleaf deciduous gallery forest along the lake edge and inflowing streams. In general, vertebrate fossils are rare and known mostly from a few localities in the Pliocene portion of the formation, reflecting an early Blancan land mammal age (Czaplewski 1987a, 1987b, 1990). However, some localities in the Verde Formation might bear a late Hemphillian fauna (Lindsay and Czaplewski, this volume).

Twenter (1962) mentioned some of the first vertebrate fossils known from the Verde Formation. At one locality east of Cottonwood on the south flank of House Mountain, Yavapai County (Figures 2, 3), he recovered fossils of small mammals, which were sent to C.W. Hibbard, who identified teeth of the rodents *Dipodomys* (= *Prodipodomys*), *Bensonomys*, and *Sigmodon* (Twenter and Metzger 1963). In 1979 I relocated this site and removed sediments from it. The sediments amounted to less than 10 kg of rock, but when

FIGURE 3. MNA locality 318 on the south flank of House Mountain, Arizona. 3.1. View northward from across the canyon. Fossils were collected from the light-colored mudrocks in the center of the photograph beneath the horizontal limestone ledges extending across the photo. K. Davies points out the hollow in the outcrop behind him from which the blocks were quarried and plaster-jacketed for this study. 3.2. Close-up view northeastward of the same outcrop. K. Davies' right hand is on the level that contained the richest assortment of microvertebrate bones.

screened underwater by standard techniques, produced a dozen isolated rodent molars from at least four different taxa. Further screening produced abundant rodent teeth and small vertebrate bone fragments. When small discrete samples of sediment were screenwashed, complete or nearly complete "sets" of maxillary or mandibular teeth showing equivalent degrees of wear and similar preservation were recovered. These results suggested that complete skulls and lower jaws of individual rats and mice were present but were destroyed during screenwashing. Part of the deposit was quarried in 1979-1980 in order to recover unique taphonomic data. The site is Museum of Northern Arizona (MNA) locality 318 in Coconino National Forest; all specimens are cataloged with MNA numbers.

Fluvial transport and accumulation by predators are often invoked as mechanisms involved in the accumulation of vertebrate bones (e.g., Dodson 1973; Wolff 1973; Mellett 1974; Mayhew 1977; Hunt 1978; Korth 1979; Hanson 1980; Andrews and Nesbit Evans 1983; Hoffman 1988). Owl pellets are commonly cited as a source for accumulations of small vertebrate fossils (Kusmer 1990; Denys et al. 1996; Terry 2004). However, effects such as weathering, disintegration, disturbance by insects or other invertebrates, transport, and burial of pellets after they have been regurgitated can bias analyses of owl pellet remains and might influence paleoecological interpretations (Terry 2004).

Cursory examination of the House Mountain fossils suggested that the assemblage represented an accumulation of bones from owl pellets. Although accumulation by owls is sometimes invoked as the cause when a concentration of microvertebrate fossils is discovered, few authors have actually attempted to support such claims with empirical data in open-air localities, probably because of the time and difficulties involved in quarrying microvertebrates localities. (However, some authors have addressed microvertebrate taphonomy in cave localities, e.g., Andrews 1990; Hockett 1991; Hoffman 1988; Jass 2002.) Walton (1990) gave a few examples of microvertebrate sites where owl pellet accumulation was implied, including mention of the House Mountain assemblage in the Verde Formation before the present analysis was completed.

Different taphonomic agents, including vertebrate predators, impose distinctive effects on vertebrate skeletons such that it may be possible for the paleontologist to identify the agent of accumulation of a given suite of bones (Dodson and Wexlar 1979). The purpose of the present paper is to document the concentration of early Pliocene small vertebrate remains at MNA locality 318 and to evaluate the taphonomic character of the assemblage. Production of microvertebrate quarry maps provided the opportunity to assess taphonomic data often unavailable from microvertebrate localities (e.g., bone orientation patterns). Few previous researchers have quarried sites with microvertebrate concentrations for the purpose of mapping the bones in situ (Irwin et al. 1997; Wilson 2006), rather than screenwashing quarried rock and thereby losing taphonomic information. No such studies, and no microvertebrate quarry maps, appear to have been published previously.

METHODS AND MATERIALS

Quarried Blocks with Microvertebrate Fossils

MNA locality (loc.) 318 (Figure 3.1) occurs in a 2 m high exposure (8 m in lateral extent) of calcareous grayish-green mudrocks interbedded between white biogenic limestones (micrites) containing occasional external molds of freshwater gastropods. Screenwashing of the mudrocks from the locality and inspection in the field had previously indicated that abundant microvertebrate fossils and rare gastropod fragments were exposed on edge in a single bedding plane for about 1 m along the face of the outcrop (Figure 3.2). Screened samples from above this bedding plane had produced no small vertebrate remains, and samples screened below the bedding plane produced very few. Therefore, the fossiliferous horizon in the cliff face was quarried by blocks.

A relatively large block of matrix, including the fossiliferous level, was exhumed with hammers and chisels, plaster jacketed, and prepared in the laboratory. Several small blocks were collected and prepared in the same manner. The blocks were numbered, labeled with north arrows, and their position relative to other blocks was sketched. Sedimentary matrix was painstakingly removed to the level of the fossils with carbide needles and insect pins under a dissecting microscope over an eight-month period. Once prepared, blocks were individually mapped while maintaining their relative positions, and a master map of those portions of the quarried deposit was drawn. A grid pattern of 10 cm x 10 cm squares was superimposed on the map. The general aspect of the microvertebrate deposit and the quality of bones preserved in it are shown in Figure 4.

FIGURE 4. One of the small blocks that was prepared and mapped into the overall quarry map of the microvertebrate deposit at MNA locality 318, showing the general quality of bones. Scale is numbered in centimeters. This piece is also shown in Figure 8.2.7.

Taphonomic data collection followed Munthe and McLeod (1975), and data analyses followed approaches much like those of Maas (1985) and Dodson and Wexlar (1979), along with the application of biological as well as taphonomic criteria (e.g., Korth and Evander 1986).

The trend (compass orientation) of the proximal end of 82 identifiable, elongate bones was measured, and their frequencies among 24 sectors of 15° each was plotted on a circular histogram. If proximal and distal ends were broken off or indiscernible, the azimuth of the larger end was measured. If there was no difference in size between ends, the bone was not used in the analysis. Plunge was not measured because all the bones were lying essentially horizontal on a relatively flat bedding plane. Nevertheless, the circular distribution data were treated as a diametrically bimodal distribution (Zar 1984) in case no significant direction of orientation occurred and a mean angle of orientation could still be calculated. The nonparametric Rayleigh test (Zar 1984) was used to test the null hypothesis that the sampled population of bones is uniformly (randomly) distributed.

An attempt was made to identify all skeletal elements, and where possible, to identify the species to which certain skeletal elements belonged. Some teeth, dentaries, and skull fragments were carefully removed from the prepared quarried blocks after mapping. This procedure was necessary to identify small mammals whose tooth crowns were either buried in the sediment or lying obliquely, thereby preventing detailed in situ evaluation with a microscope. The removed elements were assigned numbers that were recorded on individual block maps. These fossils were then completely prepared, usually with the aid of water-soluble Carbo-Wax (General Electric Co.). All fossils were examined for signs of abrasion and transport by water.

In quantifying the vertebrate taxa at the House Mountain fossil locality, the relative abundance was based on crania, dentaries, and isolated premolars and molars (Table 1). No attempt was made to count symmetrical pairs of paired elements or greatest number of ipsilateral elements. Nor was any attempt made to match or to separate pairs of contralateral elements based on similar degrees of tooth wear. A simple total number of halves for each paired element was counted and divided by two in order to determine the MNI represented. Thus, Table 1 may slightly underestimate the actual numbers present in the deposit.

Modern Owl Pellets for Comparison

Recent owl pellets were collected from several localities in Arizona in order to make taphonomic comparisons with the fossil assemblage from House Mountain. Owl pellets analyzed in the greatest detail came from three localities. The first two localities, occupied by the barn owl (*Tyto alba*), occurred in agriculturalized mesquite grassland between Portal, Arizona, and Rodeo, New Mexico. These materials were analyzed by generally following the methods of Dodson and Wexlar (1979) on pellets gathered from captive owls. Counts were made of each skeletal element except ribs, and the degree of completeness and breakage patterns of specific elements were noted. Mammal, bird, reptile, and amphibian skeletal elements were tallied separately. No species identifications were made for postcranial bones of mammals from these sites, but cranial elements were identified at lower taxonomic levels. A count of the minimum number of individuals (MNI) was based on major elements (e.g., dentary, femur). Data from the modern owl

TABLE 1. Relative abundance of vertebrates at MNA locality 318 based on crania, dentaries, and isolated premolars and molars. Taxa are arranged from most abundant to least abundant from top to bottom.

Taxon	Crania	Cranial Bones			All Cheek Teeth		Molars Only		Overall MNI	Percent of Overall MNI
		Maxilla	Dentary	MNI	Quarried	Screened	No.	MNI		
Prodipodomys idahoensis	4	5	11	6	68	52	82	7	7	20
Geomys minor	2	0	7	4	24	0	18	2	4	11.4
Bensonomys arizonae	0	0	5	3	7	5	12	1	3	8.6
Sigmodon minor	2	1	4	2	19	14	33	3	3	8.6
Passeriformes					coracoids N = 5				3	8.6
Perognathus strigipredus	0	1	2	1	13	21	24	2	2	5.7
Onychomys bensoni	0	1	2	1	10	5	15	2	2	5.7
Reithrodontomys cf. *wetmorei*	0	0	2	1	5	0	5	1	1	2.9
Neotoma vaughani	0	1	1	1	8	0	8	1	1	2.9
Postcopemys sp.	0	0	0	0	1	4	5	1	1	2.9
Jacobsomys verdensis	0	0	0	0	0	4	4	1	1	2.9
Soricidae	0	0	1	1	0	1	1	1	1	2.9
Lasiurus cf. *blossevillii*	0	0	0	0	0	5	2	1	1	2.9
Prosigmodon holocuspis	0	0	0	0	0	1	1	1	1	2.9
Urodela					jaw fragments N = 2				1	2.9
Cricetidae indet.					6	19	25	3	3	8.6
Total									35	100.4

pellets, including prey taxa represented, proportional representation of skeletal elements, and patterns of bone breakage were compared with published studies and with the fossils from House Mountain. Expected number of individual bones (NIb) was based on the number of the elements found in a typical small mammal skeleton multiplied by the minimum number of individual small mammals. This result was then compared to the number of individual specimens (NISP); NISP often exceeds the "expected" NIb because of multiple fragmentations of a given element (see Results and Discussion).

The third modern pellet locality was a habitual roost for barn owls at a short cliff south of Sugarloaf Mountain, Yavapai County, Arizona. Along the base of this cliff was an accumulation of small vertebrate bones from regurgitation pellets (Figure 5.1-5.4) representing prey remains from many seasons. The exact duration of accumulation is unknown, but probably represents at least one season of occupation of the roost. Small vertebrate bones at this site were spread across an area of ground estimated at 12 m^2. The density of bones varied greatly in different portions of the area. Compass orientation of an arbitrary sample of long bones was determined as in the fossil sample. I measured the trend of 95 bones in a sparsely vegetated area that sloped slightly downhill away from the cliff. Because of the slope, there was reason to expect that a specific mean direction might result. Therefore, a modification of Rayleigh's test was used (Durand and Greenwood 1958; Zar 1984) to consider the null hypothesis that the population angles are randomly distributed. Two 0.25 m^2 segments (approximately equal to the quarried area of the Pliocene deposit) within the densest concentration of bones were sampled in 25 increments each 10 cm x 10 cm (Figures 6.1-6.4). Data on prey species present, prey sizes, and proportional representation of all skeletal elements (including ribs) were collected also.

A few modern pellets were collected opportunistically near Camp Verde, Arizona, from a great

FIGURE 5. A modern barn owl roost in a cliff near Sedona, Arizona. 5.1. Guano streaks are visible at the top of the photo, and the surface of the ground below shows part of the accumulation of prey animals' bones weathered out of the owls' regurgitation pellets. 5.2. View of the ground below the roost with numerous scattered microvertebrate bones. A dark, intact pellet is below and to the left of the feather, and a grayish, partially weathered pellet is at left center. Feather is 23 cm long. 5.3. A finch skull is visible at the top and a woodrat (*Neotoma*) skull in the center of the photo, with a decomposing pellet between them and to the left of the feather. 5.4. In this view, a woodrat skull is visible at the top, a finch skull is at lower left center, and a weathering pellet can be seen as the gray mass at the lower right. Numerous other skeletal elements are discernible on close inspection.

horned owl (*Bubo virginianus*) roost. These pellets were examined in less detail than were the barn owl pellets from the other localities, but some incidental results are mentioned below.

Age-Frequency Profiles

Age-frequency profiles were produced for *Prodipodomys idahoensis*, the most abundant rodent in the House Mountain fossil assemblage. In order to determine the ontogenetic age of individual kangaroo rats, arbitrary tooth-wear categories similar to those used by neontologists were established (see Figure 7). In addition, tooth crown-height measurements of certain cheek teeth were made (Table 2). Crown heights were measured from the apices of the dentine tracts as follows (terminology is from Barnosky 1986; see also Czaplewski 1990): P4, from labial dentine tract to metacone and from lingual tract to entostyle; M1, from labial tract to paracone and from lingual tract to protostyle; p4, from labial tract to hypostylid and from lingual tract to entoconid; m1, from labial tract to protostylid and from lingual tract to metaconid.

