

The Taphonomy of Owl-Deposited Fish Remains and the Origin of the Homestead Cave Ichthyofauna

Jack M. Broughton*, Virginia I. Cannon, Shannon Arnold
*Department of Anthropology, University of Utah, 270 South 1400 East, RM 102,
Salt Lake City, UT 84112, USA*

Raymond J. Bogiatto
Department of Biological Sciences, California State University, Chico, CA 95929-0515, USA

Kevin Dalton
Department of Anthropology, California State University, Chico, CA 95929, USA

Journal of Taphonomy 4 (2) (2006), 69-95.

Manuscript received 29 September 2005, revised manuscript accepted 18 October 2005.

We report a case of fish prey dominating the diet of modern barn owls (*Tyto alba*) and conduct a descriptive taphonomic analysis on the fish remains the owls deposited. From a sample of 14 barn owl pellets collected on the floor of a Nevada barn, we identified 3294 tui chub (*Gila bicolor*) bones. These remains, derived from very small-sized fish, comprised nearly 90% of the total pellet NISP and were characterized by relatively complete skeletal part representation, and minimal bone fragmentation and digestive surface damage. We use this data-set, along with tui chub samples deposited by other agents, to evaluate the origin of fish remains derived from late Quaternary deposits of Homestead Cave, located in the northern Bonneville Basin, Utah. Quantitative comparisons of skeletal part representation and digestive damage show that the Homestead Cave fish assemblage is statistically indistinguishable from the owl-derived collection but different from chub samples originating from coyote (*Canis latrans*) scat and human faeces. Qualitative evaluations of other agents also suggest an owl-based origin of the fauna. Our analysis calls attention to the important role that owls can play in depositing fish in caves and rockshelters and provides useful information to researchers interested in deciphering the taphonomic history of fish remains recovered from these settings around the world.

Key words: BARN OWL, FISH REMAINS, GREAT BASIN, HOMESTEAD CAVE, OWL PELLETS, RAPTOR DEPOSITS, TAPHONOMY, TUI CHUB

Introduction

Fish remains are frequently represented in cave and rockshelter faunas around the world (e.g., Driver, 1988; Nagaoka, 2005;

Muñoz & Casadevall, 1997; Rick *et al.*, 2001; Smith, 1985) yet their value to inform on ancient human foraging behavior or paleoenvironmental conditions in these contexts often depends on understanding

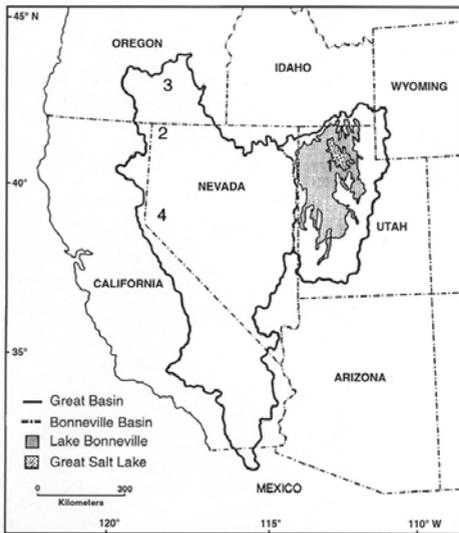


Figure 1. Map of southwestern USA showing the Great Basin, Bonneville Basin, Great Salt Lake and sites discussed in the text (from Madsen et al. 2001). 1) Homestead Cave, 2) Bitner Ranch, 3) Harney Lake, 4) Hidden Cave.

their depositional origin. This remains a challenge, however, since the signs of human processing can be subtle (e.g., Butler, 1993, 1996; Van Neer & Morales 1992; Wheeler & Jones, 1989:68) and there has been little research conducted on the taphonomy of cave-derived ichthyofaunas. And while owls are widely recognized for the role they play in the deposition of small mammal and bird materials in caves (e.g., Andrews, 1990; Bochenski & Tomek, 1997; Bochenski & Nekrasov, 2001; Hockett, 1995; Lyman et al., 2003), they are rarely considered as potential contributors of fish remains in these settings.

We were recently compelled to such a consideration during analyses of the small vertebrate fauna from Homestead Cave located in the northern Bonneville Basin,

Utah (Figure 1; Broughton, 2000a, b; Broughton et al., 2000; Grayson, 1998, 2000a, b; Livingston, 2000; Madsen, 2000; Madsen et al., 2001). At Homestead Cave, the lowest late Pleistocene-aged stratum produced a substantial small vertebrate fauna that included nearly 14,000 identified fish specimens. Both roosting owls and piles of owl pellets—regurgitated casts of indigestible fur and bone—were observed in the cave when the excavation began (Figures 2-3). Signs of other bone accumulating agents (people, canids) in the assemblage were limited, and there was no evidence for water-laid sediments. Finally, the deep, enclosed cave context would seem to have precluded the occupation of such piscivorous raptors as bald eagles (*Haliaeetus leucocephalus*) or osprey (*Pandion haliaetus*). All of this pointed to owls as the depositional agent of the Homestead fish remains, but we could find no evidence in the literature that North American owls utilize fish in appreciable quantities and no taphonomic analyses of owl-deposited fish remains were available for us to evaluate this suggestion.

We fill both those gaps here by 1) documenting a case in which fish dominated the diets of modern barn owls (*Tyto alba*; family Tytonidae) living in northwestern Nevada, and 2) conducting a taphonomic analysis on the fish materials deposited by those owls. In particular, we describe a variety of osteological characteristics commonly used to address issues involving the mode or agent of deposition with archaeological and paleontological faunas including skeletal part representation, fragmentation, size structure, and digestive modifications. We then compare taphonomic patterns of the Homestead Cave fish remains with those from the barn owl sample and other bone accumulating agents to evaluate the



Figure 2. Western screech owl (*Megascops kennicottii*) on a perch in Homestead Cave (photograph by M.W. Shaver III).



Figure 3. View of an owl pellet cone beneath the perch (Figure 2) on the floor of Homestead Cave (photograph by M. W. Shaver III).

Table 1. Numbers of identified specimens (NISP) and minimum numbers of individuals (MNI) per taxon for the Bitner Ranch barn owl pellets.

Taxon	NISP	%NISP	MNI	%MNI
<i>Gila bicolor</i>	3294	89.2	48	73.0
Passeriformes	62	1.68	2	3.0
<i>Sturnella neglecta</i>	7	<1	1	1.5
<i>Sorex</i> sp.	2	<1	1	1.5
Rodentia	128	3.47	-	-
<i>Thomomys talpoides</i>	86	2.33	5	7.5
<i>Peromyscus</i> sp.	31	<1	3	4.5
<i>Microtus</i> sp.	84	2.27	6	9.0
Total	3694	100	66	100

depositional origin of that fauna. The data and analyses presented here should be useful to researchers interested in deciphering the taphonomic history of fish remains in cave and rockshelter faunas around the world.

A case of fish dominating the diet of modern owls: the Bitner Ranch barn owl pellets

Pellet sample and context

In July of 2002, we (J.M.B., R.J.B., and K.D.) collected 14 owl pellets in various stages of decomposition from the floor of an abandoned barn at Bitner Ranch, Washoe County, Nevada. Bitner Ranch (1747m asl) sits at the south end of a long (10 km) meadow (Badger Creek Meadow) in the southern Guano Basin. Big sage (*Artemisia tridentata*) dominates the vegetation community surrounding the ranch. The pellets were consistent in size with those of barn owl and retained the dried saliva film or cemented appearance diagnostic of tytonid pellets (König *et al.*, 1999:26). Barn

owls had also been recently observed in the structure (P. Van Ornum, pers. comm.), but it is unknown whether they used the site for nesting. The varying states of pellet preservation suggested they had accumulated over an extended, but unknown, period of time. We found no additional pellets on revisits to the barn in July of 2003 and 2005.

Cursory inspection of the pellets in the field revealed that fish bones were an abundant constituent. The pellets were bagged as a unit in the field and returned to the Zooarchaeology Laboratory (Department of Anthropology, University of Utah) for examination; the analyses that follow focus on the bones derived from the aggregated assemblage of 14 pellets. In the lab, the dried pellets were dissected with forceps and all of the osteological materials visible under 5x magnification were separated for identification. Our identifications are based on comparisons with Recent vertebrate specimens from the Utah Museum of Natural History and criteria described below.

Taxonomic composition

Fish remains, namely tui chub (*Gila bicolor*; family Cyprinidae), comprise an overwhelming majority of the pellet-derived bones, representing 89.2% of the total number of identified specimens (3294 of 3694 total NISP) and 73% of the sample of identified individuals (48 of 66 total MNI; Table 1). No other fish species is present in the collection.

We distinguished tui chub from other cyprinid species (e.g., speckled dace [*Rhinichthys osculus*], Lahontan redbreast [*Richardsonius egregius*]) by obvious differences in the pharyngeal tooth row

formulae and morphology of the bony arch (see Butler, 2001; Follett, 1970; Smith, 1985). Given that all of the pharyngeals present in the sample were from tui chub, we assigned the remaining cyprinid elements to that taxon as well.

