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# Inferring predator identity from skeletal damage of small-mammal prey remains

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## ABSTRACT

**Questions:** Do predator-derived small-mammal skeletal assemblages record statistically distinguishable predator-specific damage signatures? Can a given skeletal assemblage of unknown origin be correctly attributed to a specific predator based on skeletal damage? Has the type of predator responsible for creating the Holocene faunal sequence at Homestead Cave, Utah, remained constant over the depositional history of the record?

**Data incorporated:** Two data sets were compiled from published counts of small-mammal skeletal material recovered from modern scatological assemblages produced by a variety of predators from around the world. One data set contained skeletal part frequencies, whereas the other contained proportional fragmentation information. Skeletal part frequencies and proportional fragmentation data were also compiled for 15 strata spanning the Holocene from Homestead Cave, Utah.

**Method of analysis:** Principal components analysis and discriminant function analysis with cross-validation of predator classification success rates.

**Conclusions:** Modern small-mammal skeletal assemblages produced by owls are reliably differentiable from those produced by diurnal raptors and mammalian carnivores. Owl-produced assemblages are characterized by a low frequency of fragmentation and the survival of a high proportion of fragile skeletal specimens, whereas assemblages produced by diurnal raptors and mammalian carnivores exhibit increased bone destruction and a residual concentration of teeth. The ability to perform species-specific predator identifications is not supported, but skeletal damage patterns are extremely useful for identifying the general type of predator responsible for creating a skeletal concentration of unknown origin, with classification success rates of 70–100%. Finally, application of the method indicates that owl prey were the dominant source for skeletal material over the entire depositional history of the Holocene Homestead Cave record.

*Keywords*: Homestead Cave (Utah), discriminant function analysis, paleoecology, predation, principal components analysis, skeletal damage patterns, small mammals, taphonomy.

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## INTRODUCTION

A full understanding of the response of species to long-term changes in their environment requires data from the recent fossil record (Swetnam *et al.*, 1999; National Research Council, 2005). Small mammals (rodents, insectivores, and some lagomorphs) have long been recognized as exceptionally suitable for studying climatically driven habitat transitions on both neontological and paleontological time-scales (Avery, 1995; Brown, 1995; Vigne and Valladas, 1996; Grayson, 2000; Hadly, 2003). Predation on small mammals is an important mechanism leading to the concentration of their skeletal remains and the formation of modern and fossil small-mammal death-assemblages (Mellet, 1974; Mayhew, 1977; Dodson and Wexlar, 1979; Maas, 1985; Andrews, 1990). Long-term predator roost and latrine sites thus provide unparalleled opportunities to establish 'natural' (pre-human) baselines of small-mammal community composition, if their records can be confidently dissected into ecological snapshots within longer-term ecological archives (e.g. Hadly, 1996; Grayson, 1998, 2000; Vigne and Valladas, 1996; Schmitt *et al.*, 2002). Such data are critical for addressing mammalian responses to environmental change at the time-scales most relevant to broad-scale conservation efforts (hundreds to thousands of years) (Hadly, 1996, 1999; Swetnam *et al.*, 1999; National Research Council, 2005).

Modern predators of small mammals include mammalian carnivores, diurnal raptors, and nocturnal owls (Mellet, 1974; Mayhew, 1977; Andrews, 1990). While mammalian carnivores concentrate their prey's skeletal remains in scat, avian predators produce pellets: regurgitated masses of the undigested components of a bird's meal, including bones, claws, and teeth held together by matted fur. Many of these predators show high roost, den or latrine fidelity ranging from seasonal to millennial time-scales (Bent, 1961; Andrews, 1990), which can lead to a significant build-up of stratified prey material (e.g. Hadly, 1996; Vigne and Valladas, 1996; Grayson, 2000). The ecological information recorded in such faunal archives, however, may be biased by an array of factors. These include time-averaging [the incorporation of multiple generations into a single stratigraphic horizon (Kidwell and Bosence, 1991)], spatial averaging (the incorporation of prey from multiple habitats), and/or shifts in the dominant type of predator occupying a roost/latrine site (Grayson, 1981).

Depending on the scale of the question under investigation, some spatial averaging, and time-averaging ranging from hundreds to thousands of years, may actually be beneficial to reconstruction efforts, providing a more complete picture of the available prey community by incorporating pellets from multiple predators into single assemblages. Nevertheless, different predator species hunting over the same habitat can affect both the taxonomic composition and relative abundance structure of prey death-assemblages if they occupy roost sites sequentially and exhibit different activity patterns or prey selectivities (Grayson, 1981). Thus dramatic shifts in roost occupation, involving nocturnal versus diurnal predators, for example, may still mask or produce spurious temporal patterns of environmentally driven small-mammal community restructuring at these coarser temporal scales. To date, paleoecological reconstruction efforts in such systems have typically rested on the assumption that the identity of the dominant predator or suite of predators at a site has remained constant over the depositional history of its faunal sequence.