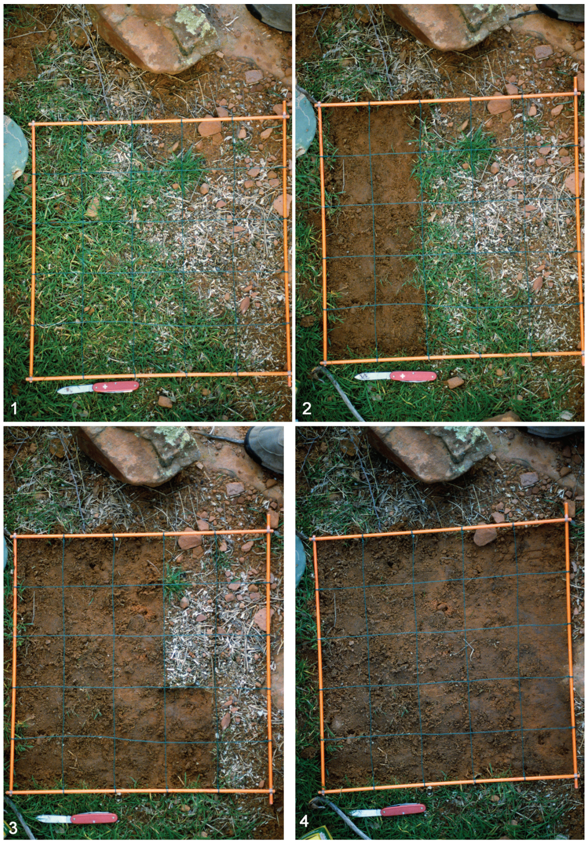

FIGURE 6. Bones beneath a modern owl roost near Sugarloaf Mountain, Arizona, sampled for comparison with Pliocene microvertebrate bones from the House Mountain locality in the Verde Formation. 6.1-6.4. Photos show removal of successive samples from Plot 1. A second plot was sampled similarly. Outer orange frame is 0.5 m x 0.5 m, approximately the size of the Pliocene deposit, with the smaller grid squares delimited by green wires each measuring 10 cm x 10 cm.

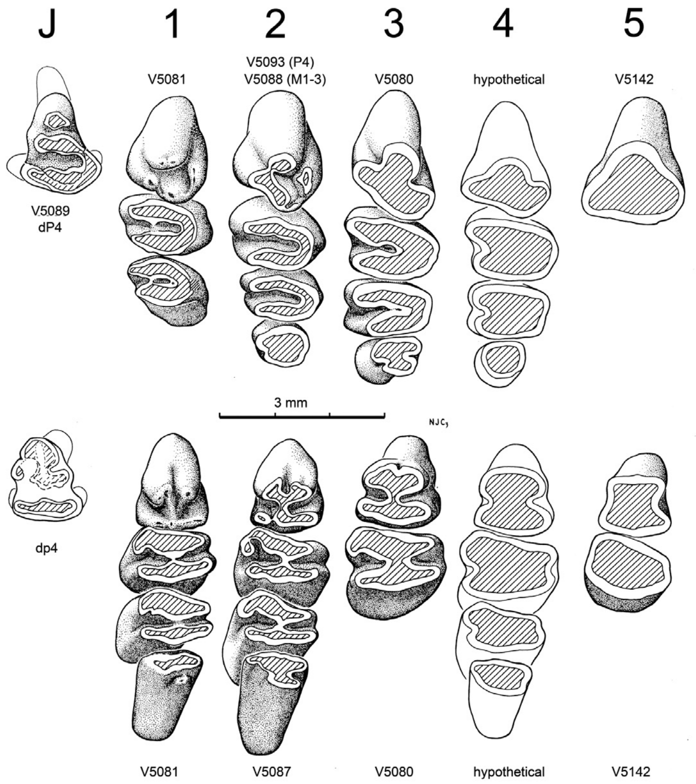

FIGURE 7. Partial and complete cheek-tooth rows of *Prodipodomys idahoensis* showing arbitrary tooth-wear stages used to determine the age-frequency distribution of this species at MNA locality 318. All specimens shown are from MNA loc. 318; associated upper and lower jaws were used where possible to ensure equivalency of wear. The deciduous p4 (juvenile, stage J) and teeth in wear stage 4 were not recovered in the deposit; hypothetical drawings are provided for these categories (the dp4 of *P. idahoensis* is unknown; a drawing of dp4 from a modern *Dipodomys merriami* is shown). Drawings are realigned and are reversed from original specimens where necessary in order to be shown as right upper teeth and left lower teeth. See also Table 2 for crown height measurements of P4, p4, M1, and m1 at each of these stages of wear. White and stippled areas indicate enamel; hatched areas indicate dentine.

RESULTS AND DISCUSSION

The overall quarried and mapped area comprises about 0.25 m^2 (Figure 8.1). Most of the fossil material exposed on the prepared bedding plane is too fragmentary for taxonomic identification. In general, fossil bone from the House Mountain locality is brittle and easily pulverized, whereas tooth enamel is better preserved, but teeth still may be brittle and occasionally cracked. Close-up views of portions of the fossil accumulation are shown enlarged in Figures 8.2.1-8.2.11 and 8.3.1.

Predominant Orientation of Bones

The fossils tend to lie along a diameter line with a mean angle of 171°, and the bones show no predominant directional orientation (Figure 9.1; Rayleigh's $z = 1.368$, $p > 0.05$). Sedimentary structures characteristic of high-energy fluvial activity are absent in the outcrop, nor is abrasion obvious on any of the bones. Some bones are roughened ("feathered") about the edges, an effect that could have resulted from limited subaerial weathering prior to burial, poor preservation, or damage during preparation. Evidence of hydrodynamic sorting of bones of differing sizes or shapes is absent. All elements of the skeleton are present. However, there is a high representation of fossil rodent incisors, the most obvious departure from modern pellet counts. Incisors are frequently the most abundant element in fluvial assemblages of disarticulated rodent remains. The fossil incisors are no more fragmentary than those in the modern pellets, so post-depositional breakage does not account for the difference. The cause of the discrepancy between fossil and modern incisors is unknown,

TABLE 2. Crown heights (in mm) of *Prodipodomys idahoensis* teeth at different stages of tooth wear. Arbitrary wear stages are shown in Figure 6. Teeth at Stage 4 were not recovered. lab. = labial; lin. = lingual; O.R. = observed range.

		Stage 1			**Stage 2**			**Stage 3**			**Stage 5**		
Tooth	**Side**	**N**	**O.R.**	**Mean**	**N**	**O.R.**	**Mean**	**N**	**O.R.**	**Mean**	**N**	**O.R.**	**Mean**
P4	lab.	4	1.67-1.97	1.83	9	1.44-1,90	1.67	1	1.30		2	0.24-0.92	0.58
	ling.	6	1.44-1.67	1.59	9	1.41-1,77	1.59	1	1.44		1	0.98	
M1	lab.	3	1.21-1.54	1.42	7	1.28-1.59	1.45	1	1.06		0		
	ling.	2	1.27-1.34	1.30	4	0.98-1.39	1.24	1	1.15		0		
p4	lab.	2	1.70-1.79	1.74	3	1.34-1.90	1.55	3	1.23-1.45	1.33	1	0.59	
	ling.	4	1.34-1.64	1.50	4	1.25-1.65	1.48	4	1.14-1.44	1.27	4	0.56-0.95	0.73
m1	lab.	3	1.15-1.21	1.18	1	1.24		3	0.98-1.21	1.10	0		
	ling.	4	0.98-1.29	1.21	2	1.11-1.25	1.18	4	1.11-1.31	1.21	1	0.24	

although winnowing of the assemblage by weak fluvial currents might explain the high proportion in the fossil assemblage. Substantial fluvial transport can be eliminated as a possible mechanism in the accumulation of the bones at House Mountain.

The weight of overlying sediments or diagenetic compaction appears to have flattened and crushed the fossils in situ once they were deposited. Many of the long bones, dentaries, skulls, etc., were crushed into a number of fragments, yet the various pieces retain their positions relative to each other so that the overall shape of the original element is preserved or at least can be readily visualized. For example, skulls of *Prodipodomys* (Figure 8.2.1, 8.2.2, 8.3.1), *Geomys* (Figure 8.2.3), and *Sigmodon* (Figure 8.2.4) are broken into many pieces but the fragments have not been dispersed by water transport. Undoubtedly, the cracking and fragmentation occurred after burial, because exposure even to light rainfall, wind, or wave action would have scattered the fragments. In fact, for the *Sigmodon* skull just mentioned, both dentaries remain in nearly articulated positions, and a humerus and ulna are associated (Figure 8.2.4). Virtually all but the smallest and relatively densest bones (unguals and other short phalanges, some metapodials) and teeth are crushed in this manner. All bones were crushed in a vertical direction perpendicular to the bedding plane on which the fossils were deposited. For purposes of comparison and quantification, the crushed and splintered fossil bones were considered to be "complete" as long as no significant portion was missing.

Unlike the bones in the fossil bed, bones from the modern owl pellets at Sugarloaf Mountain did not exhibit a uniform circular distribution (Figure 9.2; modified Rayleigh test, u = 2.455; $0.005 < p < 0.01$; Zar 1984). Mean angle was 87°, but this angle is aligned neither parallel nor perpendicular to the downslope direction (approximately 40°). The hydraulic properties of microvertebrate bones have been studied in flowing water (Dodson 1973; Korth 1979), in which they are highly susceptible to transport for considerable distances. Different skeletal elements have different "competent velocities" that are required to transport them depending on the hydrodynamic properties of the element. Below their competent velocities many bones orient themselves to a current in positions of minimum resistance (Dodson 1973). The hydrodynamic behavior of microvertebrate bones on dry land that are subjected to periodic rainfall, or in shallow standing water that are subjected to gentle wave action, has not been studied. On dry land, their orientation could be changed radically in three-dimensional space by the impact of a single drop of rain. Relative to the microtopography of the ground surface and plants growing in it, small long bones might stand on end propped up in vegetation as readily as to lie flat on the ground. If these standing bones became buried and fossilized, they might remain uptilted or laid flat depending on energy in the process burying them, and could also become flattened through compaction by the overlying sediments. Because of the lack of actualistic data concerning the hydrodynamic behavior of microvertebrate bones on dry land, the importance of the significant orientation trend of bones in the modern owl deposit remains unknown.

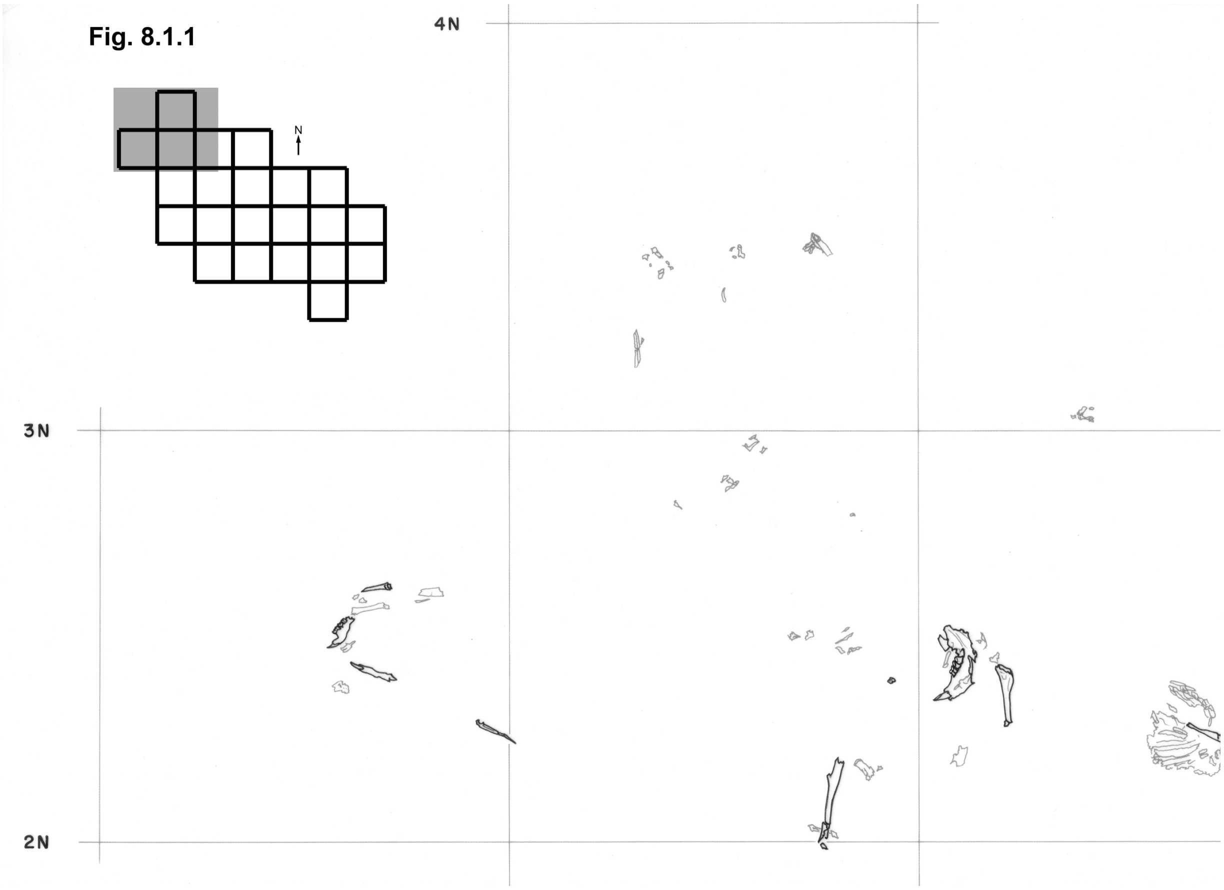

FIGURE 8.1.1-8.1.8. Quarry map of the early Pliocene microvertebrate fossil accumulation at MNA locality 318 in the Verde Formation near House Mountain, Yavapai County, Arizona. Identifiable skeletal elements are outlined with a solid line, unidentifiable elements as a lighter line. Each grid square is designated according to the intersection of grid lines at its southwestern corner.