The chubs almost surely originated from Badger Creek, an intermittent stream located ~100 m west of the barn. By mid-summer, most sections of Badger Creek are dry, at which time fish are restricted to deeper water-retaining pools in the stream bed. Sheldon tui chub (*Gila bicolor eurysona*), a subspecies endemic to the Guano Basin of northwest Nevada and southeast Oregon (Williams and Bond, 1981), is the only fish taxon that has been collected from the creek in recent surveys (E. Flores, pers. comm.). As is typical for tui chub populations inhabiting springs, ponds, and small creeks, Sheldon tui chub are very small with the average length of adults only 63.8 and 70.6 mm, for males and females, respectively (E. Flores, pers. comm.; Williams & Bond, 1981).

Fish and barn owl foraging behavior

To our knowledge, this case represents the only well-documented example of a North American owl species relying heavily on fish prey. And while we have no data on the overall role of fish in the annual diet of these owls, or how and in what contexts they were captured, it is clear that when they roosted or nested in the Bitner Ranch barn, tui chub was the principal prey species used. Of course, micromammals inhabiting open areas—usually rodents and insectivores ranging between 20 and 70 g—are by far the most common prey taken by barn owls over their nearly cosmopolitan range (Johnsgard, 2002:69; König *et al.*, 1999:195; Marti,

1990). Smaller and larger prey—less than 10 and up to 500 g—are also taken depending on local densities and the availability of prey in the preferred size range (Derting & Cranford, 1989; Ille, 1991; Janes & Barss, 1985; König *et al.*, 1999:195; Marti, 1974:54). In the Great Basin, voles (*Microtus*) are the favored prey in most areas with other important taxa including *Sorex*, *Thomomys*, *Perognathus*, *Dipodomys*, *Reithrodontomys*, and *Mus* (Marti, 1990).

Barn owls are known, however, to exploit unusual prey opportunities and switch to new prey species as they become available. Barn owls roosting in caves, for instance, will prey heavily upon bats that share their sites (Andrews, 1990:29). And barn owls residing near seabird nesting colonies have been known to prey intensively on small seabirds (e.g. Leach's Storm-petrels [*Oceanodroma leucorhoa*]; Bonnot, 1928). Frogs and other amphibians are occasionally taken in abundance as well (Lenton, 1984; Esteban *et al.*, 1998).

The only previously published detailed account of barn owls taking fish was provided by Gallup (1949:150) near Escondido, in southern California (San Diego Co.). Gallup noted that: "Barn owls are common birds in this region. I have seen as many as 30 on the beach at night feeding on grunion when these were running". California grunion (*Leuresthes tenuis*) are well known for their unusual spawning habits in which adults spawn en masse on sandy beaches at night during high tides (Eshmeyer *et al.*, 1983:119). The few available accounts of other North American owls taking fish (e.g., great horned owl [*Bubo virginianus*]) also suggest that fish prey are exploited opportunistically when capture costs are substantially reduced as

Table 2. *Tui chub skeletal element representation from the Bitner Ranch barn owl pellets.*

Anatomical region	Skeletal element	NISP	MNE	MAU	%MAU	Anatomical region	Skeletal element	NISP	MNE	MAU	%MAU	
Neurocranium	Ethmoid	10	10	10.0	21.74	Gill and throat	Opercle	74	74	37.0	80.43	
	Frontal	33	33	16.5	35.87		Interopercle	41	41	20.5	44.56	
	Parietal	48	48	24.0	52.17		Preopercle	61	57	28.5	61.96	
	Supraoccipital	13	13	13.0	28.26		Subopercle	18	18	9.0	19.57	
	Exoccipital	43	43	21.5	46.74		Pharyngeal	92	91	46.0	100.00	
	Parasphenoid	29	22	22.0	47.83		Basihyal	1	1	1.0	2.17	
	Basioccipital	42	41	41.0	89.13		Ceratohyal	77	77	38.5	83.69	
	Mesa-						Hypohyal	15	15	7.5	16.30	
	metapterygoid*	26	26	13.0	28.26		Epithyal	49	49	24.5	53.26	
	Otolith	123	123	30.8	66.85		Urohyal	37	37	18.5	40.22	
	Post-temporal	16	16	8.0	17.34		Branchiostegal ray	60	60	10.0	21.74	
	Palatine	20	20	10.0	21.74		Total for region	525	520	241.0		
	Prefrontal	22	22	11.0	23.91							
	Sphenotic	38	38	19.0	41.30		Post-cranial	Cleithrum	114	84	42.0	91.30
	Pterotic	65	65	32.5	70.65			Supracleithrum	32	32	16.0	34.78
	Epiotic	28	28	14.0	30.43			Coracoid	9	9	4.5	9.78
	Pterosphenoid	20	20	10.0	21.74			Scapula	48	48	24.0	52.17
	Prootic	29	29	14.5	31.52			Pectoral fin spine	39	39	19.5	42.39
	Supraorbital	3	3	1.5	3.26			Basiplerygium	62	62	31.0	67.39
	Vomer	3	3	3.0	6.52			Pterygiophore	31	31	1.9	4.22
Total for region	611	603	315.3		Vertebra 1 & 2	72		72	36.0	78.26		
Jaws	Maxilla	70	69	34.5	75.00	Vertebra 3 - penultimate vert.		1214	1214	32.8	71.30	
	Premaxilla	33	32	16.0	34.78	Ultimate vertebra		37	37	37.0	80.43	
	Dentary	85	85	42.5	92.39	Weberian apparatus		92	82	41.0	89.13	
	Articular	64	64	32.0	69.57	Hypural		29	29	4.8	10.43	
	Quadrate	63	63	31.5	68.48	Total for region		1779	1739	290.5		
	Hyomandibular	64	64	32.0	69.56	Grand total	3294	3239	1035.3			
	Total for region	379	377	188.5								

* Includes both metapterygoids and mesopterygoids.

when fish are stranded—dead or alive—on shorelines or partially exposed in very shallow streams (Bogiatto *et al.*, 2003; Broughton, 2000a:104-105; Errington, 1940).

In sum, Barn owls usually take small mammals but are clearly opportunistic hunters and will take a variety of prey, including fish that fall within their targeted size range. We hypothesize that the Bitner Ranch barn owls scavenged tui chub carcasses that resulted from periodic summer dessications or winter freezes of Badger Creek.

The taphonomy of barn owl-deposited fish remains

Previous barn owl taphonomic work with small mammal and avian prey shows that ejected pellets contain materials typically characterized by a high degree of skeletal completeness, with comparatively low degrees of bone fragmentation, and corrosion caused by digestion (e.g., Andrews, 1990; Dodson & Wexler, 1979; Hoffman, 1988; Kusmer, 1990; Lyman *et al.*, 2003; Raczynski & Ruprecht, 1974; but see Saavedra & Simonetti, 1998 for intraspecific variation in barn owl bone deposits). In this section, we conduct a taphonomic analysis of the tui chub remains derived from the Bitner Ranch barn owl pellets describing patterns in skeletal part representation, size structure, fragmentation, and surface digestion damage. To facilitate subsequent comparisons, we follow the methods used in Butler's (Butler, 1996; Butler & Schroeder, 1998) taphonomic work with tui chub materials deposited by mammalian predators.

Table 3. Fragmentation of selected tui chub elements derived from the Bitner Ranch barn owl pellets.

Skeletal element	Degree of element completeness			
	0-33%	33-67%	67-100%	% > 67%*
Basioccipital	6	1	34	83
Articular	0	0	63	100
Opercle	16	16	26	45
Pharyngeal	2	9	80	88
Ceratohyal	0	2	75	97
Vertebra	15	56	1111	94
Total	39	84	1389	92

*Column 3/Σ columns 1-3.

Skeletal part representation

We measured relative skeletal abundances from the pellet-derived tui chubs by comparing the number of observed elements to the number expected. These values are derived from minimal animal units (MAU)—counts per element normed by the number of times the latter occurs in the body of a single individual (see Binford, 1984; Mollhagen *et al.*, 1972). The MAU values are based, in turn, on MNEs, or the minimum number of individual elements needed to account for a collection of element fragments. In this case, the best-represented element was the pharyngeal, with an MAU of 46; the abundances of all other elements were scaled to this value, accordingly (i.e., % MAU for the basioccipital = $41/46 = 89.13\%$).