It has long been known that bone destruction patterns can contribute unique insights regarding the accumulation history of skeletal debris (e.g. Mayhew, 1977). Prey death-assemblages from pellets and scat are commonly thought to record predator-species-specific patterns of digestive modification, and much previous work has been done investigating patterns of etching and pitting due to acid and enzymatic attack and patterns of bone

destruction as evidence for determining predator identity from field assemblages (Cummings *et al.*, 1976; Mayhew, 1977; Dodson and Wexlar, 1979; Andrews and Nesbit Evans, 1983; Hoffman, 1988; Rensberger and Krentz, 1988; Andrews, 1990; Kusmer, 1990; Denys *et al.*, 1995, 1996; Saavedra and Simonetti, 1998). Many of these studies were limited, however, by a qualitative approach, small sample size (pellets collected from only a few different predator species), or a lack of explicitly defined and consistent quantitative units (reviewed by Lyman, 1994b).

Here I present the first large-scale quantitative synthesis of skeletal damage patterns recorded in modern scatological assemblages and statistically evaluate the utility of these damage patterns for predator identification purposes. I address the following two questions: Do small-mammal skeletal assemblages record statistically distinguishable predator-specific signatures in terms of skeletal part frequencies and fragmentation patterns? And is it possible to use these taphonomic signatures to correctly attribute a modern small-mammal skeletal assemblage of unknown origin to a specific predator? Finally, as a case study, I apply the statistical methods used here to the Holocene faunal record from Homestead Cave, Utah, to test the assumption of constant predator identity over the depositional history of this record.

## METHODS

### Data sets

I compiled data on skeletal part frequencies and fragmentation from the published literature (from Dodson and Wexlar, 1979; Andrews and Nesbit Evans, 1983; Hoffman, 1988; Andrews, 1990; Terry, 2004). Both data sets contain counts of small-mammal skeletal material recovered from modern scatological assemblages produced by a variety of predators from around the world, encompassing a wide range of body sizes (150–3056 g) and a wide range of depositional environments (temperate forests to desert rock outcrops).

#### *Skeletal part frequency data set*

For this data set, I compiled the number of paired skeletal specimens (mandible, scapula, humerus, radius, ulna, innominate, femur, tibia), skulls, ribs, vertebrae, metapodials, phalanges, and teeth (molars and incisors) recorded in 38 different skeletal assemblages produced by 21 different predator species (11 owls, 3 diurnal raptors, and 7 mammalian carnivores) (see Appendix 1). In contrast to the term *skeletal element* – 'a single complete bone or tooth in the skeleton of an animal' – I use the term *skeletal specimen* to refer to 'a bone or tooth or fragment thereof' following Grayson (1984, p. 16). Thus counts of 'specimens' contain no explicit information about bone breakage, but a 'specimen' can be (but is not required to be) a 'skeletal element'. A count of 'specimens', therefore, that places equal weight on all bone fragments, is the same as the quantitative unit NISP (Number of Identified Specimens) (Lyman, 1994a).

Not all data sources included here contained explicit information about whether broken bones ('specimens') were included in their bone tally data. However, Lyman (1994b) suggested that skeletal counts presented by Andrews (1990) are based on NISP values ('specimens'), thus incorporating broken elements and providing a maximum estimate of the number of bones present in an assemblage. Because the majority of the records included in my analyses come from Andrews (1990), I thus assumed that his skeletal counts represent NISP values. For other studies, where information on breakage frequency was provided (e.g. Terry, 2004),

I pooled counts of complete skeletal elements and counts of specimens, thus generating NISP estimates in an effort to maximize consistency between data sets.

For each assemblage I calculated an estimate of the minimum number of prey individuals (MNI) as the highest number of specimens per bone type present in an assemblage divided by the frequency of that bone type in the mammalian body. I did not, however, include information on fragmentation or which side of the body a bone came from, since that information was not always available. I then transformed the data into skeletal part frequencies by dividing the number of tallied specimens by the number of specimens expected given the estimated MNI for the assemblage. Skeletal part frequencies often are presented this way, although there is no consistency in what this statistic is called (see, for example, Dodson and Wexlar, 1979; Korth, 1979; Shipman and Walker, 1980; Andrews, 1990; Kusmer, 1990).

Because left/right and fragmentation information was not available, I was unable to use Minimum Number of Elements (MNE) to construct skeletal part frequency values as recommended by Badgley (1986) for when the probability of association of bone fragments is high. However, using the statistical methods presented below, I conducted a preliminary analysis of data from Lyman (1994b), where skeletal part frequencies based on NISP and MNE counts were both provided for the same assemblages. There was no significant difference in the scores of owls along the first discriminant axis regardless of the initial counting method used (Kolmogorov-Smirnov test, $P = 0.1259$), supporting my use of skeletal part frequencies based on NISP counts for the analyses presented here.

### *Fragmentation data set*

For this data set, I compiled breakage patterns for humeri, ulnae, femora, and tibiae recovered from 18 different assemblages produced by 12 different predator species (3 nocturnal owls, 3 diurnal raptors, and 6 mammalian carnivores) (see Appendix 2). Fragmentation data are expressed as the proportion of specimens exhibiting a certain type of breakage (e.g. the proportion of humeri that are broken distally).

## Statistical analyses

Analyses to investigate the similarity of assemblages produced by different predators in terms of skeletal damage patterns consisted of: (1) principal components analysis and (2) discriminant function analysis with posterior comparison of median scores on the ordination axes, and a cross-validation of classification success results. All analyses were performed in the statistical program R (R Core Development Team, version 2.2.1). A list of the variables used in the analyses can be found in Table 1.