Microvertebrate Taxa Representation

At least 16 taxa of vertebrates occur in the House Mountain assemblage, including a salamander (Urodela), a small finch (Passeriformes), a shrew (Soricidae), a bat (*Lasiurus*), and 11 kinds of rodents (Table 1). The House Mountain bone accumulation is remarkable for the relatively large number of small-bodied species represented in such a small sample area. Body-size range varies from an estimated 5 to 7 grams (shrew and salamander) to 154 to 177 grams (woodrat; Martin 1984). The combination of the small sample area, limited body-size range, and high taxonomic diversity implies that some selective factor, such as a vertebrate predator, accumulated these bones.

Potential Collectors of Microvertebrate Bones

The nature of the bone assemblage suggests that a small terrestrial vertebrate predator accumulated the bones. Potential candidates are medium-sized reptilian carnivores, small to medium-sized mammalian carnivores, diurnal or nocturnal raptors, or other large predatory or carrion-feeding birds such as gulls and terns (Laridae), egrets and herons (Ardeidae), and crows and jays (Corvidae).

Reptilian carnivores large enough to prey on vertebrates the size of woodrats are unknown as fossils in the Verde Formation, although beaded lizards (Helodermatidae) and some snakes (Boidae, Colubridae, Crotalidae) are capable of preying on woodrats and are known as fossils from the Neogene of North America (Holman 1979; Pregill et al. 1986). However, the stomachs of reptilian carnivores strongly acid-etch their prey's bones and teeth (Fisher 1981), digesting the bones and leaving little or nothing to identify in their scats (Figure 10). The lack of etching and relatively good preservation of bones and teeth in the Verde assemblage eliminates reptiles as possible agents of accumulation. It also seems unlikely that reptiles

Fig. 8.1.2

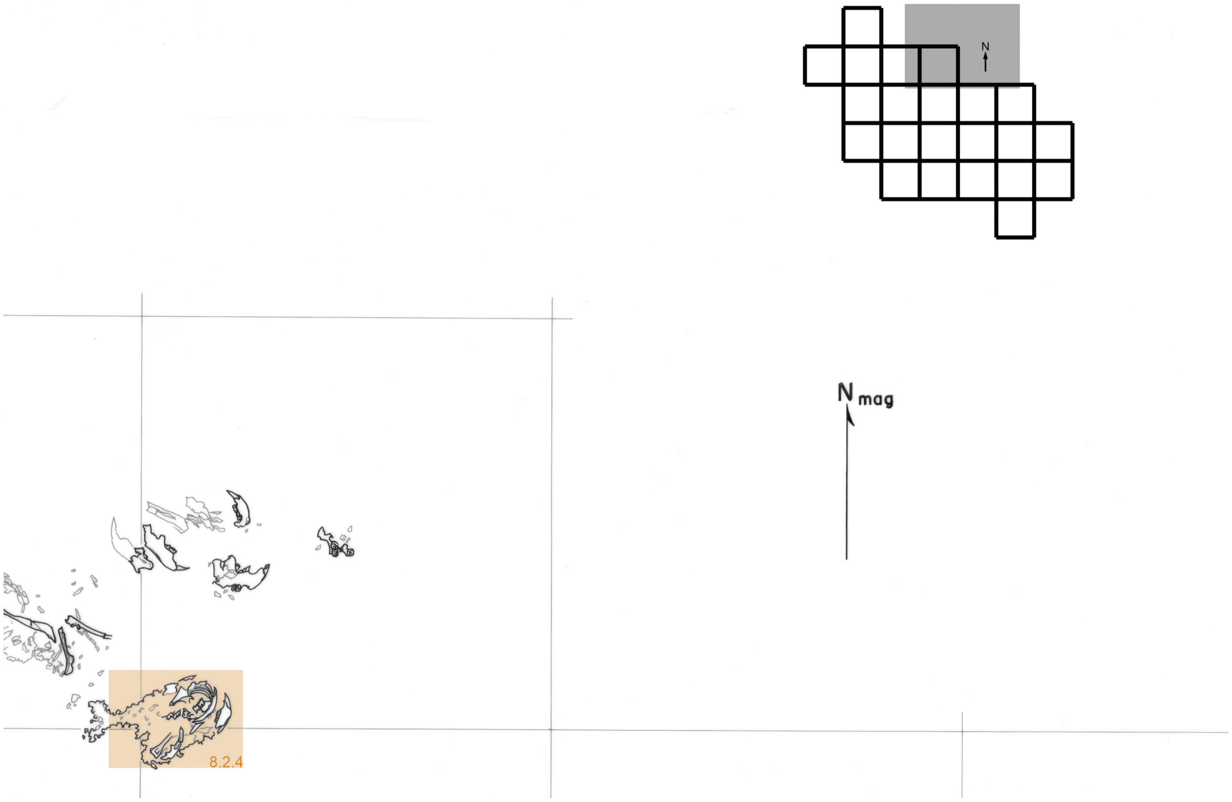

FIGURE 8.1.2 (continued). Kangaroo rat (*Prodipodomys idahoensis*) anterior portion of cranium in ventrolateral aspect, and associated right dentary in lingual aspect located at 1S+2W; also present are the left p4-m1 to the right of the tip of the i1 in the dentary, and other unassociated bones and fragments. Arrow points northward.

would accumulate such a high diversity of prey items over such a small area during a given time period.

Many kinds of birds produce pellets of undigestible food materials (Leahy 1982; Elbroch et al. 2001). Among these, raptors (owls, hawks, eagles, vultures) are well known to produce pellets containing the remains of small vertebrates. Gulls (Laridae), herons and egrets (Ardeidae), and ravens and crows (Corvidae) occasionally eat mammalian prey, but usually not to the extent that they produce large accumulations of pellets containing bones. Furthermore, ardeids have powerful digestive systems that are capable of eliminating practically all bones when digesting prey (Glue 1970).

If the House Mountain fossils actually represent prey remains, then another look at the list of taxa is instructive. Based on modern analogues, all organisms in the fossil assemblage are primarily nocturnal except for the finch or sparrow. This pattern suggests a nocturnal agent of accumulation, such as mammalian carnivores or nocturnal raptors (owls), and helps to eliminate diurnal raptors (hawks, falcons). Some extant owl species (e.g., hawk owl, *Surnia ulula*) often forage by day. Other owls are crepuscular or primarily nocturnal. Even nocturnal owls occasionally forage in the daytime (Vaughan 1954); barn owls and long-eared owls often raid communal roosts of small birds during winter (Glue 1972; Fritzell and Thorne 1984). This habit can account for the presence of diurnal organisms like songbirds in their diets. James (1963) believed that nocturnality of microvertebrates in the Cuyama badlands of California, USA, suggested that an owl accumulated the Cuyama fauna, and Worthy and Holdaway (1994) found mostly nocturnal ground-dwelling birds among other small vertebrates in a Quaternary bone deposit in New Zealand, where the only native mammals are bats.

Perhaps the strongest evidence for a specific kind of predator is in the condition and association/dissociation of bones in the House Mountain assemblage at MNA loc. 318. First, all elements of

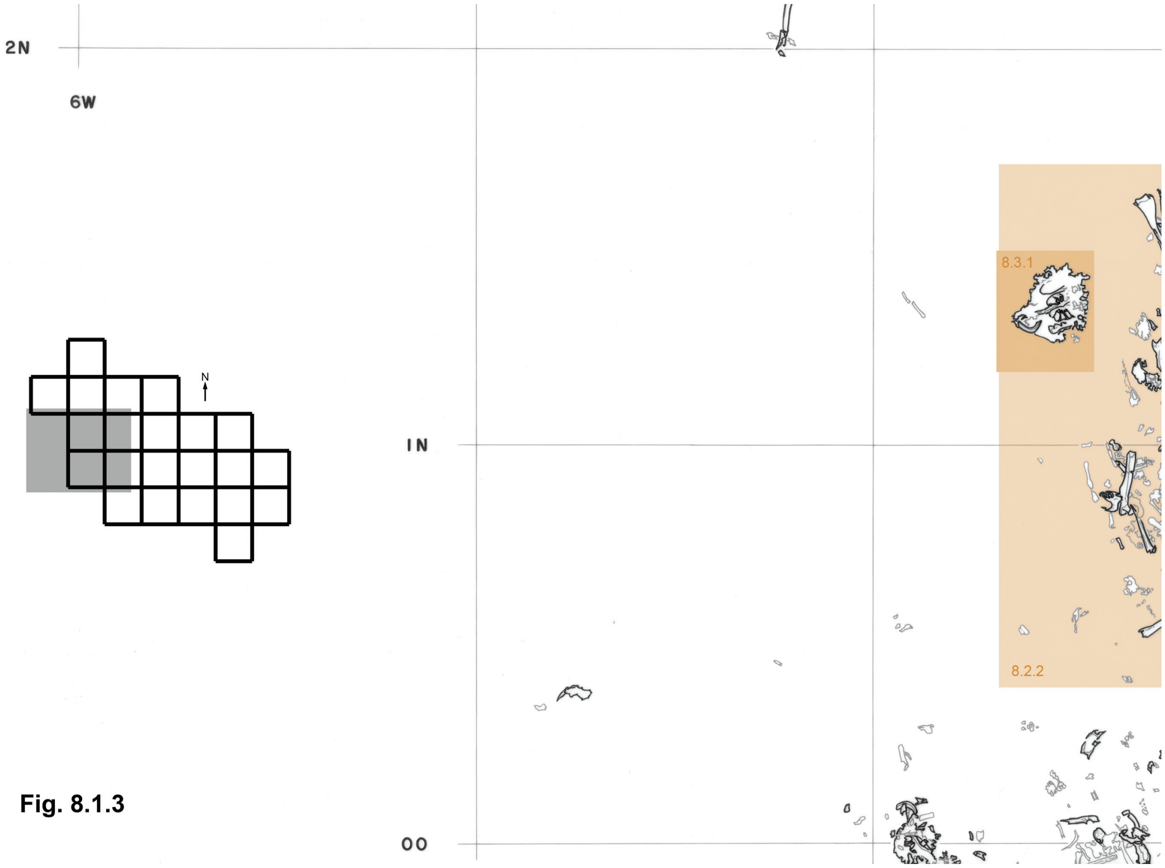

Fig. 8.1.3

FIGURE 8.1.3 (continued).

the skeleton of prey animals, including elements not often recovered in the fossil record, are represented. Second, except for the post-burial fracturing of some elements, the bones are intact including relatively tiny and fragile ones. Third, partial association of skeletal elements originating from individual animals is frequently seen. These three points further help to eliminate diurnal raptors and eliminate mammalian carnivores as the predators responsible for the Verde assemblage, because diurnal raptors and mammalian carnivores typically chew and break up the bones of their prey (Glue 1970; Mayhew 1977; Korth 1979; Andrews and Nesbit Evans 1983). Diurnal raptors also cause considerably more corrosion to bones than owls because their gastric juices are stronger (Duke et al. 1975).

Owls typically do little physical or chemical damage to prey bones (Glue 1970; Mayhew 1977; Dodson and Wexlar 1979). Owls often produce one pellet per prey item (but this varies; see below) and, given the rate at which they hunt and kill prey, they can produce several pellets in a day. During cyclic irruptions in high-latitude populations of arvicoline rodents (voles and lemmings), some owls can gather large numbers of prey very quickly (Hanski et al. 1991, 2001; Klemola et al. 2002; Korpimäki and Norrdahl 1991; Korpimäki et al. 2004). The pellets are usually cast beneath the daytime roost or nest, where large numbers of pellets can accumulate. Sometimes owls cast pellets in their nocturnal hunting grounds, and the pellets may be concentrated at habitual night roosts or scattered. The size and shape of pellets roughly reflect body size and internal anatomy. These characteristics as well as the condition of the contents can be helpful in identifying the producer of modern pellets (Elbroch et al. 2001). When owls eat, their prey is swallowed whole or torn into chunks, which is then swallowed with varying degrees of bone breakage (depending on the species of owl; Elbroch et al. 2001). Large prey may be partly consumed and the uneaten portions cached for later consumption (Forsman et al. 1984). In the proventriculus, flesh and skin are digested but bones, fur, or feathers are usually little corroded and are formed into a pellet that is then spewed onto the ground (Duke et al. 1976; Duke and Rhoades 1977; Rhoades and

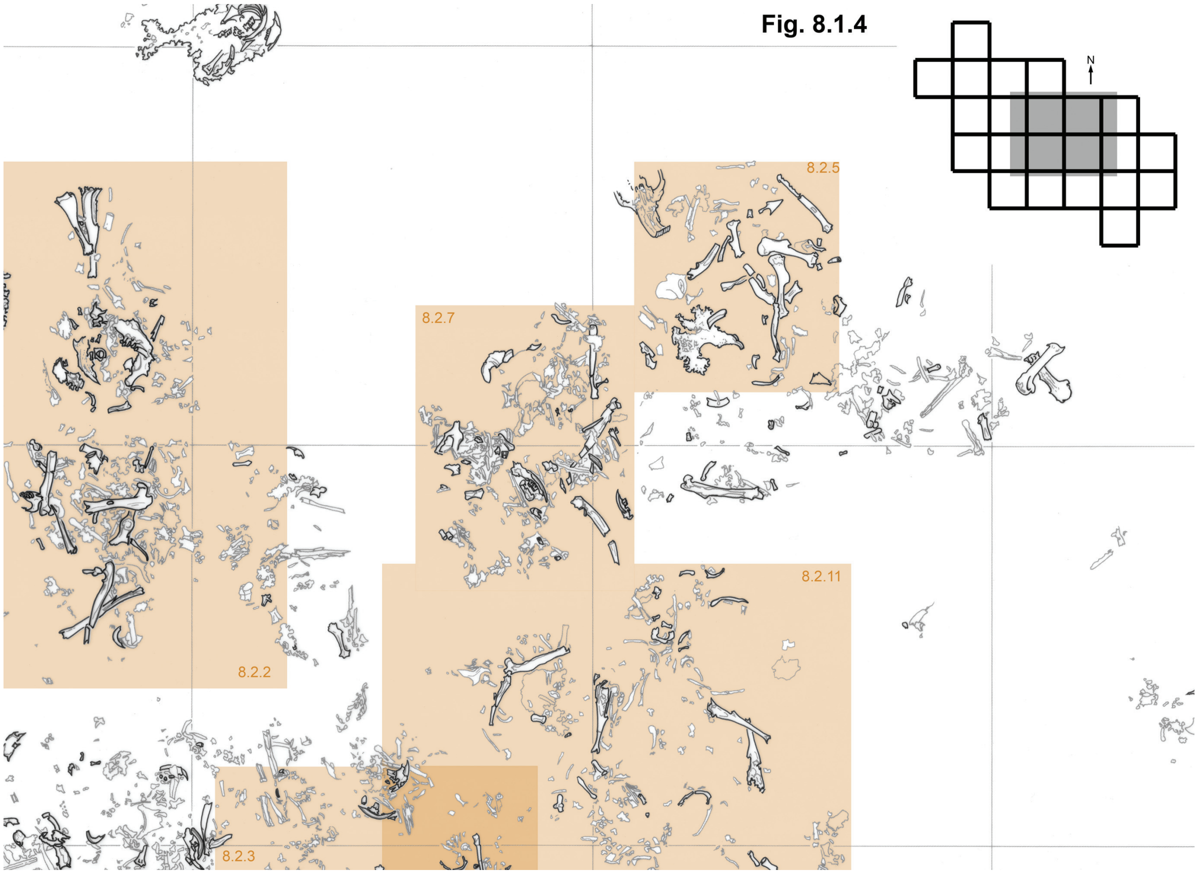

FIGURE 8.1.4 (continued).