In general, element survivorship is high with 18 different elements represented by 60% or greater of the expected values (Table 2). Moreover, each major region of the skeleton is represented by an element with a value greater than 89%, suggesting

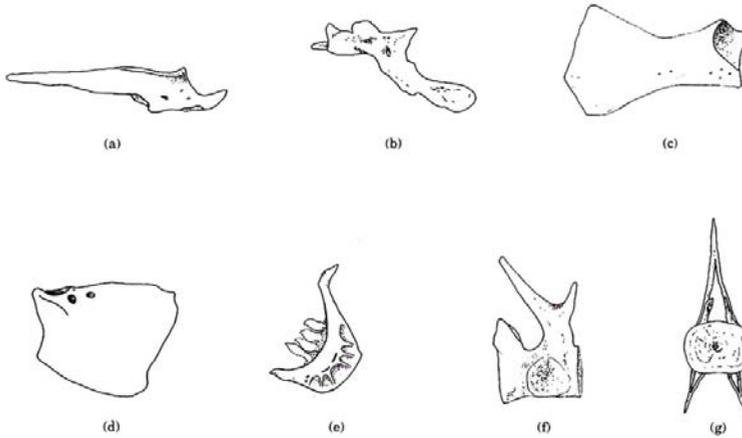


Figure 4. Tui chub elements included in the analysis of bone digestive damage (all paired elements are from the left side). Not drawn to scale. (a) Articular, lateral; (b) basioccipital, lateral; (c) ceratohyal, medial; (d) opercle, medial; (e) pharyngeal, dorso-lateral; and abdominal vertebrae, lateral (f), and posterior (g) views (from Butler and Schroeder, 1998).

that whole fish were consumed and relatively complete skeletons were regurgitated in pellets. Still, some elements are underrepresented. The supraorbital, vomer, basihyal, coracoid, and pterygiophore, for instance, are each represented by 10% or less of their expected values.

Although element destruction is often correlated with structural bone density (e.g., Lyman 1994; Butler 1993), the limited available density data suggests this is not a factor here. Using bone density values for large sucker (*Catostomus macrocheilus*, family Catostomidae; from Butler 1996), a species in the same order (Cypriniformes) as tui chub, there is no correlation between element survivorship (%MAU) and mineral bone density in this assemblage ($r_s = 0.13$, $P = 0.64$). The underrepresented elements in the collection are, however, the smaller, seemingly more delicate bones of the skeleton and we suspect their scarcity is related to variables such as size and shape

and their affect on preservation, recovery, and identifiability (see Butler & Schroeder, 1998; Darwent & Lyman, 2002; Lyman & O'Brien 1987; Nagaoka, 2005).

In sum, these skeletal part data are consistent with previous barn owl field research and pellet analyses focused on mammalian prey and suggest that small fish prey are swallowed whole with the materials contained within ejected pellets being characterized by a high degree of skeletal completeness.

Tui chub size structure

We reconstructed the size profile of the barn owl-deposited tui chubs by using the logarithmic regression formula:

$$\ln SL = 2.51260 + .90851(\ln OL),$$

where SL is the estimated standard length (end of snout to end of hypural bone), and OL is the opercle length (maximum length of anterior border of the

Table 4. Frequency (NISP) of selected tui chub elements showing surface digestion damage from the Bitner Ranch barn owl pellets.

Skeletal element	Pitting			Rounding			Deformation		
	Present	Absent	% present	Present	Absent	% present	Present	Absent	% present
Basioccipital	-	-	-	7	34	17.1	-	-	-
Articular	0	63	0.0	-	-	-	-	-	-
Opercle	0	58	0.0	-	-	-	-	-	-
Ceratohyal	9	68	11.7	-	-	-	-	-	-
Pharyngeal	-	-	-	10	81	11.0	-	-	-
Vertebra	-	-	-	237	944	20.07	62	1116	5.26
Total	9	189	4.5	254	1059	19.35	62	1116	5.26

opercle bone). This formula was derived by Butler (1996:704) from a modern sample of tui chubs ($n = 143$) collected from western Nevada.

A total of 46 opercles in the Bitner Ranch tui chub sample were intact enough to measure their maximum anterior lengths. Consistent with recent fish survey work in Badger Creek, the represented individuals are very small fish, ranging between 88.41 and 167.67 mm SL, with a mean of 109.931 mm SL. The distribution does not differ significantly from a normal one (Kolmogorov-Smirnov normality test; $X^2 = 2.78$, $P = 0.49$). Using established length-weight relationships for tui chub (Kimsey, 1954:407), fish of these lengths correspond to weights between about 10 and 75 g—well within the preferred prey size range of barn owl mammalian prey. So while the tui chub is an unusual prey type for barn owls, the size range of the exploited individuals is typical for the species.

Element fragmentation

To measure element fragmentation here, we assigned selected elements to one of three categories of skeletal completeness based on the percentage of the element present:

$\leq 1/3$; $1/3$ to $2/3$; and $\geq 2/3$. Following Butler and Schroeder (1998), we selected for this analysis a subset of elements that exhibit different shapes and sizes and are located at different parts of the skeleton: the basioccipital, articular, opercle, pharyngeal, ceratohyal, and vertebra (Figure 4). A total of 1449 specimens were examined for fragmentation (Table 3). These data suggest a minimal degree of fragmentation: 92% of the elements examined were at least $2/3$ complete. There is some variation in completeness among the elements, however, with, not surprisingly, the widest, thinnest element in the sample—the opercle—showing the greatest degree of fragmentation.

Digestive processes and bone surface damage

Bones and teeth ingested by avian and mammalian predators often show distinctive surface modifications caused by mastication, acid corrosion, or physical abrasion with associated gritty food items. Importantly, the degree of such damage has been shown in many cases to be predator-specific (e.g., Andrews, 1990; Bochenski & Tomek, 1997; Mayhew, 1977). Following Butler & Schroeder's (1998) work with tui chub

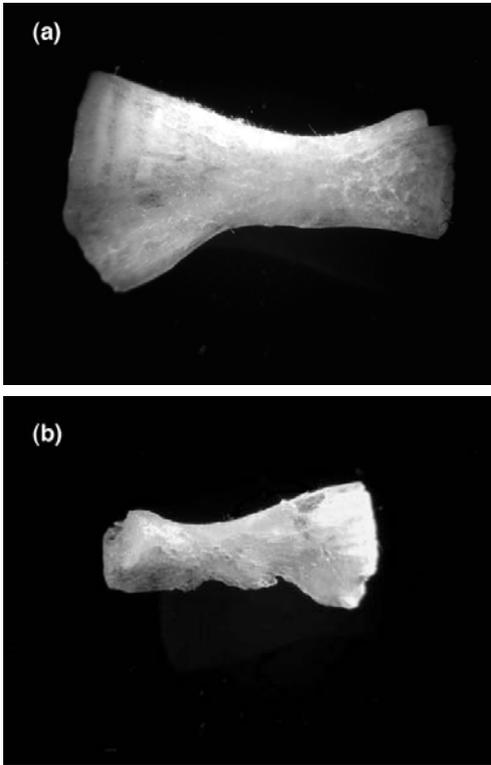


Figure 5. (a) Unmodified tui chub ceratohyal (35 x), lateral view, from the Bitner Ranch barn owl pellets. (b) Tui chub ceratohyal (35 x), medial view, from the Bitner Ranch barn owl pellets showing pronounced pitting.

materials derived from mammalian scat, we selected the basioccipital, articular, opercle, pharyngeal, ceratohyal, and vertebra from the Bitner Ranch tui chub materials for analysis of bone digestion damage (Figure 4). [Butler & Schroeder](#) (1998) found that the primary digestive damage attributes, including pitting, rounding, and deformation — features commonly reported and described for both mammalian scat and avian pellet samples— were variously evident on this subset of tui chub elements. Accordingly, pitting was examined here for

the articular, opercle and ceratohyal (Figure 5); rounding was recorded for the basioccipital, pharyngeal, and vertebrae (Figure 6); and deformation was observed on the vertebrae (see [Butler & Schroeder](#) [1998] for further details on the nature of these attributes). The entire element surfaces were examined for these features under 8-50 x magnification with a dissecting microscope.

The data show that the barn owl-derived chub elements exhibit, with some exceptions, little evidence of digestion damage (Table 4). The presence of pitting and vertebral deformation —two out of the three damage categories— was observed on less than 5% of the elements examined. Rounding, however, was a bit more commonly exhibited on these materials, occurring on 19% of the elements studied. These data are consistent with previous taphonomic studies on barn owl deposited mammalian prey that have also shown low frequencies of digestive-based surface damage. This is apparently due to the fact that barn owls swallow small prey whole and produce gastric secretions with comparatively low acidity ([Andrews](#), 1990; [Duke et al.](#), 1975; [Kusmer](#), 1990; [Mayhew](#), 1977). This generally low degree of digestive damage contrasts sharply with mammalian predators and many other raptors (e.g., [Andrews](#), 1990; [Duke et al.](#), 1975; [Kusmer](#), 1990; [Schmitt & Juell](#), 1994).

Owls and the depositional origin of the Homestead Cave ichthyofauna

The barn owl-derived fish data set can now be employed along with cyprinid samples deposited by other predators to evaluate the origin of the Homestead Cave ichthyofauna.