Principal components analysis is an ordination technique that is used to summarize multidimensional (multivariable) data by producing a lower dimensional ordination space in which the proximity of two points reflects their similarity (Gauch, 1982; ter Braak, 1995). Principal components analysis calculates synthetic variables that minimize the total residual sum of squares by extracting the eigenvectors and eigenvalues from the variance–covariance matrix of the original data matrix (ter Braak, 1995; Davis, 2002). Groupings in the data that emerge from principal components analysis are not known beforehand: death-assemblages are free to enter any of the resulting clouds of points in the ordination space.

I used R-mode principal components analysis with no rotation to assess the similarity of small-mammal death-assemblages produced by different predator species. If predator-

**Table 1.** Variables used in the different analyses

| Skeletal part frequencies | | Fragmentation |
|---|---|---|
| PCA/DFA | HS analysis | PCA/DFA/HS analysis |
| Mandibles | Mandibles | Humerus complete |
| Maxillae | Maxillae | Humerus broken |
| Incisors | Incisors | Ulna complete |
| Molars | Molars | Ulna broken |
| Scapulae | Scapulae | Femur complete |
| Humeri | Humeri | Femur broken |
| Radii | Radii | Tibia complete |
| Ulnae | Ulnae | Tibia broken |
| Ribs | Innominates | |
| Vertebrae | Femora | |
| Innominates | Tibiae | |
| Femora | CTMP | |
| Tibiae | | |
| CTMP | | |

*Note*: Due to a lack of information, proportional representations of ribs and vertebrae were excluded from the Homestead Cave analysis of skeletal part frequencies. PCA = principal components analysis, DFA = discriminant function analysis, HS = Homestead Cave. CTMP represents the grouping of carpals, tarsals, metapodials, and phalanges.

species-specific damage patterns exist, death-assemblages produced by individual predator species should cluster together tightly in multidimensional space.

I used discriminant function analysis to address the utility of assemblage-level damage patterns for classifying prey death-assemblages of unknown origin and discriminating between predators that belong to three *a priori* groups: (1) nocturnal owls, (2) diurnal raptors, and (3) mammalian carnivores. Discriminant function analysis differs from techniques such as principal components analysis in requiring that observation classifications be set *a priori* (Davis, 2002), and finding the linear combination of variables (i.e. the function) that produces the maximum difference between the predefined groups.

Discriminant function analysis assumes that variables follow a normal distribution (Davis, 2002). To test this assumption, I applied a Shapiro-Wilk normality test to all variables used in the analyses and a square-root arcsine transformation to reduce heteroscedasticity when necessary. Once the data were projected into the multivariate space as discriminant scores, I used a Kruskal-Wallis rank sum test to test for significant differences between the medians of each predator cluster.

I then assessed the utility of this approach for predator identification through cross-validation (Davis, 2002) by testing how well certain linear combinations of variables classified a subset of the data into the correct *a priori* predator groups. To do this, I randomly split the data sets into thirds. Two-thirds of the data were used as a training set to build the discriminant functions using different combinations of variables. These functions were then used to classify the remaining 'unknown' third of the data, and thus to tally the proportion of samples classified correctly. I used multiple combinations of variables for each data set to determine which variables were most important for correct discrimination between

predators. For the data set of skeletal part frequencies, variable combinations included all bones, robust bones only (defined here as the humerus, innominate, femur, and tibia), fragile bones only (defined here as the scapula, radius, ulna, and ribs), and teeth only (incisors and molars). For the fragmentation data set, variable combinations included all bones, forelimb bones only (humerus and ulna), hindlimb bones only (femur and tibia), and femora only. The cross-validation procedure was iterated 1000 times for each combination of variables for each data set. I then compared differences in the mean proportion of correct classifications for the different variable combinations using both a parametric one-way analysis of variance (ANOVA) with Tukey-Kramer *a posteriori* pairwise comparisons, and a non-parametric Kruskal-Wallis rank sum test. Statistical significance was set at $P < 0.05$.

## RESULTS

### Principal components analysis

Principal components analysis of the skeletal part frequency data set separated predator taxa along the first axis (Fig. 1). In general, owls exhibited lower scores on principal component 1 (PC1 < 0.5) than diurnal raptors and mammalian carnivores (PC1 > 0.3), with these latter two groups restricted to a narrower total range on this axis as well. All groups were characterized by a wide range of scores on principal component 2 (PC2), with no clear separation among groups on this axis. The correlations of the original variables with the principal components (the 'loadings') indicate which variables are primarily responsible for determining the spread of predator taxa along the axes (i.e. what the principal component axes represent). Teeth were characterized by high positive loadings on PC1, while fragile skeletal specimens were characterized by high negative loadings on PC1 (Table 2). Thus the proportion of teeth in these assemblages explained 55% of the variance in PC1 ($r = 0.740$), while the proportion of fragile skeletal specimens explained 91% of the variance in PC1 ($r = -0.952$).