Duke 1977). Regurgitated owl pellets often exhibit association of elements from individual prey skeletons unless prey was torn up in order to be swallowed; the degree of breakage also varies between and within owl species (Dodson and Wexlar 1979; Hoffman 1988). Lyman et al. (2003) noted that, as the size of the most abundant mammalian prey taxon in a barn owl pellet decreases, the mean number of individuals per pellet increases, and that larger barn owl pellets contain more individual prey than smaller pellets.

If the pellets lie on open ground for a time, they can be disintegrated by rainfall, wind, and/or by the activities of scavenging insects and other invertebrates, so that the associated bones they contain become dissociated and scattered (Terry 2004). Weather and associated moisture strongly affect the speed with which an owl pellet breaks down, and the enclosed bones become separated (Elbroch et al. 2001). Many of the bones in the modern owl pellet accumulation I examined at Sugarloaf Mountain were also trampled and broken by cattle.

When mammalian carnivores and diurnal raptors eat vertebrate prey, the prey's bones are always broken to a much greater degree than seen in the Verde fossil assemblage, and bones are usually dissociated in the process (Andrews and Nesbit Evans 1983). An exception is the bat hawk (*Macheiramphus alcinus*, Accipitridae) of South Africa, Indonesia, and New Guinea, a unique crepuscular kite that is a dietary specialist preying on bats, swallowing them whole and in rapid succession (Black et al. 1979; H.L. Black, personal commun). As a result of its feeding style few prey bones are damaged, and bat hawks' regurgitation pellets often include nearly intact, fragile dentaries of bats. For the rodents occurring in the House Mountain fossil deposit, every possible skeletal element is represented except hyoids and sternebrae (Tables 3, 4, 5), though not necessarily in the proportions with which they occur in the skeleton. Even tiny elements not often recovered as fossils, but which occasionally are preserved in modern owl pellets, occurred. These include a baculum (Figure 8.2.2) and several middle ear ossicles of *Prodipodomys* (5 mallei and 7 incudes, most of

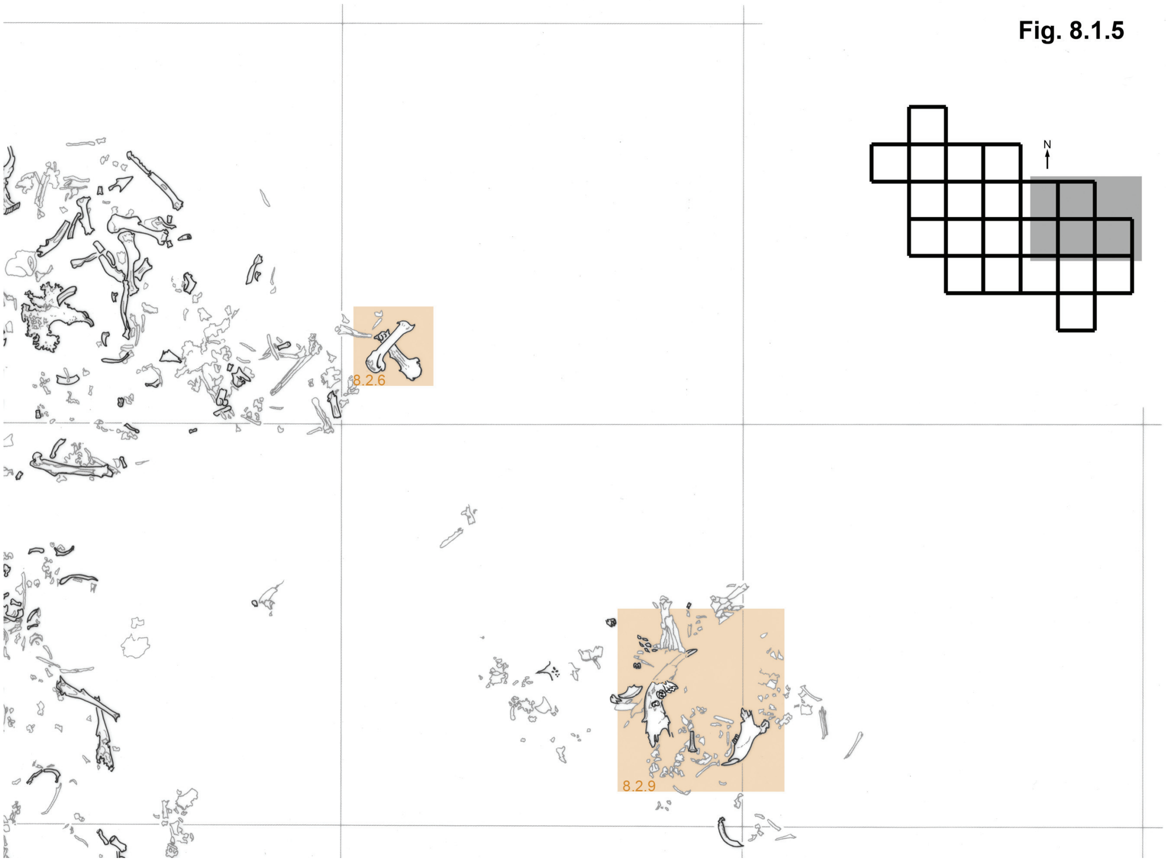

FIGURE 8.1.5 (continued).

which were found in the screenwashed material; e.g., Figure 11, Table 5).

By comparison, in about one liter of the modern barn owl pellets collected near Rodeo, New Mexico, one baculum and one malleus of *Dipodomys spectabilis* were found among the remains of a minimum of three individuals of that species (based on number of skulls, auditory bullae, and dentaries); one baculum and one malleus of *Dipodomys merriami* were recovered among remains of a minimum of nine individuals of that species (based on cranial elements). In addition, at Rodeo, 1 baculum, but no auditory ossicles, were found per four *Chaetodipus hispidus* skulls, and one baculum was found per 26 *Perognathus flavus* right dentaries. No other bacula or auditory ossicles were recovered, even though skeletal elements of a pocket gopher and seven genera of cricetid rodents (among other taxa) occurred.

In modern great horned owl pellets collected near Camp Verde, Arizona, two bacula and one malleus were found per 18 *Dipodomys ordii* crania; one baculum per 17 *Peromyscus* dentaries; one incus per 7 *Thomomys bottae* crania; and one cricetid incus fragment of indeterminate genus from among a total of 47 individuals of *Reithrodontomys*, *Peromyscus*, and *Onychomys*. No bacula or auditory ossicles of *Perognathus* or *Neotoma* were recovered per one and 22 skulls, respectively.

Although most of the House Mountain fossils are isolated bones (disarticulated and dissociated), many examples can be found which represent partial association of elements or partial skeletons from individual animals. In the master taphonomic map (Figure 8.1.1-8.1.8), much of the west half of grid square 2N+1W is occupied by a slightly dissociated anterior appendicular skeleton and skull of a pocket gopher, *Geomys* (*Nerterogeomys*) *minor* (Figure 8.2.5). In this area there is no redundancy of elements, indicating that the anterior half of a single prey animal is preserved.

Additional examples of partial association are evident: In the southwest corner of grid square 2N+00 and northeast half of adjacent grid square 2N+1W are a right and left humerus (Figure 8.2.6), a scapular fragment, right tibiotarsal fragment, right coracoid, right ulna, and premaxilla of a small pas-

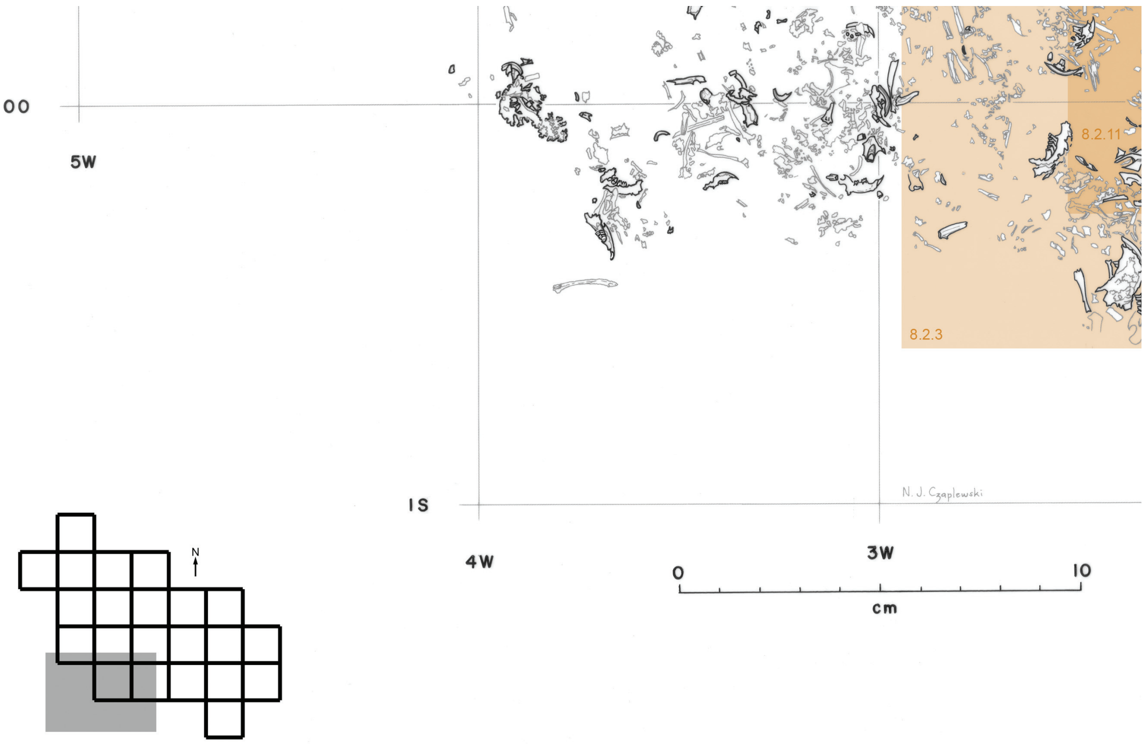

Fig. 8.1.6

FIGURE 8.1.6 (continued).

seriform bird (Emberizidae or Fringillidae). In the southwest corner of grid square 3N+2W is a crushed skull of *Sigmodon* mentioned previously (Figure 8.2.4). It retains both dentaries in articulation and an associated humerus and ulna. In the southeastern corner of grid square 1S+3W is a skull of *Prodipodomys* (Figure. 8.2.1). The well-preserved cranium is associated with a right dentary bearing the incisor and two cheek teeth, and two loose left cheek teeth with tooth wear equivalent to teeth in the cranium.

The partial association of fossil bones in the House Mountain assemblage probably reflects burial after a period of exposure to weathering long enough to cause partial pellet disintegration. Modern owl pellet accumulations in unprotected sites normally include pellets in various stages of disintegration, ranging from freshly cast, intact pellets to completely disintegrated pellets (Figure 5.2).

Age-Frequency of Prey

Prey individuals of different ontogenetic ages are differentially vulnerable to predation by owls (Lay 1974; Longland and Jenkins 1987). Nevertheless, age-frequency profiles are sometimes used to indicate whether a fossil assemblage was the result of catastrophic or attritional death (Voorhies 1969; Shipman 1981; Klein 1982; Korth and Evander 1986; Kos 2003; McFarlane and Blake 2005). Catastrophic death assemblages are those that result from a relatively instantaneous killing that is not age-selective, and all members of a species are likely to be killed equally. An attritional death assemblage is one that is the result of selective death of the most vulnerable individuals of a population (very young and very old).