Homestead Cave is a limestone cavern located on the northwestern margin of the Lakeside Mountains, several kilometers west of Great Salt Lake (Figs. 1-3; 7) in the northern Bonneville Basin. The cave sits at an elevation of 1406 m and is 17 m in length and varies from 1 to 4.5 m wide and 5 to 6 m high. No active springs or permanent streams are located near the site. In 1993 and 1994, a 1 m² sample column was excavated to a depth of ~3 m toward the back of the cave. Materials excavated from the column were passed through a nested series of 1/4" (6.4 mm) and 1/8" (3.2 mm) screens (Madsen, 2000). Analyses of the site's massive vertebrate faunal data set have substantially increased our understanding of late Quaternary paleoecology in the Great Basin (e.g., Broughton, 2000a, b; Grayson, 1998, 2000a, b; Livingston, 2000; Madsen, 2000; Madsen *et al.*, 2001).

The fish remains from Homestead Cave have played an important role in those analyses as the site provided the largest, well-stratified, and richest late Pleistocene and Holocene ichthyofaunal sequence from the entire Great Basin (Broughton 2000a, b; Broughton *et al.*, 2000). Perhaps of broadest interest, the fish-based trends in moisture history have been shown to co-vary positively with paleontologically derived fluctuations in artiodactyl populations and ultimately patterns in human foraging behavior and associated hunting technology in the region (Byers & Broughton, 2004; Byers *et al.*, 2005).

Importantly, the paleoclimatic inferences derived from the Homestead ichthyofauna are based on the suggestion that owls deposited the fish in the cave. Specifically, it is argued that insofar as owls only utilize fish in unusual circumstances —such as when they

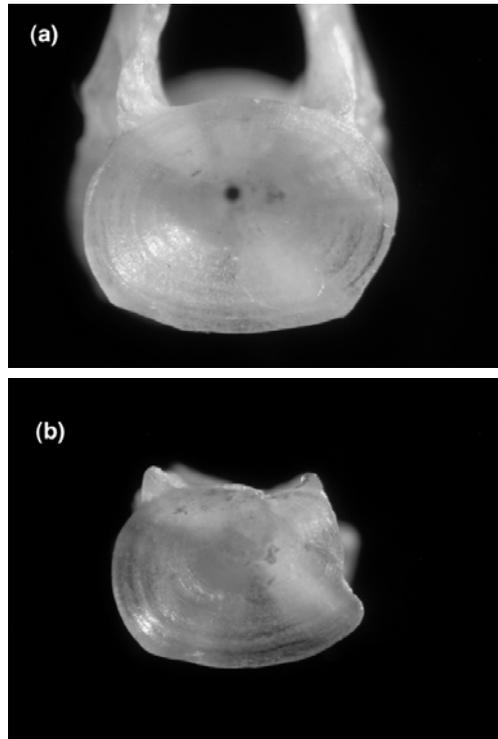


Figure 6. (a) Unmodified tui chub abdominal vertebra (79 x), anterior view, from the Bitner Ranch barn owl pellets. (b) Abdominal vertebra (79 x), anterior view, from the Bitner Ranch barn owl pellets showing pronounced rounding. Note rounded, scalloped edge on the right.

are stranded dead or dying on shorelines—spikes in fish abundances across the Homestead Cave deposits should reflect periods characterized by enhanced scavenging opportunities. Since this is a closed-basin lake context, these would result from climate-based recessions from high-stands of Lake Bonneville or Great Salt Lake and the ensuing fish die-offs associated with increases in lake-water salinity and temperature. Peaks in fish abundances in the cave deposits would not, however, be tied to recessions from high-stands if the fish were

Owl-deposited fish remains

collected and deposited by active piscivores capable of extracting live fish from open water (e.g., humans, osprey, bald eagle). Below, we evaluate to what degree the taphonomic patterns in the Homestead Cave ichthyofauna are consistent with those derived from the barn owl-deposited fish bones described above and distinct from those of other bone accumulating agents.

The Homestead Cave ichthyofauna

Although the entire Homestead Cave deposit is rich in bone, fish remains were most abundant in stratum I, the basal stratum of the deposit. This layer consists primarily of degraded organic material, including vast quantities of unfossilized small vertebrate materials. The analyses below focus on the fish remains recovered from the 1/4" and 1/8" fractions of stratum I. Six radiocarbon dates constrain the deposition of the materials from stratum I between ~11,200 and ~10,100 ¹⁴C yrs B.P. These dates correspond with the Gilbert level of Lake Bonneville: the shoreline of the lake at that time would have been located less than ~1 km from the mouth of the cave (Madsen, 2000).

Nine species are represented by the 13,536 identified fish specimens from stratum I of Homestead Cave (Broughton 2000a, b). Collectively, it is a deep-water lacustrine fauna, strikingly similar to that of modern Bear Lake, a cold, deep, high-elevation lake located on the Utah-Idaho border. In addition to the fishes, 23 species of small mammals (Grayson, 2000; Madsen, 2000) and 28 species of birds (Livingston, 2000) have also been identified from the stratum I deposits. Over 99% of the ~184,000 identified mammalian specimens from the site are small rodents and

lagomorphs; and 78% of these specimens represent taxa smaller than *Lepus* (Grayson, 2000a).

Cyprinid deposits produced by known agents

In addition to the barn owl collection described above, quantitative taphonomic data on cyprinid remains deposited by known agents are limited to skeletal part representation and digestive damage attributes for tui chub materials derived from coyote scats, modern human faeces, and archaeological human coprolites (Butler & Schroeder, 1998). The coyote sample consists of four scats collected along the shore of Harney Lake, southeastern Oregon (Figure 1), after a series of tui chub die-offs. The remains from the modern human faeces resulted from taphonomically-oriented experimental work, and the coprolites include ten specimens recovered from Hidden Cave, western Nevada (Figure 1). The tui chub remains from these collections were recovered by sieving through 1/8" (3.2mm) and 1/16" (1.6 mm) mesh screens (see Butler & Schroeder [1998] for



Figure 7. View of the mouth of Homestead Cave.

Table 5. Element abundances by major anatomical region for tui chubs derived from different agents.

Anatomical region	Barn owl pellets*		Coyote**		Human** faeces (experimental)		Human** coprolites (Hidden Cave)	
	MNE	%MAU†	MNE	%MAU†	MNE	%MAU†	MNE	%MAU†
Neurocranium	603	36.06	349	37.47	7	6.85	151	30.03
Jaws	377	68.29	219	62.83	6	16.60	84	47.28
Gill and Throat	520	47.63	168	51.67	7	22.18	111	56.07
Post-cranial	1679	52.63	1017	61.50	61	45.99	433	46.38
Total	3179		1753		81		779	

* This study.

** Data from Butler & Schroeder (1998).

† %MAU is the mean of %MAU values derived for the individual elements that comprise a major anatomical region.

Table 6. Matrix of chi-square values for comparisons of tui chub skeletal part representation between different known agents (raw data are MNE values from Table 5).

	Barn owl pellets	Coyote scat	Human faeces (experimental)
Barn owl pellets	–	–	–
Coyote scat	***43.65	–	–
Human faeces (experimental)	**16.23	*10.71	–
Human coprolites (Hidden Cave)	3.32	*12.6	*12.06

* Significant at $P \leq 0.01$.

** Significant at $P < 0.001$.

*** Significant at $P < 0.000$.

Owl-deposited fish remains

Table 7. Adjusted residuals for comparisons of skeletal part representation among known-agent control samples.

a. Barn owl vs. coyote scat

	Barn owl	Coyote scat
Neurocranium	-0.80	0.80
Jaws	-0.65	0.65
Gill and throat	6.57	-6.57
Post-cranial elements	-3.51	3.51

b. Barn owl vs. human faeces (experimental)

	Barn owl	Human faeces (experimental)
Neurocranium	2.35	-2.35
Jaws	1.23	-1.23
Gill and throat	1.86	-1.86
Post-cranial elements	-4.01	4.01

c. Coyote scat vs. human faeces (experimental)

	Coyote scat	Human faeces (experimental)
Neurocranium	2.51	-2.51
Jaws	1.36	-1.36
Gill and throat	0.28	-0.28
Post-cranial elements	-3.09	3.09

d. Coyote scat vs. human coprolites (Hidden Cave)

	Coyote	Human coprolites (Hidden Cave)
Neurocranium	0.31	-0.31
Jaws	1.22	-1.22
Gill and throat	-3.46	3.46
Post-cranial elements	1.14	-1.14

e. Human faeces (experimental) vs. human coprolites (Hidden Cave)

	Human faeces (experimental)	Human coprolites (Hidden Cave)
Neurocranium	-2.38	2.38
Jaws	-0.95	0.95
Gill and throat	-1.40	1.40
Post-cranial elements	3.42	-3.42

details); our quantitative comparisons with the Homestead fishes are made with these collections and the barn owl sample described above. Although we have reasons to doubt that people or coyotes played a significant role in depositing the Homestead fauna, as we discuss below, these collections provide an important frame of reference to compare with our barn owl-derived control sample.

Skeletal part representation

Before turning to the Homestead fauna, we compare element abundances among the tui chub known-agent control samples (Table 5). To facilitate comparisons, we conduct the analysis on aggregated sets of elements that comprise four major regions of the fish skeleton: the neurocranium, jaws, gill and throat, and the post-cranial skeleton.