Principal components analysis of predator taxa based on fragmentation patterns revealed a clear separation of owls from both diurnal raptors and mammalian carnivores (Fig. 2), with owls characterized by higher scores along the first principal component (PC1 > 0.0). Broken skeletal specimens were characterized by negative loadings on PC1, while complete skeletal specimens exhibited strong positive loadings on this axis (Table 3). Thus the proportion of bone breakage in these assemblages explained 99% of the variance in PC1 ($r = -0.998$). There did not appear to be any biologically meaningful separation of predators along PC2.

Scatological prey assemblages are commonly thought to record patterns of skeletal part frequencies and fragmentation that are uniquely tied to the specific predator species responsible for creating the assemblage (Dodson and Wexlar, 1979; Andrews and Nesbit Evans, 1983; Hoffman, 1988; Andrews, 1990; Kusmer, 1990). However, results from the principal components analysis presented here indicated a significant amount of variation within assemblages produced by individual predator species even within the same geographic region. Assemblages produced by Barn Owls (*Tyto alba*) in England, for example, were scattered throughout the ordination space (see Fig. 1). This lack of clear sorting casts doubt on the utility of skeletal part frequency patterns as an effective means of predator identification at the species-specific level.

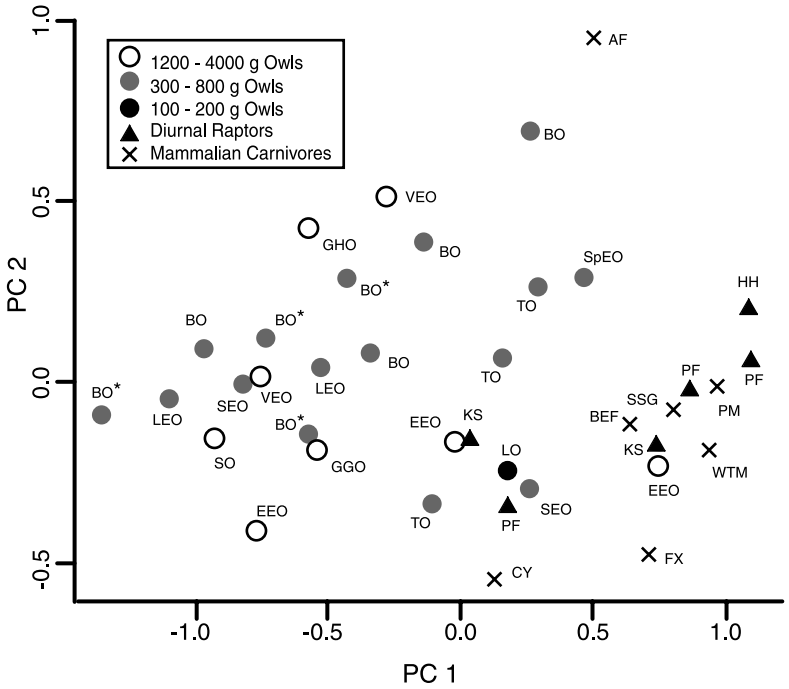


**Fig. 1.** Principal components analysis of predator taxa based on skeletal part frequencies. Owls are coded by body size. Amount of variance explained: PC1 = 0.598, PC2 = 0.125. Assemblages denoted as BO* represent Barn Owl assemblages from England. Based on the distribution of these assemblages throughout the ordination space occupied by owls, there does not appear to be any obvious clustering based on geographic location. EEO = European Eagle Owl, VEO = Verreaux Eagle Owl, SO = Snowy Owl, GGO = Great Grey Owl, GHO = Great Horned Owl, BO = Barn Owl, LEO = Long-eared Owl, SEO = Short-eared Owl, TO = Tawny Owl, SpEO = Spotted Eagle Owl, LO = Little Owl, HH = Hen Harrier, PF = Peregrine Falcon, KS = Kestrel, WTM = White-tailed Mongoose, PM = Pine Martin, SSG = Small-spotted Genet, FX = Red Fox, AF = Arctic Fox, BEF = Bat-eared Fox, CY = Coyote.

To determine if there was an alternative taphonomic explanation for the lack of clear clustering of predators at the species level, I re-analysed the data both by predator body size (see Fig. 1) and by type of collection site (e.g. temperate forest vs. arid rock outcrop). There appeared to be no clustering based on either set of variables, suggesting that the lack of distinct species-level clustering is not due to differences in predator size-selectivity or differences in the post-mortem destruction histories of skeletal remains due to different depositional environments.

## Discriminant function analysis

The discriminant analysis of predator groups based on skeletal part frequencies separated mammalian carnivores, characterized by negative scores on the first linear discriminant (LD1), from diurnal raptors (centred around a score of zero) and owls (primarily restricted to positive scores on LD1) (median scores: owls = 1.37, diurnal raptors = –0.15,

**Table 2.** Loadings of the skeletal part frequency variables on the principal components

| | PC1 | PC2 |
|---|---|---|
| Mandibles | −0.100 | 0.075 |
| Maxillae | −0.096 | 0.087 |
| Incisors | 0.278 | −0.218 |
| Molars | 0.029 | −0.023 |
| Scapulae | −0.223 | −0.014 |
| Humeri | −0.145 | −0.069 |
| Radii | −0.254 | −0.024 |
| Ulnae | −0.198 | −0.051 |
| Ribs | −0.191 | 0.018 |
| Vertebrae | −0.079 | 0.008 |
| Innominates | −0.255 | −0.045 |
| Femora | −0.173 | −0.147 |
| Tibiae | −0.231 | −0.067 |
| CTMP | −0.075 | 0.007 |