The age-frequency distributions of *Prodipodomys* based on the data from MNA loc. 318 are shown in Figure 12. Compared to age-frequency profiles for rodents and rabbits provided by Korth and Evander (1986), the House Mountain *Prodipodomys* show an attritional age-frequency distribution based on the representation of juveniles (stage J) and very old individuals (tooth wear stage 5) and on the non-representation of adult category 4 (which is completely absent; teeth at this stage were not recovered). Yet young adults of stages 2 and 3 are the most common as would be expected in a catastrophic assemblage. Thus, the age-frequency distribution of *Prodipodomys* is inconsis-

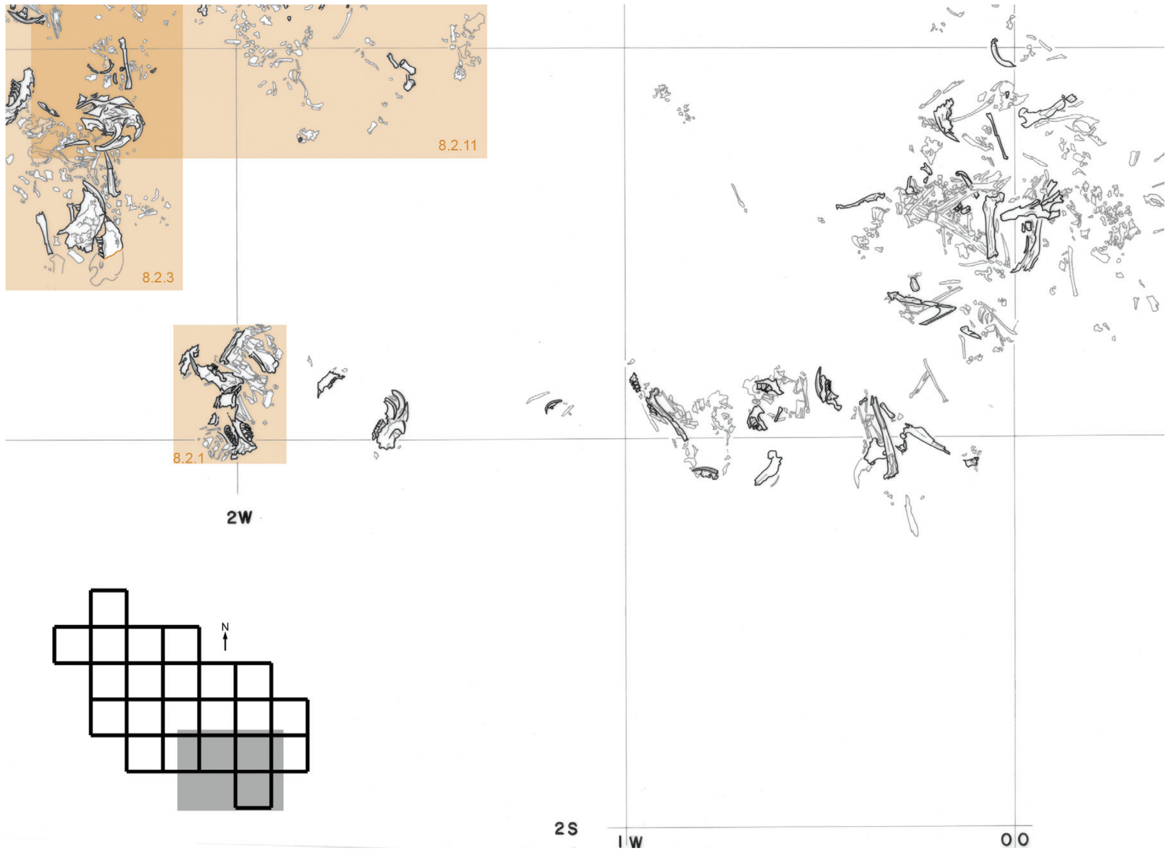

FIGURE 8.1.7 (continued).

tent with other available information for MNA loc. 318 that suggests an owl as the accumulator of the fossils and is equivocal in terms of its utility for demonstrating selective killing in this instance. The reasons for this are not clear but may be related to small sample size or other factors.

Owl Pellets, Owl Diets, and Microvertebrate Fossil Accumulations

As noted above, owl pellets probably are the source of microvertebrate assemblages in many previous studies, especially Pleistocene sites in caves or sinkholes (Mayhew 1977; Walton 1990), although some assemblages may represent scats, pellets, or caches made by other carnivores (Mellett 1974; Mead and Van Devender 1981; Andrews and Nesbit Evans 1983). Owls have a fossil record dating back to the Paleocene, and at least four genera are known in the Pliocene of North America (Brodkorb 1971; Rich and Bohaska 1976, 1981; Walton 1990). Extant owls, Strigidae and Tytonidae collectively, inhabit all land surfaces of the world except for a few oceanic islands and Antarctica. In fact the barn owl, *Tyto alba*, is one of the most widespread of all land bird species (Van Tyne and Berger 1976; Marti et al. 2005). Studies of owl diets using regurgitation pellets have been nearly as widespread as owls themselves (e.g., Cowan 1942; Hawbecker 1945; Anderson and Long 1961; Glue 1967, 1970; Haverschmidt 1970; Buden 1974; Marti 1974; Czaplewski 1976; Herrera and Hiraldo 1976; Mayhew 1977; Thomas and Thomas 1977; Jaksíc and Yañez 1979; Dickerman and Brash 1980; Herrera and Jaksíc 1980; Justo and DeSantis 1982; DeSantis et al. 1983; Baker 1986; Taberlet and Fumagalli 1996; Fernandez-Jalvo et al. 1999; Bilney et al. 2006; Goodman and Griffiths 2006) and are routinely conducted in high school and elementary school classes as basic ecology lessons. Undoubtedly, their wide range and their habit of forming pellets of well-preserved bones have resulted in owls being major contributors to the global fossil record of small vertebrates.

In a study of modern owl pellets decomposing on a forest floor, Terry (2004) noted that as owl pellets disintegrate the skeletal composition changes from a high proportion of small and fragile elements to a high proportion of larger, more robust skeletal elements. She concluded that the small, fragile bones initially are protected within the mat-

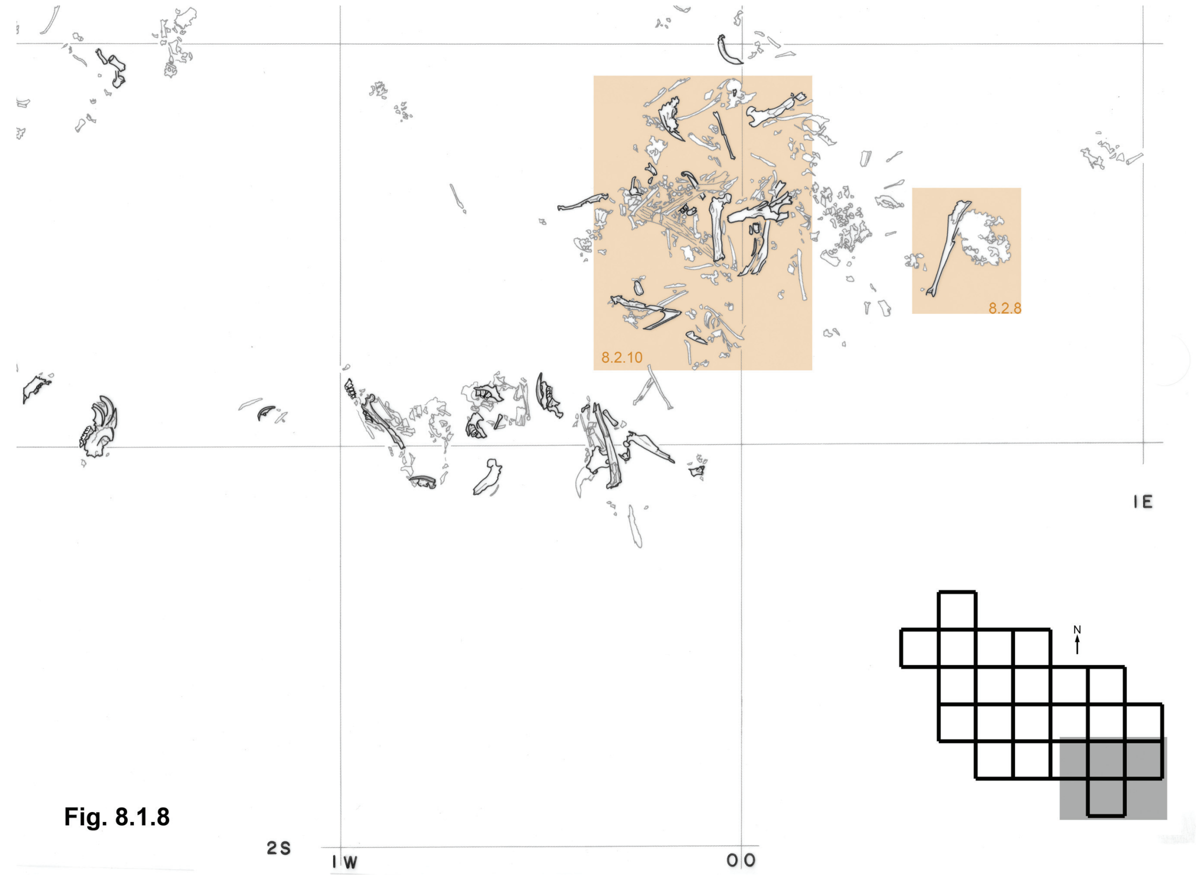

Fig. 8.1.8

FIGURE 8.1.8 (continued).

ted hair of the regurgitated pellet but, as they become exposed by physical and chemical weathering on the ground, their previous etching and pitting in the owl's digestive tract makes them more prone to fragmentation and disappearance than the larger bones. Dodson and Wexlar (1979) calculated the proportional representation of skeletal elements in pellet-derived bone concentrations from pellets of captive owls. I tried to repeat their methods with field data for modern and fossil owl pellets, and found a greater loss of information under the less ideal and older circumstances in the fossil deposit. A larger proportion of the bones were broken, possibly due to trampling by large hoofed mammals (although there is yet no evidence of this in the fossil record), or weathering, or perhaps greater breakage by the owls. In the House Mountain assemblage, post-burial crushing has rendered species identification of most postcranial elements difficult or impossible.

The breakage also made it difficult to accurately estimate the actual number of bones present. Instead of a count of complete (intact) elements, I counted a number of identifiable specimens (NISP), fragmented and intact. As a basis for comparison, I counted the minimum number of individual (MNI) rodents indicated by the most numerous element, maxillae, dentaries, or cheek teeth. The percentage present (percent representation) expresses the proportion of individual specimens present relative to the potential or expected number of intact bones (NIb) per rodent skeleton (Table 5). Very few elements in the House Mountain fossil accumulation were complete due to postdepositional flattening and breakage. As a result, in both the disintegrated modern pellets and the microvertebrate fossils, the NISP often is excessive relative to the potential Nib because of multiple fragmentation of a given element (Table 3 gives percentages of intact quarried elements at House Mountain). Thus, a single incisor broken four times would give an NISP = 5, overestimating the expected NIb by 500 percent.

As widespread organisms, the dietary diversity of owls is variable. For barn owls, it is highly variable among different continents and localities (Jaksíc 1983), even more so than in other owl species investigated. In a study of 107 previously pub-

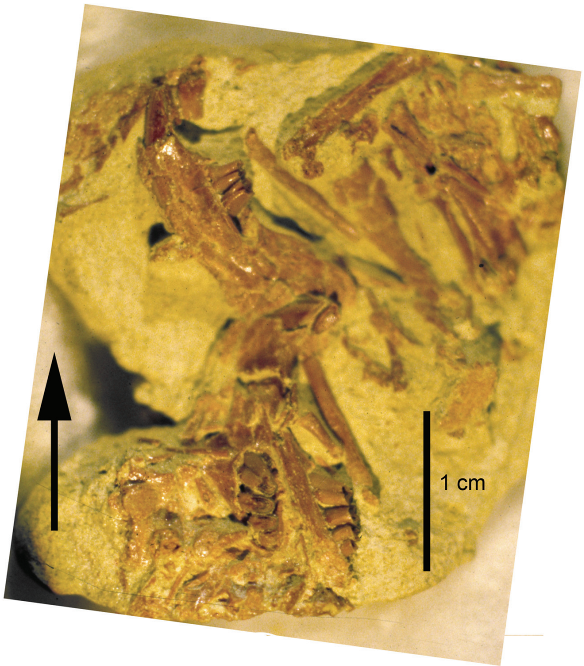

FIGURE 8.2.1 (continued).

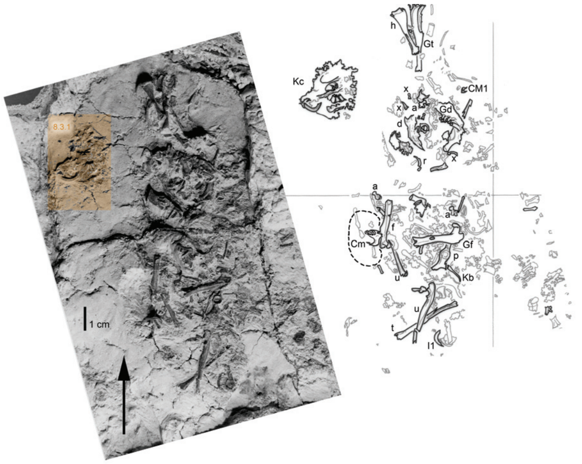

FIGURE 8.2.2 (continued). Area in the south half of 1N+4W and northeast corner of 00+4W showing a *Geomys minor* dentary (Gd), tibia (Gt), and femur lacking the distal epiphysis (Gf), cricetid maxilla and loose molars (Cm; shown on map but it had been removed before the photograph was made. There is now a small hole in the matrix where the maxilla had been, represented by a dashed line in the key.), cricetid M1 (CM1; also removed), *Prodipodomys* baculum (Kb), and cranium (Kc; see also Figure 8.3.1), rodent astragali (a),dentary (d), femur (f), humerus (h), incisor (I1), innominate (p), phalanges (x), rib (r), tibia (t), ulnae (u), and other bones. Click on the orange rectangle to see a close-up of that area.