Chi-square comparisons show that skeletal part abundances are dramatically distinct among these agents with one notable exception; the barn owl and Hidden Cave coprolite samples are indistinct (Table 6). To explore the specific sources responsible for the differences in element abundances between these collections, we examine adjusted residuals. These indicate which cells — in this case, different anatomical regions— are responsible for the significant overall chi-square values.

Adjusted residuals are read as standard normal deviates—values that exceed ± 1.96 and ± 2.57 are significant at the 0.05 and 0.01 levels, respectively (Everitt, 1992:47). The analysis shows that the barn owl and Hidden Cave collections are consistently overrepresented by gill and throat elements compared to the coyote control (Table 7). In addition, the barn owl collection is underrepresented by post-cranial elements compared to the coyote sample. These patterns may be related in part to a more thorough destruction of fish skeletons in the coyote digestive system, insofar as post-cranial elements such as vertebrae are more resistant to breakdown from mechanical and biochemical processes. Vertebrae, we observe, are among the more dense elements of the cypriniform skeleton, to judge from analyses of mineral bone density on largescale sucker (Butler, 1996). Indeed, density and survivorship (%MAU) are uncorrelated in each of the collections with the exception of the coyote scat sample (Table 8). This suggests that the distinctiveness of the coyote and barn owl samples is due to a greater degree of density mediated destruction in the former and is consistent with previous taphonomic work with small mammal, bird, and fish prey recovered from these predators (e.g., Dodson & Wexlar, 1979; Andrews 1990; Schmitt & Juell, 1994; Butler & Schroeder,

Table 8. Spearman's rank order correlation coefficients for tui chub element survivorship (%MAU) and bone density from different agents; density values are from Butler (1996).

Assemblage	Rho	P
Barn owl pellets	0,13	0,64
Coyote scat	0,66	0,02
Human faeces (experimental)	0,30	0,35
Human coprolites (Hidden Cave)	0,05	0,86

Table 9. Skeletal part abundances for the Homestead Cave (Stratum I) Cypriniformes.

Anatomical region	Skeletal element	NISP	*Normed NISP	%Normed NISP
Neurocranium				
	Ethmoid	31	31.0	20.26
	Frontal	92	46.0	30.07
	Parietal	81	40.5	26.47
	Supraoccipital	27	27.0	17.65
	Exooccipital	4	2.0	1.31
	Parasphenoid	42	42.0	27.45
	Basioccipital	69	69.0	45.10
	Meso/meta-pterygoid	33	16.5	10.78
	Palatine	94	47.0	30.72
	Posttemporal	10	5.0	3.27
	Sphenotic	21	10.5	6.86
	Pterotic	79	39.5	25.82
	Epiotic	38	19.0	12.42
	Supraorbital	3	1.5	0.98
	Circumorbital	3	1.5	0.98
	Vomer	33	33.0	21.57
	Total for region	660	431.0	
Jaws				
	Maxilla	115	57.5	37.58
	Premaxilla	19	9.5	6.21
	Dentary	122	61.0	39.87
	Articular	51	25.5	16.67
	Quadrate	58	29.0	18.95
	Hyomandibular	66	33.0	21.57
	Total for region	431	215.5	
Gill and throat				
	Opercle	104	52.0	33.99
	Preopercle	28	14.0	9.15
	Interopercle	6	3.0	1.96
	Subopercle	4	2.0	1.31
	Pharyngeal	306	153.0	100.00
	Epihyal	28	14.0	9.15
	Ceratohyal	66	33.0	21.57
	Urohyal	38	38.0	24.84

Table 9 (continuation)

Anatomical region	Skeletal element	NISP	*Normed NISP	%Normed NISP
	Basihyal	9	9.0	5.88
	Hypohyal	21	10.5	6.86
	Branchiostegal	13	2.2	1.41
	Epibranchial	1	0.2	0.10
	Total for region	624	330.8	
Post-cranial				
	Cleithrum	88	44.0	28.76
	Supracleithrum	3	1.5	0.98
	Post-cleithrum	18	9.0	5.88
	Coracoid	12	6.0	3.92
	Scapula	27	13.5	8.82
	Pectoral fin spine	41	20.5	13.40
	Basipterygium	79	39.5	25.82
	Pterygiophore	1	0.1	0.04
	Vertebra 1-2	86	43.0	28.10
	Other vertebra	1712	46.3	30.24
	Weberian apparatus	32	32.0	20.92
	Total for region	2099	255.3	
	Grand total	3814	1232.6	

* Normed NISP represents skeletal part NISP values divided by the number of times the relevant part occurs in the tui chub skeleton (see Grayson & Frey 2004).

Table 10. Chi-square values for comparisons of tui chub skeletal part representation between different agents and the Homestead Cave Cypriniformes.

	Barn owl pellets	Coyote scat	Human faeces (experimental)	Human coprolites (Hidden Cave)
Homestead Cave	4.70	**46.64	*13.34	3.58

*Significant at $P \leq 0.01$.

**Significant at $P < 0.000$.

1998). Most importantly, it also suggests that skeletal part representation may be used as a means of distinguishing fish remains deposited by these two agents. However, because the barn owl and one of the human faecal samples were also indistinct, skeletal part representation alone may not allow us to distinguish between owl and human-derived deposits.

The Homestead Cave materials used in this analysis include all specimens identified to or below the order Cypriniformes (Table 9). This order is represented at Homestead primarily by two species: one catostomid —Utah sucker (*Catostomus ardens*)— and one cyprinid —Utah chub (*Gila atraria*). Conducting the analysis at this level was necessary because the vertebrae of cypriniform taxa are notoriously difficult to identify below the order level and no attempt to do so was made for the Homestead materials. An analysis focusing strictly on Utah chub, or even cyprinid specimens, would thus not include this important component of the fish skeleton. Finally, anatomical part representation for the Homestead collection is based on skeletal part NISP values; MNE data were not provided in the original analysis of the Homestead ichthyofauna (Broughton 2000a) that we draw from here. However, Grayson & Frey (2004) have documented a close correspondence between NISP and MNE-based measures of skeletal part representation in faunas from a variety of distinct contexts. We add to this here by observing that the relationship between NISP and MNE values for our barnowl-derived tui chub assemblage (Table 2) is astonishingly tight ($r = +1.0$, $P < 0.001$).

Chi-square comparisons of element abundances between the Homestead Cave cypriniformes and the known-agent controls

show that Homestead is significantly different from the coyote and the modern human faecal samples, but indistinct from both the barn owl and Hidden Cave coprolite collections (Table 10). Element abundances in the Homestead collection, we also note, are uncorrelated with density ($r_s = 0.25$, $P = 0.37$) suggesting that density mediated attrition is not a primary factor affecting these data. In addition, adjusted residuals show that both the coyote and modern human faeces collections are significantly overrepresented by the more durable post-cranial elements (e.g., vertebrae) than the Homestead sample (Table 11). Hence, the Homestead assemblage differs from the coyote sample in much the same way that the barn owl sample differs from it.

Whatever the underlying causes, our analyses of skeletal part representation suggests that the Homestead collection is fully consistent with a derivation from barn owls, and clearly inconsistent with an origin from coyote scat. An origin from human faeces remains ambiguous since one of the human control samples—the modern human faeces—showed a significant difference with the Homestead assemblage, yet the other—the Hidden Cave coprolites—did not.

Digestive processes and bone surface damage

Digestion-based surface damage attributes—including pitting, rounding, and deformation—appear to be less frequently represented in the tui chub materials derived from barn owl pellets, relative to the other known-agent controls (Table 12). Indeed, chi-square analysis of the total number of damaged versus undamaged specimens

Table 11. Adjusted residuals for comparisons of skeletal part representation between the Homestead Cave Cypriniformes and the coyote and human faeces (experimental) tui chub samples.

a. Homestead Cave vs. coyote scat		
	Homestead Cave	Coyote scat
Neurocranium	-2.34	2.34
Jaws	-1.29	1.29
Gill and Throat	6.72	-6.72
Post-cranial elements	-2.08	2.08

b. Homestead Cave vs. human faeces (experimental)		
	Homestead Cave	Human faeces (experimental)
Neurocranium	2.04	-2.05
Jaws	1.10	-1.10
Gill and Throat	1.87	-1.87
Post-cranial elements	-3.63	3.63

Table 12. Proportions of specimens exhibiting digestive damage from known-agent control samples.

	NISP pitted/total NISP	% pitted	NISP rounded/total NISP	% rounded	NISP deformed/total NISP	% deformed
Barn owl	9 / 198	4.5	254 / 1313	19.3	62 / 1178	5.3
Coyote	68 / 103	66.0	135 / 538	25.0	81 / 445	18.2
Human faeces (experimental)	3 / 5	60.0	1 / 23	4.3	14 / 19	73.6
Human coprolites (Hidden C.)	35 / 45	77.8	68 / 196	34.7	3 / 154	1.9
Homestead Cave	7 / 101	6.9	287 / 1764	16.3	88 / 1539	5.7

Owl-deposited fish remains

Table 13. Chi-square values for comparisons of the numbers of specimens damaged and undamaged by digestive processes for different known-agent control samples.