*Note*: CTMP represents the grouping of carpals, tarsals, metapodials, and phalanges.

mammalian carnivores = −3.52) (Fig. 3A). Assemblages produced by diurnal raptors appeared mostly separated from both assemblages produced by mammalian carnivores and owls along the second axis, with mammalian carnivores generally restricted to negative scores (except for assemblages produced by the Pine Martin and White-tailed Mongoose), and diurnal raptors mostly restricted to positive scores (except for an assemblage made by a Kestrel) (median scores: owls = −0.63, diurnal raptors = 2.55, mammalian carnivores = −0.79). All three predator groups were characterized by significantly different median scores on LD1 (Fig. 3B, $P < 0.0001$), while only diurnal raptors were characterized by significantly higher scores on the second linear discriminant (LD2) ($P = 0.0100$).

Ulnae, scapulae, and teeth were again important in separating predator taxa along the first axis. These fragile elements, and tibiae, were characterized by high positive loadings on LD1, while molars, together with vertebrae, humeri, and femora were characterized by high negative loadings on LD1. Vertebrae and humeri were characterized by high negative loadings on LD2, while ulnae were characterized by the highest positive loading on this axis (Table 4).

Classification success rates using linear discriminant functions to distinguish between owls, diurnal raptors, and mammalian carnivores based on skeletal part frequencies ranged from ~70 to 78% (Table 5; grand mean = 76%). The classification success rate obtained using all bone types was significantly worse than results obtained using robust skeletal specimens, fragile skeletal specimens, or teeth only (ANOVA, $P < 0.0001$; Kruskal-Wallis, $P < 0.0001$). Using teeth only and fragile skeletal specimens only yielded significantly higher proportions of correct classifications than when only robust skeletal specimens were used ($P = 0.0001$ and $P = 0.013$ respectively). Differences between success rates obtained using teeth only versus fragile skeletal specimens only were not significant ($P = 0.277$).

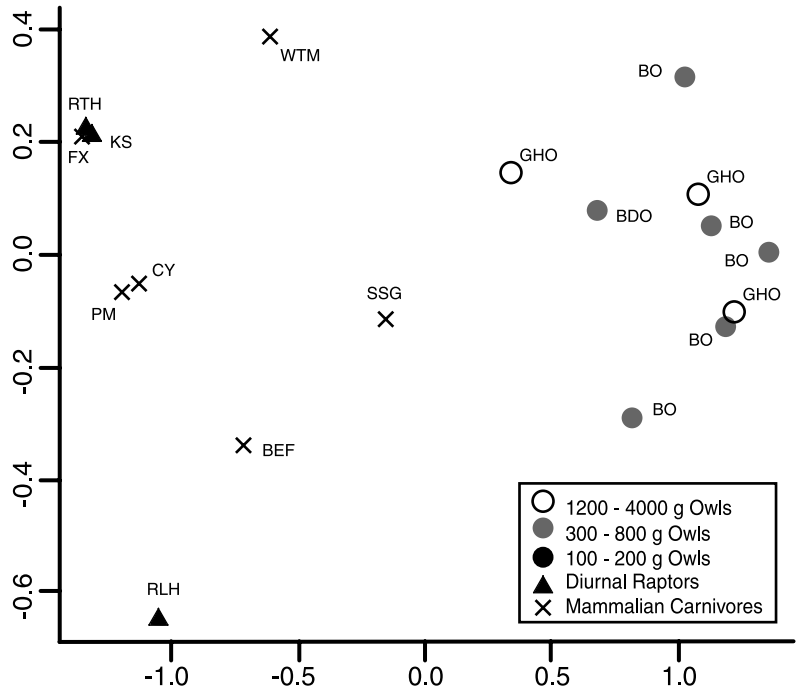


**Fig. 2.** Principal components analysis of predator taxa based on fragmentation patterns. Owls are coded by body size. Amount of variance explained: PC1 = 0.909, PC2 = 0.0515. GHO = Great Horned Owl, BO = Barn Owl, BDO = Barred Owl, RTH = Red-tailed Hawk, RLH = Rough-legged Hawk, KS = Kestrel, WTM = White-tailed Mongoose, PM = Pine Martin, SSG = Small-spotted Genet, BEF = Bat-eared Fox, FX = Red Fox, CY = Coyote.

**Table 3.** Loadings of the fragmentation variables on the principal components

| | PC1 | PC2 |
|---|---|---|
| Humerus complete | 0.359 | 0.032 |
| Humerus broken | −0.359 | −0.032 |
| Ulna complete | 0.359 | −0.072 |
| Ulna broken | −0.302 | 0.221 |
| Femur complete | 0.418 | 0.063 |
| Femur broken | −0.418 | −0.063 |
| Tibia complete | 0.399 | 0.021 |
| Tibia broken | −0.399 | −0.021 |

Classification success rates increased significantly in all cases when functions were asked to discriminate only between owls and 'other predators' (diurnal raptors and mammalian carnivores combined) (Table 5; grand mean = 88%; $P < 0.0001$). Fragile skeletal specimens only and teeth only again produced the highest proportions of correct classifications (~93% and ~91% respectively).