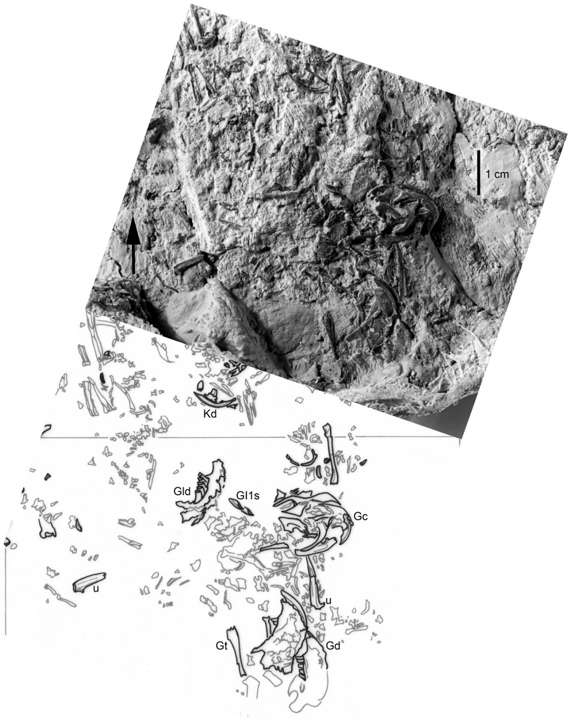

FIGURE 8.2.3 (continued). Area in the north half of 1S+3W and south-central portion of 00+3W showing *Geomys minor* partial cranium (Gc), left and partial right dentaries (Gd), an additional left dentary (Gld), tips of a pair of I1s (GI1s), tibia (Gt), ulnae (u), and a *Prodipodomys* dentary with i1 and p4 (Kd), as well as other bones.

lished collections of North American barn owl pellets, Lyman et al. (2003) noted that the generic richness of mammalian prey increases as the number of prey and number of pellets increases. Does the House Mountain assemblage (Table 1) reflect the entire range of prey species in the diet of the hypothetical fossil owl? For the 0.25 m^2 mapped in Figure 8, three different species-area curves were generated by randomly selecting 10 cm x 10 cm grid squares and plotting the cumulative number of taxa encountered. One example is shown in Figure 13. The species-area curve has not yet reached a plateau, suggesting that not all potential prey items have been preserved in the small mapped area. Four additional taxa that were not present in the quarried area were recovered by screenwashing of the same bedding plane confirm this pattern. In the quarried and mapped area, body sizes ranged from the smallest, a harvest mouse (*Reithrodontomys* cf. *R. wetmorei*) to the largest, a woodrat (*Neotoma vaughani*). As mentioned previously, fossils recovered by screenwashing include still

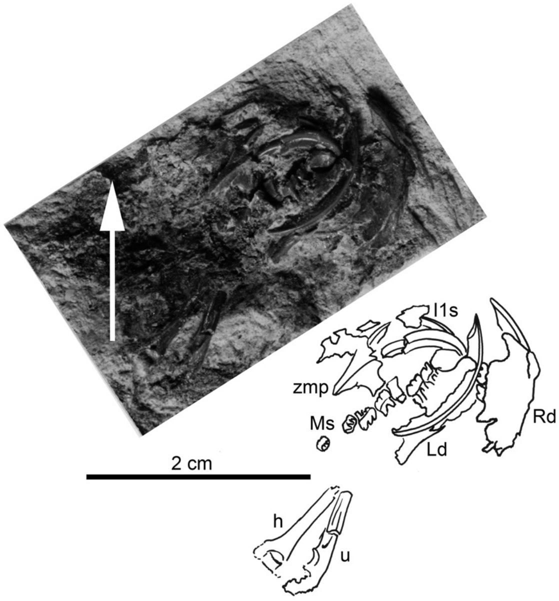

FIGURE 8.2.4 (continued). **FIGURE 8.2.4.** Crushed contents of a single fossil owl pellet containing the remains of a cotton rat (*Sigmodon minor*). Most of the cranium and possibly postcranial bones seem to have been crushed and appear as "bone hash" (area behind and beside the arrow) except for a partial rostrum with zygomasseteric plate (zmp), upper incisors (I1s), and upper molars (Ms), and associated left and right dentaries (Ld, Rd), humerus (h), and ulna (u). No other bones were found within a few cm of this group. Arrow points northward.

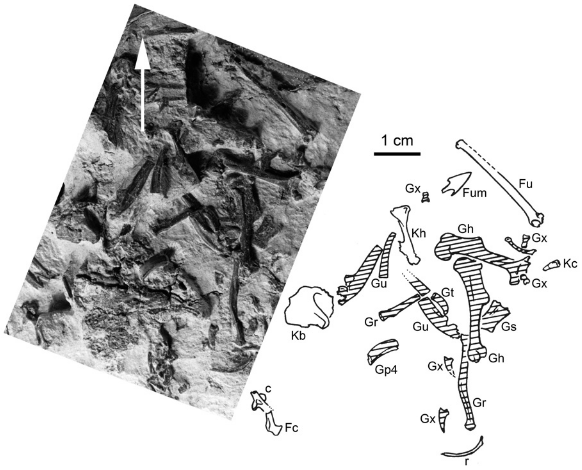

FIGURE 8.2.5 (continued).Section of the microvertebrate deposit at MNA locality 318 containing much of the anterior appendicular skeleton of a pocket gopher, *Geomys* (*Nerterogeomys*) *minor*. Gopher bones and teeth are shaded in the key and include a p4 (Gp4) and another cheek tooth (Gt), a scapular head (Gs), right and left humeri (Gh), ulnae (Gu), and radii (Gr), and several stout phalanges (Gx). In addition, another molar, the dorsal portion of a cranium with both I1s, and four more stout phalanges also belonging to the pocket gopher are not in this photograph but occurred adjacent to the area shown. Also visible in the area shown are a finch upper mandible (Fum), ulna (Fu), and partial coracoid (Fc), a *Prodipodomys* humerus (Kh), auditory bulla (Kb), and cheek tooth (Kc), a rodent calcaneus (c), and a mammal rib (r). Arrow points northward.

smaller taxa (shrew and salamander), but no species larger than woodrats.

Body Size of the Hypothetical Owl Implicated in the House Mountain Assemblage

Surprisingly, the remains of rabbits are lacking in the House Mountain assemblage, which contrasts with their occurrence at most other vertebrate fossil localities in the Verde Formation. Modern owls large enough to eat rabbits do so regularly (Earhart and Johnson 1970) and even 150 g burrowing owls were recorded to eat cottontails (Marti 1974). By analogy with extant owls, the presence of only adults of the largest prey species (*Neotoma vaughani*) suggests that the owl(s) could have preyed on juveniles of larger species (i.e., rabbits). In a Pleistocene agglomeration of bones from owl pellets in Argentina, Tonni and Fidalgo (1983) found mostly the remains of juveniles of the larger micromammals associated with adults of smaller micromammals. Young rabbit remains may possibly yet be found in the House Mountain

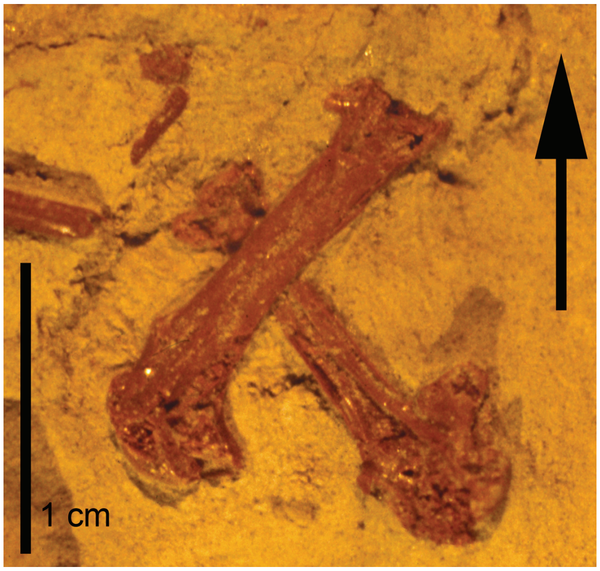

FIGURE 8.2.6 (continued). Crossed humeri of a small passeriform bird near the southwest corner of grid square 1N+1W. Arrow points northward.

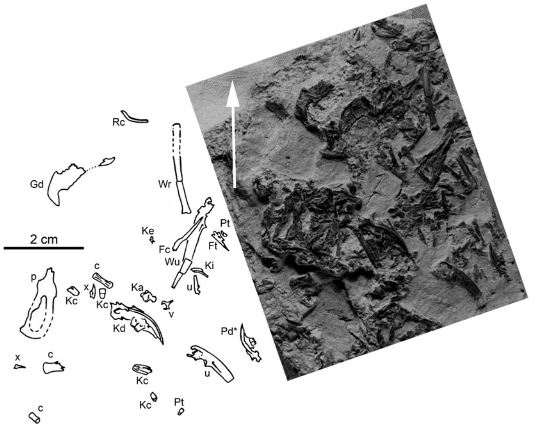

FIGURE 8.2.7 (continued). Close-up photograph and key identifying certain elements in a small portion of a Pliocene microvertebrate bone accumulation quarried from the Verde Formation at House Mountain, Arizona. c, caudal vertebra; Fc, finch coracoid; Ft, finch tarsometatarsus; Gd, pocket gopher (*Geomys minor*) dentary; Kc, kangaroo rat (*Prodipodomys idahoensis*) cheek tooth; Ke, kangaroo rat incus; Ki, kangaroo rat incisor; Ka, kangaroo rat astragalus; Pd*, pocket mouse dentary (this dentary is the holotype for *Perognathus strigipredus*, within a small block of matrix and bones cataloged as MNA V5142; Czaplewski 1990); Pt, pocket mouse tooth; p, pelvis; Rc, rodent clavicle; u, ulna; v, thoracic vertebra; Wr, woodrat (*Neotoma vaughani*) radius; Wu, woodrat ulna; x, ungual phalanx. Arrow points northward. Same view and block as in Figure 4.

deposit; the species-area curve supports this possibility.

Earhart and Johnson (1970) provided a summary of food habits and body masses of several North American owls. The body mass of the largest prey species increases with the body mass of the owl (Figure 14). Using Martin's (1984) equation for the relationship between first lower molar length and body mass in cricetine rodents, Pliocene woodrats from House Mountain weighed between 154 and 177 g. If this body mass is eye-fitted into the trend in Figure 14, it gives an approximation of the body mass of the owl between 100 and 400 g.

House Mountain Microvertebrates and Paleoecology

In the House Mountain assemblage, the microvertebrate taxa broadly reflect the putative Pliocene wetlands, grasslands, and open savanna suggested for the Verde Formation by earlier authors (Nations et al. 1981; Table 6). Based on habitat-selection similarities with phylogenetically related taxa, the unidentified shrew and red bat (*Lasiurus* cf. *L. blossevillii*; Czaplewski 1987b) could have utilized wetlands and riparian gallery forest, as well as "edge" habitats transitional between forest and grassland. *Sigmodon* spp. are grazing rodents common in grasslands and oak-savanna-grasslands of southwestern North America today, and the fossil species and *Prosigmodon* likely were also. The other small vertebrate taxa do not conflict with the other hypothesized paleocommunity types at MNA loc. 318. However, pollen and sedimentologic data from this locality provide better sources of vegetational information (Nations et al. 1981) for this portion of the Verde Formation. For example, pollen analysis of the Verde Formation sediments by Hevly (in Nations et al. 1981) previously revealed the presence of deciduous gallery forest along the lake edge and inflowing streams—possibly owl pellets were cast from a roost in a lakeside sycamore, cottonwood, or other tree. More detailed information from the vertebrate paleocommunity, however, depends on the recovery of larger samples or additional equivalent-aged samples of fossils, or possibly on studies of stable isotopes in the sediments or fossils.

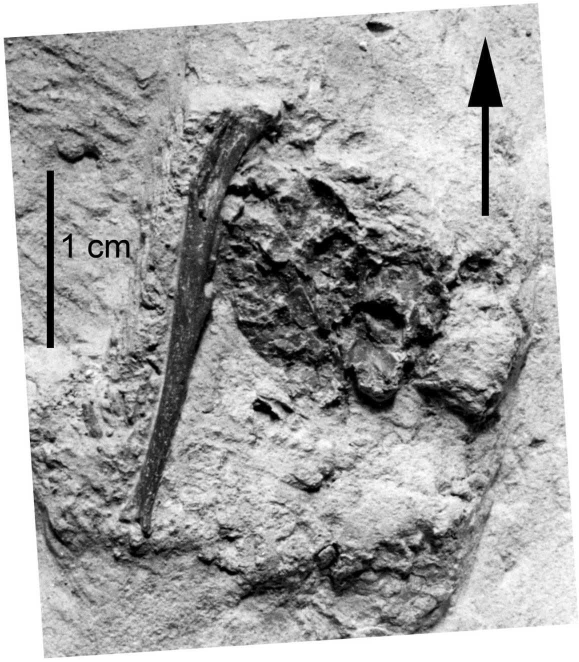

FIGURE 8.2.8 (continued). *Prodipodomys* tibia and possible crushed auditory bulla near the center of grid square 1S+00. In modern *Dipodomys* skulls found in owl pellets, the auditory bullae frequently become disarticulated from the other cranial bones.

The nearest vertebrate locality in the Verde Formation, both stratigraphically and horizontally, to MNA loc. 318 is MNA loc. 319. MNA 319 is 1.5

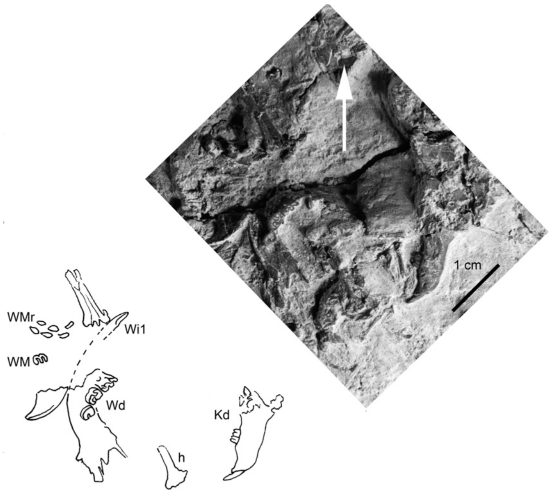

FIGURE 8.2.9 (continued). An area in the southeast corner of 2S+00 and southwest portion of 00+00 showing parts of a woodrat *Neotoma vaughani.* The right dentary (Wd) is broken and missing its diastemal region where there is a large crack in the block, but the tip of the lower incisor (Wi1) is present as well as all three heavily worn lower molars. Nearby are *Neotoma* upper molars visible in this view only by their exposed roots (WMr) and the natural impression of the occlusal surface of an upper molar that was previously removed (WM), hence the tooth does not show in the photograph. After this photograph was made, the *Neotoma* dentary and teeth were removed from the block and prepared separately to better expose the wear surfaces of the upper molars for study; these specimens serve as the holotype for *Neotoma (Paraneotoma) vaughani* (MNA V4885; Czaplewski 1990). Also visible are a *Prodipodomys* left dentary (Kd) and a probable rodent distal humerus (h).