	Barn owl pellets	Coyote scat	Human faeces (experimental)
Barn owl pellets	–	–	–
Coyote scat	*113.10	–	–
Human faeces (experimental)	*28.94	3.40	–
Human coprolites (Hidden Cave)	*62.32	0.07	2.73

*significant at $P < 0.000$

Table 14. Chi-square values for comparisons of the numbers of specimens damaged and undamaged by digestive processes for different known-agent control samples and the Homestead Cave Cypriniformes.

	Homestead Cave
Barn owl pellets	1.09
Coyote scat	*145.25
Human faeces (experimental)	*33.17
Human coprolites (Hidden Cave)	*77.07

*Significant at $P < 0.000$.

Table 15. Adjusted residuals for comparisons of the numbers of specimens damaged and undamaged by digestive processes for known-agent control samples and the Homestead Cave Cypriniformes.

	*Homestead Cave
Coyote scat	-12.05
Human faeces (experimental)	-5.76
Human coprolites (Hidden Cave)	-8.78

*The values represented are the Homestead Cave "number damaged" cells; negative values thus indicate the underrepresentation of damaged specimens at Homestead.

reveals that the barn owl sample is underrepresented by modified specimens compared to each of the known-agent controls (Table 13). Moreover, no significant differences can be detected in the frequencies of damaged specimens among the coyote and human samples. This suggests that the extent of digestion-based surface damage is a variable that can readily distinguish between deposits derived from barn owl pellets and the scats from mammalian predators.

The Homestead Cave cypriniformes assemblage exhibits a generally low degree of digestion damage; pitting, rounding, and deformation are evident on only, 6.9, 16.3, and 5.7% of the examined specimens, respectively (Table 12). This low incidence of surface damage is clearly not due to our inability to observe these damage features as a result of post-depositional weathering; the remains are exceptionally well-preserved and unabraded (Figure 8; see [Bochenski & Tomek, 1997](#) for differences between owl digestion damage and sediment erosion). Chi-square analysis of the raw numbers of specimens that do and do not exhibit these damage features shows, in fact, that the Homestead collection is indistinguishable from the barn owl sample but significantly different from each of the other comparative samples (Table 14). And adjusted residuals clearly show that the numbers of specimens modified by digestive processes are underrepresented at Homestead Cave compared to each of the mammalian control samples (Table 15).

Summary and discussion of quantitative comparisons

No significant differences could be detected in skeletal part representation or digestive

damage between the owl-derived tui chub assemblage and the Homestead Cave cypriniform fauna. However, significant differences were found in these variables between the Homestead assemblage and the human and coyote scat control samples. However, for reasons unclear, skeletal part representation from one of the two human fecal samples—the Hidden Cave coprolite collection—was not detectably different from either the barn owl control or the Homestead fishes. Yet, overall, an anthropogenic origin is not supported by these analyses since skeletal part data from the modern human faeces was different than the Homestead collection, as was the degree of digestive damage evident in both the human samples compared to Homestead. There is no suggestion from any of these analyses that coyotes played a role in the deposition of the Homestead fish fauna.

Qualitative comparisons with other potential depositional processes

The analyses above were necessarily restricted to skeletal part representation and

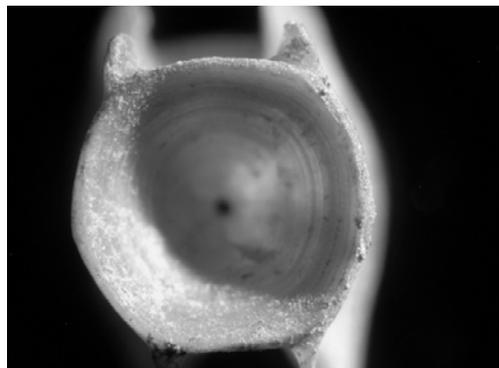


Figure 8. Cypriniformes caudal vertebra (79 x), posterior view, from Homestead Cave (stratum I). This specimen shows no signs of digestive damage.

digestion damage from the few well-documented cyprinid assemblages produced by known agents. Here, we briefly evaluate with more qualitative criteria other potential processes for the deposition of the Homestead Cave fishes. These include a consideration of non-scatological anthropogenic fish deposits and other mammalian and avian predators.

Non-fecal anthropogenic deposits. Our quantitative comparison with human-derived chub remains focused on materials collected from human faecal deposits. Of course, human foragers routinely transport, process, and consume fish carcasses without ingesting their bones. An anthropogenic origin of the Homestead fish of any sort is, however, very unlikely. Only a handful of cultural artifacts were found from the site and all of those were derived from late Holocene deposits (Shaver, 2000). Further, not a single burned or butchered bone was recorded among over 204,000 identified vertebrate specimens from the site (Schmitt, 2000).

Other mammalian predators. Taphonomic work with small mammal and bird prey recovered from scats produced by a variety of carnivores (e.g., other canids, mustelids, ursids, felids) suggests that such deposits are characterized by incomplete skeletal part representation, high degrees of fragmentation, and substantial digestive surface damage (e.g., Andrews, 1990; Andrews & Evans, 1983; Schmitt & Juell, 1994). These patterns contrast with the minimal damage and skeletal completeness of the Homestead fish and suggest a scatological origin for the fauna is unlikely. Carnivores can, however, transport and deposit bones without digesting them and

such remains would thus not reflect the substantial digestive damage that characterize these taxa. Other evidence bearing on carnivore activity from the Homestead fauna suggests they were not a factor. For instance, evidence of carnivore involvement is limited to three —out of over 204,000 vertebrate NISP— gnawed artiodactyl phalanges (Broughton, 2000a; Grayson, 2000a; Livingston, 2000).

Other avian agents. As a result of differences in feeding behavior and digestive physiology, pellets cast by diurnal raptors (Falconiformes) contain substantially less bone and the surviving materials are characterized by a relatively high degree of fragmentation, incomplete skeletal representation, and pronounced surface digestive corrosion compared to owls. These patterns, derived from analyses of avian and mammalian prey remains, are due not only to the lower gastric pH and greater bone digestion capabilities that characterize falconiform taxa, but to the fact that most diurnal raptors remove the flesh from larger prey and thus ingest less bone to begin with (Andrews, 1990; Bochenski *et al.*, 1998, 1999; Duke *et al.*, 1975; Hoffman, 1988; Mayhew, 1977). As a result, substantial bone deposits produced by Falconiformes are more likely to result from uneaten prey remains than they are from pellets (Bochenski *et al.*, 1997, 1999; Bochenski & Tornberg, 2003).

Taphonomic work with fish remains deposited by hawks and eagles is very limited but consistent with observations derived from bird and mammal prey remains. And although we are unaware of work conducted on fish remains from such piscivorous North American falconiform taxa as osprey or bald eagle, Stewart *et al.*

(1999) have provided detailed analyses of fish materials collected from the roosts of African fish eagles (*Haliaeetus vocifer*) in Kenya. Most notably, the fish materials—dominated by cichlids and catfish (*Clarias*)—are characterized by extensive breakage and extremely low element survivorship with, overall, only 6.7% of the bones surviving eagle consumption and digestive processes.

The overall taxonomic composition of the Homestead vertebrate fauna and the cave microhabitat context are also inconsistent with diurnal raptors and other potential avian agents. For instance, the fact that stratum I contains not only fish but an enormous stratigraphically intermixed assemblage of small, nocturnal, rodents (e.g., *Peromyscus*, *Dipodomys*, *Perognathus*, *Neotoma*; Grayson, 2000a) would seem to rule out not only obligate piscivores such as osprey or cormorants (*Phalacrocorax*), but also more generalist raptors such as bald eagle and golden eagle (*Aquila chrysaetos*) that focus on much larger prey items (Kochert et al., 2002; Poole et al., 2002). Finally, the deep enclosed cave context is inconsistent with the behavior of a number of hawks and eagles that favor more exposed nest site contexts, such as trees, or ledges on cliff faces, that provide unobstructed access to nests from above and views of the surrounding landscape (e.g., Bechard & Schmutz, 1995; Buehler, 2000; England et al., 1997; Kochert et al., 2002; Poole et al., 2002; Preston & Beane, 1993).