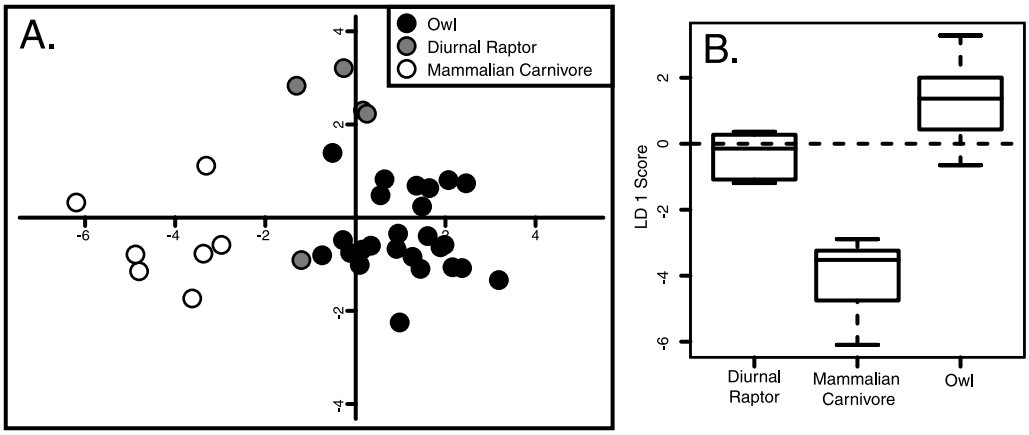


**Fig. 3.** Discriminant function analysis of predator taxa based on skeletal part frequencies. (A) Discriminant scores of predator taxa. Amount of variance explained: LD1 = 0.828, LD2 = 0.172. (B) Kruskal-Wallis rank sum test results comparing the median scores of the different predator groups on LD1. The outlier box plots represent the minimum and maximum scores, the median score, and the 25th and 75th quantiles. Owls show significantly higher median scores on LD1 than diurnal raptors and mammalian carnivores ($P < 0.0001$).

**Table 4.** Loadings of the skeletal part frequency variables on the discriminant axes

| | LD1 | LD2 |
|---|---|---|
| Mandibles | 0.743 | −0.522 |
| Maxillae | −2.097 | 0.066 |
| Incisors | 0.811 | 2.426 |
| Molars | −5.171 | 1.452 |
| Scapulae | 7.867 | 0.536 |
| Humeri | −8.210 | −5.542 |
| Radii | −0.018 | −1.658 |
| Ulnae | 8.771 | 7.084 |
| Ribs | −3.880 | 2.998 |
| Vertebrae | −8.899 | −8.944 |
| Innominates | −1.498 | 1.289 |
| Femora | −6.289 | −3.326 |
| Tibiae | 7.381 | 0.257 |
| CTMP | 1.899 | 1.899 |

*Note*: CTMP represents the grouping of carpals, tarsals, metapodials, and phalanges.

Based on fragmentation patterns, owls were characterized by positive scores on LD1, while diurnal raptors and mammalian carnivores were restricted to negative scores on LD1 (median scores: owls = 3.11, diurnal raptors = −4.14, mammalian carnivores = −2.17) (Fig. 4A). Owls showed significantly higher median scores on LD1 than diurnal raptors and mammalian carnivores ($P = 0.0009$) (Fig. 4B). Diurnal raptors showed significantly

**Table 5.** Classification success rates (± standard error) based on skeletal part frequencies

| Bone combinations | Owl vs. DR vs. MC | Owl vs. 'other predators' |
|---|---|---|
| All bones | 0.698 ± 0.128 | 0.783 ± 0.111 |
| Robust bones only | 0.763 ± 0.120 | 0.893 ± 0.085 |
| Fragile bones only | 0.777 ± 0.118 | 0.927 ± 0.082 |
| Teeth only | 0.783 ± 0.121 | 0.914 ± 0.084 |

*Note*: Classification results when functions were asked to discriminate between owls, diurnal raptors (DR), and mammalian carnivores (MC): grand mean = 0.76. Classification results when functions were asked to discriminate between owls and 'other predators' (diurnal raptors and mammalian carnivores combined): grand mean = 0.88. 'Bone combination' categories of 'All bones', 'Robust bones only', 'Fragile bones only', and 'Teeth only' represent discriminant functions built using select variable combinations.