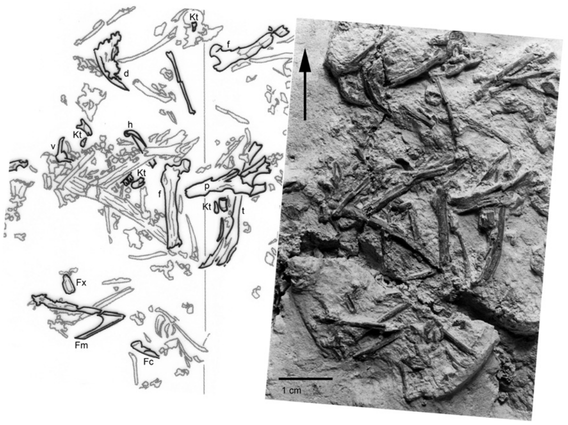

FIGURE 8.2.10 (continued). Area in the east half of grid square 1S+1W and west edge of 00+1E showing a finch mandible (Fm), manual phalanx (Fx), and partial coracoid (Fc), several *Prodipodomys* cheek teeth (Kt), humerus (h), innominate (p), femur (f), tibia (t), and proximal caudal vertebra (v), and a rodent dentary with i1 (d).

km from 318 (Czaplewski 1987b); paleomagnetically, MNA 319 is just below the base of the Nunivak normal polarity zone (Bressler and Butler 1978; now chron C3n.2n of Berggren et al. 1995; Bell et al. 2004), about 4.62 million years old, or roughly 300,000 years older than MNA loc. 318. The vertebrate assemblage from MNA 319 differs in some taxa from that of 318 and includes Leporidae, *Prodipodomys idahoensis*, *Postcopemys* n. sp. (Lindsay and Czaplewski, this volume), *Sigmodon minor*, *Neotoma (Paraneotoma) vaughani*, *Ogmodontomys* cf. *poaphagus*, a second indeterminate arvicoline, and *Bassariscus* sp. (Czaplewski 1990). Most of these taxa are rare except for *Ogmodontomys*. Perhaps this assemblage reflects the biases inherent in the diet of a different predator (the ringtail, *Bassariscus*?), as well as a different time period, but with partial overlap of prey selection and habitat selection in that *Prodipodomys*, *Postcopemys*, *Sigmodon*, and *Neotoma* are shared between the two localities.

Time-Averaging

The phenomenon of time-averaging is often a consideration in taphonomic studies of vertebrate fossil accumulations. Assemblages of mammal bones by predators are generally considered to represent durations from 10^{-1} to 10^{2} years (Behrensmeyer and Chapman 1993). It seems possible that suitable roosting and nesting sites could be at a premium for owls, and particularly good sites might be used for many generations. With respect to the duration of modern owl pellet accumulations, some investigators have revisited a site to collect owl pellets on occasions up to 46 years apart, which presumably was continuously occupied by the owls during that interval (Kittredge et al. 2006; Marti 1973; Baker 1986). Conceivably, owls might occupy a favorable site and accumulate prey remains for months to tens or even hundreds of years. One of the modern owl roosts sampled for this study showed a sizeable accumulation of prey-animal bones in the 1980s (Figures 5, 6); however, bones were virtually absent, and this roost had been abandoned when revisited in 2007, possibly due to the construction of a resort nearby and increased human activity in the formerly remote area. Not surprisingly, the density of bones at the modern sites visited varied across the ground surface beneath the roosting cliff, along which many different perches were available. Terry (2004)

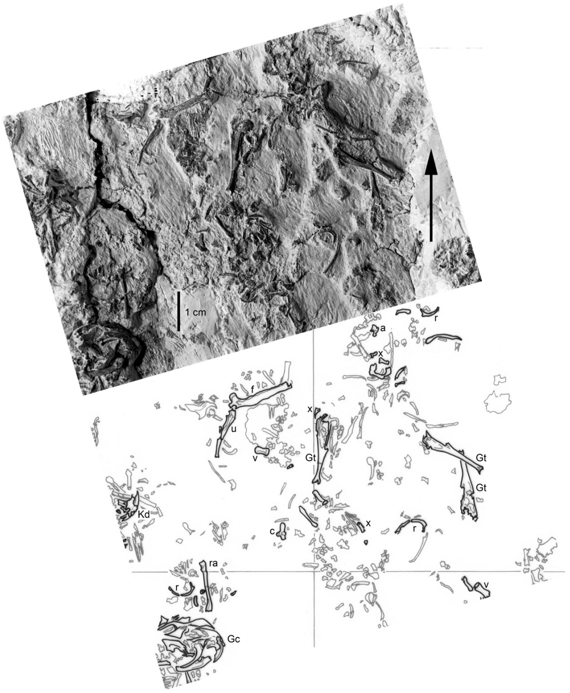

FIGURE 8.2.11 (continued). Area in the southeast corner of 00+3W, southwest portion of 00+2W, and northeast portion of 1S+3W showing *Geomys minor* partial cranium (Gc; the same one as seen in Figure 8.2.3) and three tibiae (Gt), *Prodipodomys* partial dentary (Kd), and rodent astragalus (a), calcaneus (c), femur (f), phalanges (x), radius (ra), ribs (r), ulna (u), and vertebrae (v).

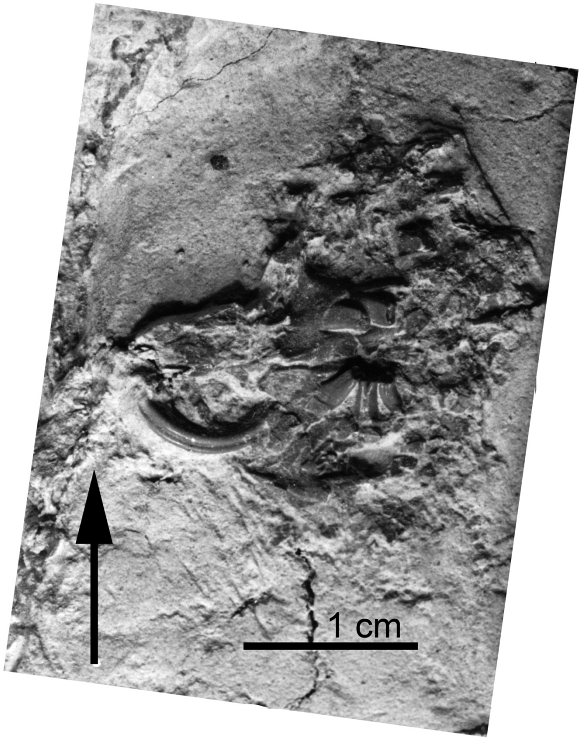

FIGURE 8.3.1 (continued). *Prodipodomys idahoensis*, ventral aspect of cranium. Crushing has forced the maxillary tooth rows inward; the upper incisor has slipped from its alveolus. Located at center of grid square 1N+4W. Arrow points northward.

showed that the density of skeletal elements derived from owl pellets decreases with the distance from the base of a roost tree. In the very small area (approximately one-fourth of a square meter) of the fossiliferous bedding plane quarried and mapped at House Mountain, the density of fossil bones varied from none in some grid squares to full coverage in other grid squares. It is impossible to know the distance from a conjectural owl roost and whether or not bone density in this area is representative of the entire (unquarried and unscreenwashed) microvertebrate deposit. However, the available evidence indicates that the deposit represents a time-averaged duration within the same range (months to hundreds of years) as other predator-accumulated assemblages noted by Behrensmeyer and Chapman (1993). Because the fossiliferous deposit is virtually restricted to one thin bedding plane, with very few microvertebrate bones found by screenwashing the strata immediately above and below it, the deposit might represent a relatively short-term (10^{-1} to 10^{1} years) accumulation of bones followed by sedimentary burial of the bones and pellets and abandonment of the local roost by the owl.

CONCLUSIONS

Taphonomic studies of modern owl pellets are common, but few investigators have directly applied these methods and conclusions to specific open-air fossil deposits. In this study, quarrying blocks of matrix followed by preparing the microvertebrate bones in a single bedding plane provided taphonomic evidence that was lost when screenwashing was used as the sole method of recovering fossils. Several lines of evidence suggest that the microvertebrate assemblage the Verde Formation at House Mountain, Arizona, MNA loc. 318, represents an accumulation of owl pellets deposited at the edge of the ancient Lake Verde on dry land or perhaps in shallow water at the lake's edge. Weathering of the pellets prior to burial probably was limited to relatively brief exposure to invertebrate activity, rainfall, or slight wave action in shallow water that was sufficient to disintegrate the pellets but not sufficient to completely

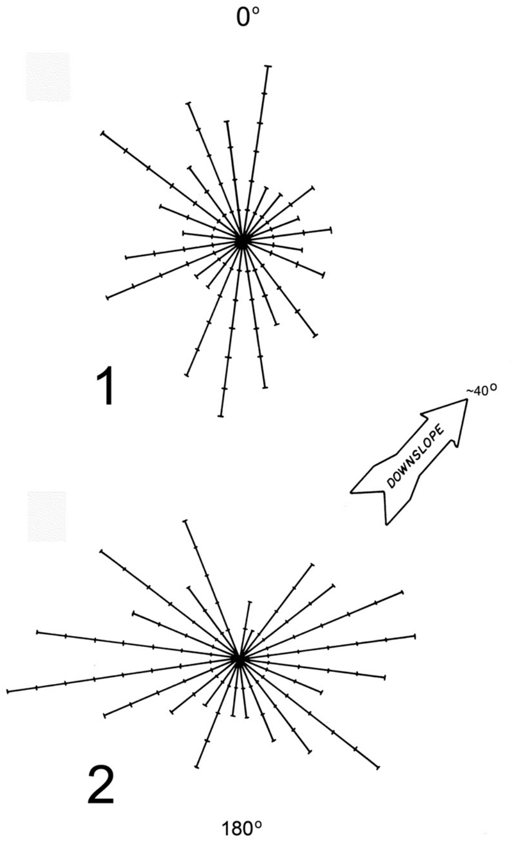

FIGURE 9. Circular histograms of the trend (directional orientation) of long bones: 9.1, for microvertebrate fossils from MNA locality 318, Verde Formation (N = 82); 9.2, for prey remains in a modern accumulation of great horned owl pellets (N = 95).

dissociate some skeletal elements of individual prey animals. During or after burial, bones were crushed in place by sediment compaction with little or no additional separation of the bone fragments. When the sediments were screenwashed, fragments of crushed bones were separated or lost and thus information on the partial association of skeletal elements was lost, by contrast with the quarrying technique. Therefore, if the recovery of taphonomic data is a prime concern in working a microvertebrate locality, field recovery methods should not be limited to underwater screening only, and much more time for preparation will be necessary.

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F.R. Twenter originally discovered and collected microvertebrates at House Mountain locality MNA 318 in the late 1950s. He provided these specimens to me in 1985 and they were placed in the MNA collection. I thank W.R. Downs for expertly and painstakingly preparing most of the blocks of matrix and a number of other specimens, and for the use of his screenwashing equipment at the Museum of Northern Arizona, Flagstaff. My wife C.D. Czaplewski ably and cheerfully helped collect fossils and modern owl pellets and data. K.P. Dial, L.L. Jacobs, and R.M. Warner also helped with fieldwork, especially plaster-jacketing and collecting the largest block of fossils amid clouds of biting juniper gnats. K. Davies helped examine and rephotograph field localities in 2007. D. Gillette and J. Gillette provided access to the MNA collection as well as help with rephotographing specimens and hospitality. G.C. Bateman directed me to the largest modern owl pellet accumulation and provided discussion and comments on an earlier version of the manuscript. P. Fisher, R. Burkhalter, and P.D. Polly kindly advised me about preparing electronic images from my original maps and photographs. I benefited from discussions with, and/or critical readings of, an early version of the manuscript by H.L. Black, D. Elliott, S.D. Emslie, J. Ganey, J.M. Marzluff, J.I. Mead, and T.A. Vaughan. Additional constructive criticism came from C. Bell, C. Jass and an anonymous reviewer. Finally, this paper is dedicated to the memory of Charles A. Repenning, who helped me in many ways with work on the Verde Formation and other studies that I did as a naïve young graduate student, like he did so many other students and colleagues. Rep was a teacher, scholar, POW survivor, warrior, and gentleman to the end. Thanks, Rep.

FIGURE 10. A Gila monster (*Heloderma suspectum*) scat, from a captive animal. Florida Canyon, Santa Rita Mountains, Arizona.

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TABLE 3. Total numbers of recognizable mammalian fossils recovered at MNA locality 318.

	Quarried Specimens				
Skeletal element	**N**	**Number complete (unbroken)**	**Percent complete**	**Screened specimens**	**Total**
cranium	17	0	0.0	8+	25
malleus	1	0	0.0	5	6
incus	1	1	100.0	4	5
dentary	46	18	52.9	17	63
isolated incisor	12	2	16.7	212	224
isolated premolar/molar	58	49	84.5	182	240
deciduous premolar	0	0	0.0	2	2
vertebra	24	9	37.5	156	180
rib	6	0	0.0	6	12
baculum	1	1	100.0	1?	2?
scapula	1	0	0.0	7	8
clavicle	2	1	50.0	0	2
humerus	14	6	42.9	17	31
radius	7	3	42.9	12	19
ulna	17	9	52.9	48	65
pelvis	3	0	0.0	22	25
femur	11	1	9.1	51	62
patella	0	0	0.0	1	1
tibiofibula	12	2	16.7	31	43
astragalus	6	6	100	15	21
calcaneus	3	3	100	26	29
carpal/tarsal	0	0	0.0	27	27
metapodial	7	4	57.1	108	115
phalanx	34	33	97.1	120	154
total	283	148	52.3	1078	1361

TABLE 4. Total numbers of recognizable avian fossils recovered at MNA locality 318.