Other owls. While a variety of indications point to owls as the source for the Homestead fauna, many prey in the deposit are beyond the ~500 g limit for barn owl and their presence suggests that other accumulators were involved. For example, a

number of the cutthroat trout (*Oncorhynchus clarki*) vertebrae from Homestead exceed 9.0 mm in maximum width, suggesting live weights over 2.6 kg; some exceed 11.0 mm, indicating weights over 6.2 kg (see Follet, 1980:115, 1982: figure 3). The abundance of both ducks (e.g., *Aythya*) and mature hares (*Lepus*) in the stratum I fauna also suggests the work of a more powerful predator. The great horned owl, well-known to roost and nest in caves, is most likely in this Great Basin context. This opportunistic feeder has the broadest diet of any North American owl and takes prey ranging in size from scorpions (*Scorpiones*) and mice, to hares and porcupines (*Erithizon dorsatum*; 3.8 – 18 kg); it is also known to scavenge fish (e.g., Bogiatto et al., 2003; Errington et al., 1940; Houston et al., 1998). Great horned owls bolt smaller prey but dismember larger ones at kill sites, where heads and feet are often discarded (Houston et al., 1998). Taphonomic work with great horned owl mammalian prey shows patterns similar to barn owls but with somewhat more extensive bone damage and less complete skeletal part representation (Dodson & Wexler, 1979; Hoffman, 1988; Kusmer, 1990). We note too that the large size of some of the Homestead fish bones also eliminates the possibility that they entered the cave in the stomachs of fish eating birds (e.g., *Phalacrocorax*, *Aechmophorus*) who had fallen prey to owls. Finally, we cannot exclude the possibility that other owl species contributed fish materials at Homestead—western screech owls (*Megascops kennicottii*), for instance, were observed roosting in the cave as the site was being excavated (Figure 2).

Conclusions

The ability to determine the depositional origin of fish remains recovered from cave and rockshelter faunas can be critical to understanding issues relating to ancient human foraging behavior and the reconstruction of past environments. And although owls are widely recognized for the role they play in depositing small mammal and bird materials in caves, they are rarely considered as potential contributors of fish remains in these settings. Our analysis of modern barn owl pellets from Nevada documents not only that this species—a widely regarded micro-mammal specialist—will utilize fish resources but, in certain circumstances, fish can overwhelmingly dominate their diets. In this pellet sample, tui chub bones comprise nearly 90% of the total NISP. Although we lack direct observations on the context of their acquisition, we suspect that the barn owls scavenged tui chub carcasses that resulted from periodic summer dessications or winter freezes of a nearby intermittent stream system.

In addition to documenting a case in which fish prey dominate owl diets, we have provided the first taphonomic analysis of owl-deposited fish remains. Our analysis of 3294 pellet-derived tui chub bones revealed a normal distribution of small-sized fish (10-75 gm), relatively complete skeletal part representation, and minimal bone fragmentation and digestive surface damage. These characteristics are similar to those reported for barn owl mammalian prey and suggest the patterns described here are typical for fish remains deposited by this species as well. Owls should thus be given serious consideration as potential contributors

of cave-derived ichthyofaunas that exhibit these characteristics.

Since work began at Homestead Cave, owls *have* been seriously considered as agents responsible for the site's rich fish record and far-reaching paleoenvironmental implications have been derived from that suggestion. Those implications are supported here by the documentation that fish can dominate the diets of barn owls and by our taphonomic analysis which shows that the Homestead fish sample is, overall, more consistent with a deposition by owls than by any other agent. Further actualistic work with fish remains deposited by other known agents will allow still stronger conclusions regarding the depositional origin of cave-derived ichthyofaunas.

Acknowledgements

We thank P. Moyle, J. Williams, E. Flores, P. Van Ornum, E. Miskow, N. Martinez for helpful assistance and advice; S. Miller and B. Bowman for photographic assistance; and F. Bayham, V. Butler, M. Cannon, and L. Lyman for invaluable comments on an earlier draft of the manuscript.

References

- Andrews, P. (1990). *Owls, Caves and Fossils*. Chicago:University of Chicago Press.
- Andrews, P. & Evans, E.N. (1983). Small mammal bone accumulations produced by mammalian carnivores. *Paleobiology*, 9:289-307.
- Bechard, M.J. & Schmutz, J.K. (1995). Ferruginous Hawk (*Buteo regalis*). In (A. Poole & F. Gill, Eds.) *The Birds of North America, No. 172*. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

- Binford, L.R. (1984). *Faunal Remains from Klasies River Mouth*. New York: Academic Press.
- Bochenski, Z.M., Huhtala, K., Sulkava, S. & Tornberg, R. (1999). Fragmentation and preservation of bird bones in food remains of the golden eagle *Aquila chrysaetos*. *Archaeofauna*, 8: 31-39.
- Bochenski, Z.M., Jussila, P., Pulliainen, E., Tornberg, R. & Tunkkari, P. (1998). Damage to bird bones in pellets of gyrfalcon *Falco rusticolus*. *Journal of Archaeological Science*, 25: 425-433.
- Bochenski, Z.M., Korovin, V., Nekrasov, A.E. & Tomek, T. (1997). Fragmentation of bird bones in food remains of imperial eagles (*Aquila heliaca*). *International Journal of Osteoarchaeology*, 7: 165-171.
- Bochenski, Z.M. & Nekrasov, A.E. (2001). The taphonomy of Sub-Atlantic bird remains from Bazhukovo III, Ural Mountains, Russia. *Acta zoologica cracoviensis*, 44: 93-106.
- Bochenski, Z.M. & Tomek, T. (1997). Preservation of bird bones: erosion versus digestion by owls. *International Journal of Osteoarchaeology*, 7: 372-387.
- Bochenski, Z.M., & Tornberg, R. (2003). Fragmentation and preservation of bird bones in uneaten food remains of the gyrfalcon *Falco rusticolus*. *Journal of Archaeological Science* 30: 1665-1671.
- Bogiatto, R.J., Sardella, B.A. & Essex, J.J. (2003). Food habits of great horned owls in northeastern California with notes on seasonal diet shifts. *Western North American Naturalist*, 63: 258-263.
- Bonnot, P. (1928). An outlaw barn owl. *The Condor*, 30: 320.
- Broughton, J.M. (2000a). The Homestead Cave ichthyofauna. In (D.B. Madsen, Ed.) *Late Quaternary Paleoecology in the Bonneville Basin*. Utah Geological Survey, Bulletin 130, pp. 103-121.
- Broughton, J.M. (2000b). Terminal Pleistocene fish remains from Homestead Cave, Utah, and implications for fish biogeography in the Bonneville Basin. *Copeia*, 2000: 645-656.
- Broughton, J.M., Madsen, D.B. & Quade J. (2000). Fish remains from Homestead Cave and lake levels of the past 13,000 years in the Bonneville Basin. *Quaternary Research*, 53: 392-401.
- Buehler, D.A. (2000). Bald Eagle (*Haliaeetus leucocephalus*). In (A. Poole & F. Gill, Eds.) *The Birds of North America*, No. 564. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- Butler, V.L. (1993). Natural versus cultural salmonid remains: origin of The Dalles Roadcut bones, Columbia River, Oregon, U.S.A. *Journal of Archaeological Science*, 20: 1-24.
- Butler, V.L. (1996). Tui chub taphonomy and the importance of marsh resources in the western Great Basin of North America. *American Antiquity*, 61: 699-717.
- Butler, V.L. (2001). Fish faunal remains. In (R.L. Kelly, Ed.) *Archaeological Survey and Excavations in the Carson Desert and Stillwater Mountains, Nevada*. University of Utah Anthropological Papers, No. 123, Salt Lake City, pp. 271-280.
- Butler, V.L. & Schroeder, R.A. (1998). Do digestive processes leave diagnostic traces on fish bones? *Journal of Archaeological Science*, 25: 957-971.
- Byers, D.A. & Broughton, J.M. (2004). Holocene environmental change, artiodactyl abundances, and human hunting strategies in the Great Basin. *American Antiquity*, 69: 235-256.
- Byers, D.A., Smith, C. & Broughton, J.M. (2005). Holocene artiodactyl population histories and large game hunting in the Wyoming Basin, U.S.A. *Journal of Archaeological Science*, 32: 125-142.
- Darwent, C.M. & Lyman, R.L. (2002). Detecting the postburial fragmentation of carpals, tarsals, and phalanges. In (W. D. Haglund & M. H. Sorg, Eds.) *Advances in Forensic Taphonomy*. Boca Raton, FL: CRC Press, pp. 356-377.
- Derting, T.L. & Cranford, J.A. (1989). Physical and behavioral correlates of prey vulnerability to barn owl (*Tyto alba*) predation. *American Midland Naturalist*, 121: 11-20.
- Dodson, P. & Wexlar, D. (1979). Taphonomic investigations of owl pellets. *Paleobiology*, 5: 292-296.
- Driver, J.C. (1988). Late Pleistocene and Holocene vertebrates and palaeoenvironments from Charlie Lake Cave, northeast British Columbia. *Canadian Journal of Earth Sciences*, 25: 1545-1553.
- Duke, G., Jegers, A., Leff, G., & Evanson, O. (1975). Gastric digestion in some raptors. *Comparative Biochemistry and Physiology*, 56A: 283-286.
- England, A.S., Bechard, M.J. & Houston, C.S. (1997). Swainson's Hawk (*Buteo swainsoni*). In (A. Poole & F. Gill, Eds.) *The Birds of North America*, No. 265. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- Errington, P.L., Hammerstrom, F. & Hammerstrom, F.N. (1940). The great horned owl and its prey in north-central United States. *Iowa Agricultural Experiment Station Research Bulletin*, 277: 757-850.