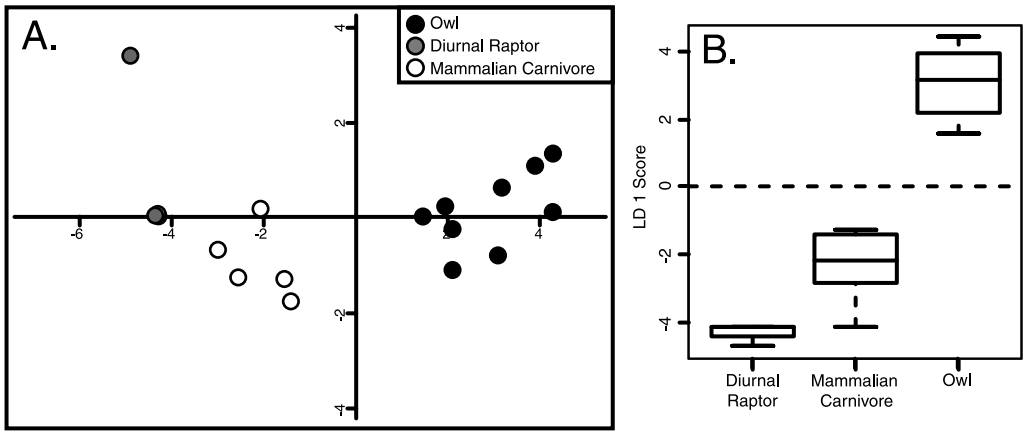


**Fig. 4.** Discriminant function analysis of predator taxa based on fragmentation patterns. (A) Discriminant scores of predator taxa. Amount of variance explained: LD1 = 0.956, LD2 = 0.044. (B) Kruskal-Wallis rank sum test results comparing the median scores of the different predator groups on LD1. The outlier box plots represent the minimum and maximum scores, the median score, and the 25th and 75th quantiles. Owls show significantly higher median scores on LD1 than diurnal raptors and mammalian carnivores ($P = 0.0009$).

higher median scores on LD2 than mammalian carnivores, although neither diurnal raptors nor mammalian carnivores were characterized by median scores that were significantly different from owls on that axis ($P = 0.0872$). Complete skeletal elements were characterized by positive loadings on LD1 (except for the tibia) (Table 6). Ulnae (both broken and complete) also showed a high negative loading on LD2.

Classification success rates when functions were asked to discriminate among owls, diurnal raptors, and mammalian carnivores based on fragmentation patterns were very high, ranging from ~85 to 94% (Table 7; grand mean = 90%; ANOVA, $P < 0.0001$; Kruskal-Wallis, $P < 0.0001$). Success rates were significantly higher when hindlimb bones or femora only were used for classification, than when other combinations of variables were used ($P < 0.0001$).

**Table 6.** Loadings of the fragmentation variables on the discriminant axes

| | LD1 | LD2 |
|---|---|---|
| Humerus complete | 0.796 | −1.040 |
| Humerus broken | −0.796 | 1.040 |
| Ulna complete | 2.846 | −3.488 |
| Ulna broken | 0.365 | −2.101 |
| Femur complete | 2.275 | 1.661 |
| Femur broken | −2.275 | −1.661 |
| Tibia complete | −1.396 | −0.038 |
| Tibia broken | 1.396 | −0.038 |

**Table 7.** Classification success rates (± standard error) based on patterns of fragmentation

| Breakage combinations | Owl vs. DR vs. MC | Owl vs. 'other predators' |
|---|---|---|
| All breakage patterns | 0.841 ± 0.181 | 0.961 ± 0.093 |
| Forelimb bones only | 0.891 ± 0.147 | 0.972 ± 0.075 |
| Hindlimb bones only | 0.937 ± 0.135 | 0.991 ± 0.045 |
| Femora only | 0.942 ± 0.122 | 1.000 ± 0.000 |

*Note*: Classification results when functions were asked to discriminate between owls, diurnal raptors (DR), and mammalian carnivores (MC): grand mean = 0.90. Classification results when functions were asked to discriminate between owls and 'other predators' (diurnal raptors and mammalian carnivores combined): grand mean = 0.90. 'Breakage combination' categories of 'All breakage patterns', 'Forelimb bones only', 'Hindlimb bones only', and 'Femora only' represent discriminant functions built using select variable combinations.

When the analysis was re-done such that the discriminant functions were used to distinguish between only two groups (owls and other predators), up to 100% of classifications were assigned correctly (when femora only were used), and again the overall increase in classification success was significant (Table 7; grand mean = 98%; $P < 0.0001$).

## DISCUSSION

### Skeletal part frequency patterns

Despite the lack of species-level clustering, the results of principal components analysis did indicate a clear separation between owls and other predators. Owl-produced prey assemblages were consistently characterized by a higher proportion of fragile skeletal specimens (scapula, radius, ulna, and ribs) relative to assemblages produced by diurnal raptors and mammalian carnivores, which were in turn characterized by a higher proportion of teeth.

A possible explanation for this higher-level taxonomic separation is differences in the digestive physiology of the different predator groups. While owls and diurnal raptors are similar in that they both regurgitate pellets, diurnal raptors exhibit more acidic stomach

conditions than owls [pH 1.6 and 2.3 respectively (Duke *et al.*, 1975)], which has been suggested as a likely contributing factor to the survival of a lower proportion of skeletal material in hawk pellets than in owl pellets (Mayhew, 1977; Dodson and Wexlar, 1979; Hoffman, 1988). In addition, diurnal raptors retain pellets in their stomach for nearly twice as long as owls before regurgitation (Duke *et al.*, 1976). This increased exposure to the digestive environment is also likely to contribute to the increased destruction of skeletal material in pellets produced by diurnal raptors, making their damage levels more like those of mammalian carnivores than those of owls. Among mammalian carnivores, skeletal remains pass through the entire digestive system, exposing them to more varied chemical environments for longer periods. This must, to some extent, have a negative influence on the amount of skeletal material that survives. Thus it is likely that the rough sorting of predator taxa along PC1 reflects a gradient of predator-specific differences in the effects of digestive processing on the survival of skeletal material.