Skeletal element	Quarried specimens N	 Number complete	Screened specimens	Total
cranium				
(premaxilla)	1	0	0	1
(quadrate)	1	1	3	4
mandible	2	0	0	2
scapula	1	0	0	1
coracoid	5	0	2	7
humerus	3	2	0	3
ulna	1	1	2	3
manual phalanx	1	1	0	1
tibiotarsus	1	0	0	1
tarsometatarsus	1	0	0	1
total	17	5	7	24

TABLE 5. Representation of rodent (other taxa not included) skeletal elements in a modern and a fossil owl pellet accumulation collected from approximately equal areas (0.25 m2; see text). MNI is estimated from a count of cranial elements (maxillae), dentaries, and cheek teeth.

		Modern Owl Pellets (MNI=56)		
Skeletalelement	**Nib per skeleton**	**Expected Nib**	**Observed NISP**	**% Representation**
cranium	1	56	318	567.9
dentary	2	112	108	96.4
cheek teeth	16[a] 12[b]	784[d]	290	37.0
incisor	4	224	210	93.7
malleus	2	112	4	3.6
incus	2	112	5	4.5
vertebra	56	3136	1325	42.2
rib	26	1456	431	29.6
sternebra	6	336	28	8.3
baculum[e]	0.5	28	7	25.0
scapula	2	112	73	65.2
clavicle	2	112	40	35.7
humerus	2	112	149	133.0
radius	2	112	103	92.0
ulna	2	112	127	113.4
pelvis	2	112	166	148.2
femur	2	112	135	120.5
patella	2	112	13	11.6
tibiofibula	2	112	157	140.2
astragalus	2	112	116	103.6
calcaneus	2	112	150	133.9
carpal/tarsal[c]	26	1456	51	3.5
metapodial	20	1120	596	53.2
phalanx	56	3136	518	16.5

[a] geomyoids

[b] cricetids

[c] other than calcaneus and astragalus

[d] based on a mean of 14 cheek teeth per rodent skull

[e] expected numbers of bacula per skeleton is based o n a 1:1 sex ratio

TABLE 5 (continued)

	Pliocene Owl Pellets					
	Quarried Specimens (MNI=16)			Screened Specimens (MNI=15)		
Skeletal element	Expected Nib	Observed NISP	% Representation	Expected Nib	Observed NISP	% Representation
cranium	16	17	106.2	15	8	53.3
dentary	32	16	143.7	30	17	56.7
cheek teeth	224	58	25.9	210	184	87.6
incisor	64	12	18.7	60	212	353.3
malleus	32	1	3.1	30	5	16.7
incus	32	1	3.1	30	4	13.3
vertebra	896	24	2.7	840	156	18.6
rib	416	6	1.4	390	6	1.5
sternebra	96	0	0.0	90	0	0.0
baculum[e]	8	1	12.5	7.5	1?	13.3
scapula	32	1	3.1	30	7	23.3
clavicle	32	2	6.2	30	0	0.0
humerus	32	14	43.7	30	17	56.7
radius	32	7	21.9	30	12	40.0
ulna	32	17	53.1	30	48	160.0
pelvis	32	3	9.4	30	22	73.3
femur	32	11	34.4	30	51	170.0
patella	32	0	0.0	30	1	3.3
tibiofibula	32	12	37.5	30	31	103.3
astragalus	32	6	18.7	30	15	50.0
calcaneus	32	3	9.4	30	26	86.6
carpal/tarsal[c]	416	0	0.0	390	27	6.9
metapodial	320	7	2.2	300	108	36.0
phalanx	896	34	3.8	840	120	14.3

[a] geomyoids

[b] cricetids

[c] other than calcaneus and astragalus

[d] based on a mean of 14 cheek teeth per rodent skull

[e] expected numbers of bacula per skeleton is based o n a 1:1 sex ratio

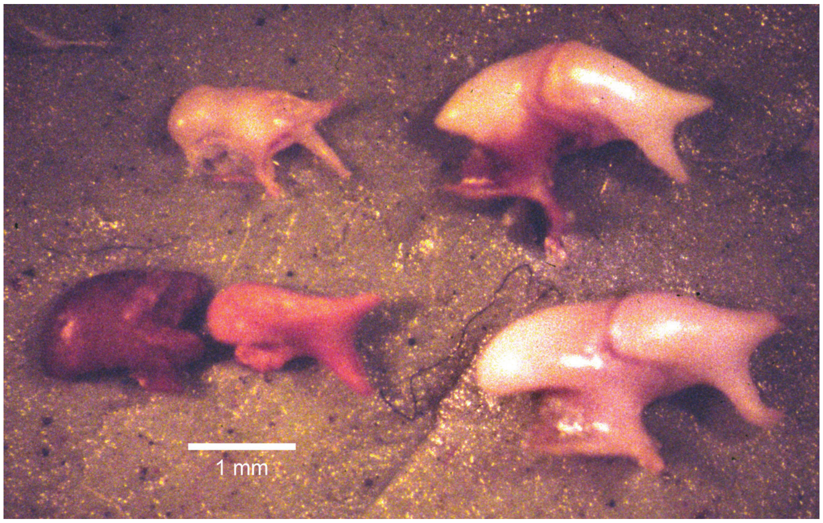

FIGURE 11. Middle ear ossicles (left malleus and incus) dissected from the skulls of several heteromyids compared with fossil ossicles of *Prodipodomys*. At upper left, modern *Chaetodipus intermedius*; upper right, modern *Microdipodops pallidus*; lower left, Pliocene *Prodipodomys idahoensis* from MNA locality 318; lower right, modern *Dipodomys merriami*. The ossicles are articulated in the modern specimens.

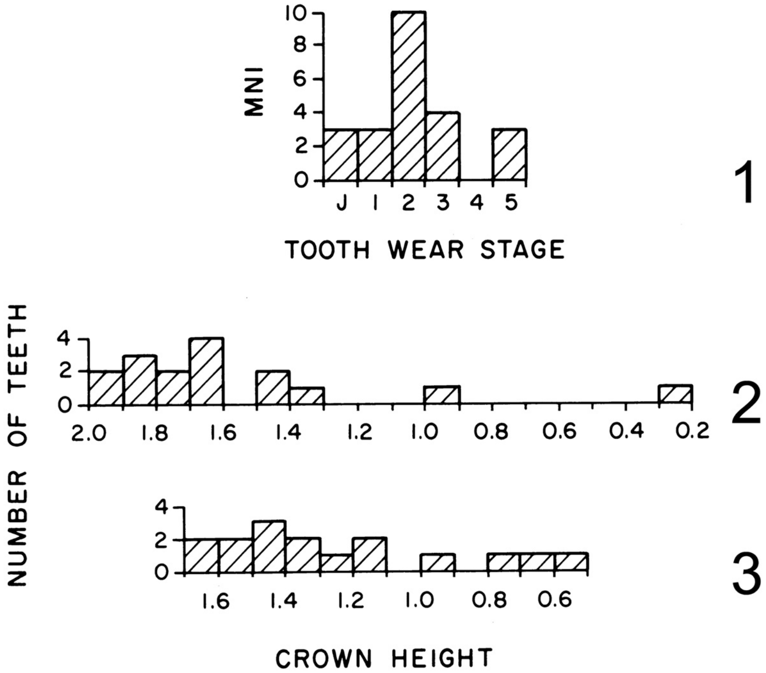

FIGURE 12. Age-frequency distribution of *Prodipodomys idahoensis* at MNA locality 318: 12.1, based on minimum number of individuals represented by dP4 and P4 in each of six arbitrary tooth-wear stages; 12.2, based on labial crown height of P4s; 12.3, based on lingual crown height of p4s. MNI = minimum number of individuals.

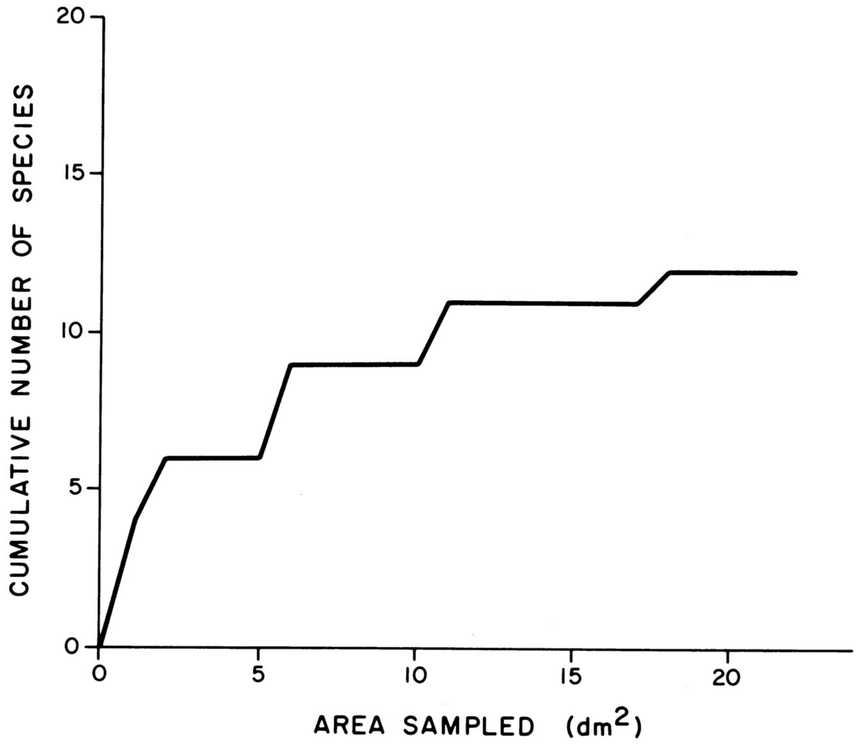

FIGURE 13. Species area curve for a randomly selected sequence of 22 grid squares (each amounting to one square decimeter, or 100 cm2) from the taphonomic map (Figure 8) for MNA locality 318.

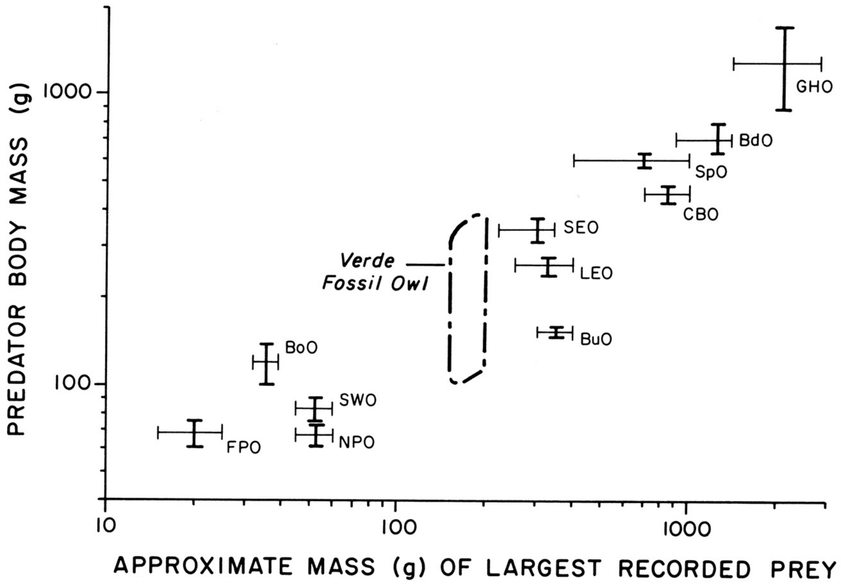

FIGURE 14. Relationship between mass of predator and mass of largest recorded prey in several North American species of owls. Range of body mass includes smallest mean male and largest mean female weights for one or more subspecies of each species presented by Earhart and Johnson (1970). Prey records are from Earhart and Johnson (1970), Marti (1974), and Forsman et al. (1984). FPO, ferruginous pygmy owl; NPO, northern pygmy owl; SWO, saw-whet owl; BoO, boreal owl; BuO, burrowing owl; LEO, long-eared owl; SEO, short-eared owl; CBO, common barn owl; SpO, spotted owl; BdO, barred owl; GHO, great horned owl. Approximate body mass of largest species (woodrat, *Neotoma*) in the House Mountain microvertebrate assemblage is 154-177 g; a body mass of ca. 100-400 g is predicted for the Verde fossil owl (dashed oval). Note logarithmic scales.

TABLE 6. Paleohabitats plausibly occupied by small vertebrate taxa at MNA locality 318, based on habitat selection by living relatives. Available plant paleocommunities based on palynological and other data compiled by Nations et al. (1981).

Vertebrate Taxa in Order of Relative Abundance	**Shallow, Open Lake/Algal Beds**	**Marshy Lake Margin**	**Deciduous Riparian Gallery Forest**	**Grasslands**	**Open Oak-Juniper Savanna**
Prodipodomys idahoensis				X	?
Geomys (Nerterogeomys) minor				X	X
Bensonomys arizonae			X	?	X
Sigmodon minor		X		X	X
Emberizidae/Fringillidae			X	X	X
Perognathus strigipredus				X	X
Onychomys bensoni				X	X
Reithrodontomys cf. *R. wetmorei*				X	X
Neotoma vaughani			X		X
Postcopemys sp.		?	X	X	X
Jacobsomys verdensis					X
Soricidae		X	X		X
Lasiurus cf. *L. blossevillii*			X		
Prosigmodon holocuspis		X		X	X
Urodela	X				