- Eshmeyer, W.N. & Herald, E.S. (1983). *A Field Guide to Pacific Coast Fishes North America*. Boston: Houghton Mifflin Co.
- Esteban, M., Castanet, J. & Sanchiz, B. (1998). Inferring age and growth from remains of fossil and predated Recent anurans: a test case using skeletochronology. *Canadian Journal of Zoology*, 76: 1689-1695.
- Everitt, B.S. (1992). *The Analysis of Contingency Tables, Second Edition*. London: Chapman & Hall.
- Follett, W.I. (1970). Fish remains from human coprolites and midden deposits obtained during 1968 and 1969 at Lovelock Cave, Churchill County, Nevada. *Contributions of the University of California Archaeological Research Facility*, 10: 163-175.
- Follett, W.I. (1980). Fish remains from the Karlo Site (Ca-Las-7), Lassen County, California. *Journal of California and Great Basin Anthropology*, 2: 114-122.
- Follett, W.I. (1982). An analysis of fish remains from ten archaeological sites at Falcon Hill, Washoe County, Nevada, with notes on fishing practices of the ethnographic Kuyuidikade Northern Paiute. *Nevada State Museum Anthropological Papers*, 18: 181-203.
- Gallup, F.N. (1949). Banding recoveries of *Tyto alba*. *Bird-Banding*, 20: 150.
- Grayson, D.K. (1998). Moisture history and small mammal community richness during the latest Pleistocene and Holocene northern Bonneville Basin, Utah. *Quaternary Research*, 49: 330-334.
- Grayson, D.K. (2000a). Mammalian responses to Middle Holocene climatic change in the Great Basin of the western United States. *Journal of Biogeography*, 27: 181-192.
- Grayson, D.K. (2000b). The Homestead Cave mammals. In (D. B. Madsen, Ed.) *Late Quaternary Paleocology in the Bonneville Basin*. Utah Geological Survey, Bulletin 130, pp. 67-89.
- Grayson, D.K. & Frey, C.J. (2004). Measuring skeletal part representation in archaeological faunas. *Journal of Taphonomy*, 2: 27-42.
- Hockett, B.S. (1995). Comparison of leporid bones in raptor pellets, raptor nests, and archaeological sites in the Great Basin. *North American Archaeologist*, 16: 223-238.
- Hoffman, R. (1988). The contribution of raptorial birds to patterning in small mammal assemblages. *Paleobiology*, 14: 81-90.
- Houston, C.S., Smith, D.G. & Rohner, C. (1998). Great Horned Owl (*Bubo virginianus*). In (A. Poole & F. Gill, Eds.) *The Birds of North America*, No. 372. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- Ille, R. (1991). Preference of prey size and profitability in barn owls *Tyto alba guttata*. *Behaviour*, 116: 80-189.
- Janes, S.W. & Barss, J.M. (1985). Predation by three owl species on northern pocket gophers of different body mass. *Oecologia*, 67: 76-81.
- Johnsgard, P.A. (2002). *North American Owls: Biology and Natural History*, Second Edition. Washington, D.C.: Smithsonian Institution Press.
- Kimsey, J.B. (1954). The life history of the tui chub, *Siphateles bicolor* (Girard), from Eagle Lake, California. *California Fish and Game*, 40: 395-410.
- Kochert, M.N., Steenhof, K., McIntyre, C.L. & Craig, E.H. (2002). Golden eagle (*Aquila chrysaetos*). In (A. Poole & F. Gill, Eds.) *The Birds of North America*, No. 684. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- König, C., Weick, F., & Becking, J.H. (1999). *Owls: A Guide to the Owls of the World*. New Haven: Yale University Press.
- Kusmer, K.D. (1990). Taphonomy of owl pellet deposition. *Journal of Paleontology*, 64: 629-637.
- Lenton, G.M. (1984). The feeding and breeding ecology of Barn Owls *Tyto alba* in peninsular Malaysia. *Ibis*, 126: 551-575.
- Livingston, S.D. (2000). The Homestead Cave avifauna. In (D.B. Madsen, Ed.) *Late Quaternary Paleocology in the Bonneville Basin*. Utah Geological Survey, Bulletin 130, pp. 91-102.
- Lyman, R.L. (1994). *Vertebrate Taphonomy*. Cambridge: Cambridge University Press.
- Lyman, R.L. & O'Brien, M.J. (1987). Plow-zone zooarchaeology: fragmentation and identifiability. *Journal of Field Archaeology*, 14: 493-498.
- Lyman, R.L., Power, E., & Lyman, R.J. (2003). Quantification and sampling of faunal remains in owl pellets. *Journal of Taphonomy*, 1: 3-14.
- Madsen, D.B. (Ed.) (2000). *Late Quaternary Paleocology in the Bonneville Basin*. Utah Geological Survey, Bulletin 130.
- Madsen, D.B., Rhode, D., Grayson, D.K., Broughton, J.M., Livingston, S.D., Hunt, J., Quade, J., Schmitt, D.N. & Shaver, M.W. (2001). Late Quaternary environmental change in the Bonneville basin, western USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 167: 243-271.
- Marti, C.D. (1974). Feeding ecology of four sympatric owls. *The Condor*, 76: 45-61.

- Marti, C.D. (1990). Barn owl (*Tyto alba*). In (A. Poole & F. Gill, Eds.) *The Birds of North America, No. 1*. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- Mayhew, D.F. (1977). Avian predators as accumulators of fossil mammal material. *Boreas*, 6: 25-31.
- Mollhagen, T.R., Wiley, R.W. & Packard, R.L. (1972). Prey remains in golden eagle nests: Texas and New Mexico. *Journal of Wildlife Management*, 36: 784-792.
- Muñoz, M. & Casadevall, M. (1997). Fish remains from Arbreda Cave (Serinyà, Girona), northeast Spain, and their palaeoecological significance. *Journal of Quaternary Science*, 12: 111-115.
- Nagaoka, L. (2005). Differential recovery of Pacific Island fish remains. *Journal of Archaeological Science*, 32: 941-955.
- Poole, A.F., Bierregaard, R.O. & Martell, M.S. (2002). Osprey (*Pandion haliaetus*). In (A. Poole & F. Gill, Eds.) *The Birds of North America, No. 683*. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- Preston, C.R. & Beane, R.D. (1993). Red-tailed Hawk (*Buteo jamaicensis*). In (A. Poole & F. Gill, Eds.) *The Birds of North America, No. 52*. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- Raczynski, J. & Ruprecht, A. (1974). The effect of digestion on the osteological composition of owl pellets. *Acta Ornithologica*, 14: 25-38.
- Rick, T.C., Erlandson, J.M. & Vellanoweth, R. (2001). Paleo-coastal marine fishing on the Pacific Coast of the Americas: perspectives from Daisy Cave, California. *American Antiquity*, 66:595-613.
- Saavedra, B. & Simonetti, J.A. (1998). Small mammal taphonomy: intraspecific bone assemblage comparison between South and North American, barn owl, *Tyto alba*, populations. *Journal of Archaeological Science*, 25: 165-170.
- Schmitt, D.N. (2000). Faunal accumulations and animal foraging behavior in the Lakeside Mountains. In (D.B. Madsen, Ed.) *Late Quaternary Paleoecology in the Bonneville Basin*. Utah Geological Survey, Bulletin 130, pp. 18-20.
- Schmitt, D.N. & Juell, K.E. (1994). Toward the identification of coyote scatological faunal accumulations in archaeological contexts. *Journal of Archaeological Science*, 21: 249-262.
- Shaver, M.W. (2000). Archaeological materials from Homestead Cave. In (D.B. Madsen, Ed.) *Late Quaternary Paleoecology in the Bonneville Basin*. Utah Geological Survey, Bulletin 130, pp. 59-66.
- Smith, G.R. (1985). Paleontology of Hidden Cave: fish. In (D.H. Thomas, Ed) *The Archaeology of Hidden Cave, Nevada. Anthropological Papers of the American Museum of Natural History*, 61: 171-178.
- Stewart, K.M., LeBlanc, L., Matthiesen, D.P. & West, J. (1999). Microfaunal remains from a modern east African raptor roost: patterning and implications for fossil bone scatters. *Paleobiology*, 25: 483-503.
- Van Neer, W. & Morales Muñoz, A. (1992). "Fish middens": anthropogenic accumulations of fish remains and their bearing on archaeoichthyological analysis. *Journal of Archaeological Science*, 19: 683-695.
- Wheeler, A. & Jones, K.G. (1989). *Fishes*. Cambridge: Cambridge University Press.
- Williams, J.E. & Bond, C.E. (1981). A new subspecies of tui chub (Osteichthyes: Cyprinidae) from Guano Basin, Nevada and Oregon. *The Southwestern Naturalist*, 26: 223-230.