Teeth, which consist of a dentin body capped by a hard mineralized enamel coat, loaded most heavily on PC2 (Table 2). Enamel is one of the hardest biological structures in the mammalian body, primarily consisting of inorganic calcium phosphate (Kardong, 2002). Although the effect of digestive enzymes on teeth is uncertain (Andrews, 1990), teeth are expected to show higher resistance to the chemical and physical processes of digestive degradation given their dense, mineralized nature. As a consequence, assemblages created by diurnal raptors and mammalian carnivores might be expected to contain a high proportional abundance of teeth relative to the proportional abundance of teeth recovered from the more skeletal-rich assemblages created by owls, as was observed here.

The importance of teeth and fragile skeletal specimens in distinguishing prey death-assemblages produced by owls from those produced by diurnal raptors and mammalian carnivores is further illustrated by the results of the discriminant function analysis. Classifications made using fragile skeletal specimens only and teeth only both resulted in significantly higher success rates than when all bones or just robust bones were used (Table 5).

Interestingly, most misclassifications of death-assemblages were between diurnal raptors and mammalian carnivores. Thus if predators are partitioned into just two groups (owls versus diurnal raptors and mammalian carnivores combined), a significantly higher proportion of correct classifications result, no matter what variables are used (Table 5).

## Fragmentation patterns

Results from the principal components analysis of predator taxa based on small-mammal skeletal breakage patterns also indicated a clear distinction between owls and other predators as a group, and again did not support distinct species-specific clustering (Fig. 2). However, prey assemblages produced by diurnal raptors and mammalian carnivores characteristically have a higher proportion of fragmented skeletal specimens (including femora) than assemblages produced by medium to large owls (Table 3).

These differences in fragmentation could be due to differences in body size, feeding behaviour, and digestive processing. Owls generally swallow their prey whole (Mayhew, 1977; Hoffman, 1988), while diurnal raptors and mammalian carnivores are prone to dismembering their prey before ingestion (Craighead and Craighead, 1956; Mayhew, 1977). This difference in feeding strategies is likely to account for the survival of a higher proportion of complete skeletal specimens in pellet-derived assemblages produced by owls. The increased residence time of

prey remains in the digestive system of diurnal raptors and mammalian carnivores results in increased exposure to physical processing through muscular contractions of the stomach, which could also result in greater fragmentation.

Results from the discriminant function analysis support the importance of hindlimb (femora and tibiae) breakage patterns in distinguishing between predator groups, because significantly higher classification success rates were obtained when using hindlimbs only and femora only than other variable combinations (Table 7).

## TEST CASE: APPLICATION TO A HOLOCENE ROCK-SHELTER RECORD

The results suggest that, assuming post-depositional breakage is minimal, skeletal part frequencies and fragmentation patterns recorded in a prey assemblage can be used with a high degree of confidence to infer whether the assemblage was primarily produced by an owl, a mammalian carnivore or a diurnal raptor. Insights into predator identity – specifically, confidence regarding the type of predator primarily responsible for producing a local record – is critical to recognizing when changes in small-mammal taxonomic composition recorded in the sediments signify true community change, rather than represent an artifact of changes in the dominant type of predator(s) responsible for concentrating skeletal remains into that record (Grayson, 1981).

As a preliminary test, skeletal damage patterns for small-mammal death-assemblages representing 15 separate horizons within the well-studied Homestead Cave record of Utah [~13,000 to 900 cal years B.P. (Madsen, 2000)] were compiled using the same counting methods as in the literature synthesis reported above. These horizons span the Holocene, over which there was an observed shift from small-mammal communities dominated by mesic taxa to communities dominated by xeric taxa (Grayson, 2000). There is also, however, an observed increase in the proportion of diurnal ground squirrels over time (Madsen, 2000). This taxonomic change has been interpreted as a response to regional climate change (Grayson, 2000), but the alternative taphonomic explanation of a change in dominant predator type at the site has not been explicitly rejected.

Using the discriminant function method described above, I found that both skeletal part frequency and fragmentation patterns in all 15 horizons indicate that the skeletal material in this record was concentrated due to predation by owls (Fig. 5). Changes in predator type can thus be rejected for this site: shifts in taxonomic composition of the small-mammal community probably reflect true biological signals, specifically a warming and drying trend through the Holocene.

With progressive burial, one might expect fragile specimens to be preferentially lost and fragmentation to increase (e.g. Terry, 2004). This would shift the oldest assemblages towards an increased proportion of robust skeletal specimens and increased breakage. In the case of Homestead Cave, no significant shifts towards an increased proportion of robust skeletal specimens are evident in terms of skeletal part frequencies. In fact, the opposite appears to be the case, with the median score of the Homestead strata shifted slightly in the opposite direction (towards increased frequencies of fragile specimens) ($P = 0.0083$; Fig. 5A). Despite this slight shift, all strata are still identified as 'owl-produced'. Breakage, however, does appear to increase with depth; the oldest strata are significantly shifted towards increased breakage ($P < 0.0001$; Fig. 5B). This difference between the behaviour of skeletal part frequencies and fragmentation may be due to the fact that NISP tallies contain no information on specimen breakage. Thus even if skeletal specimens show increased

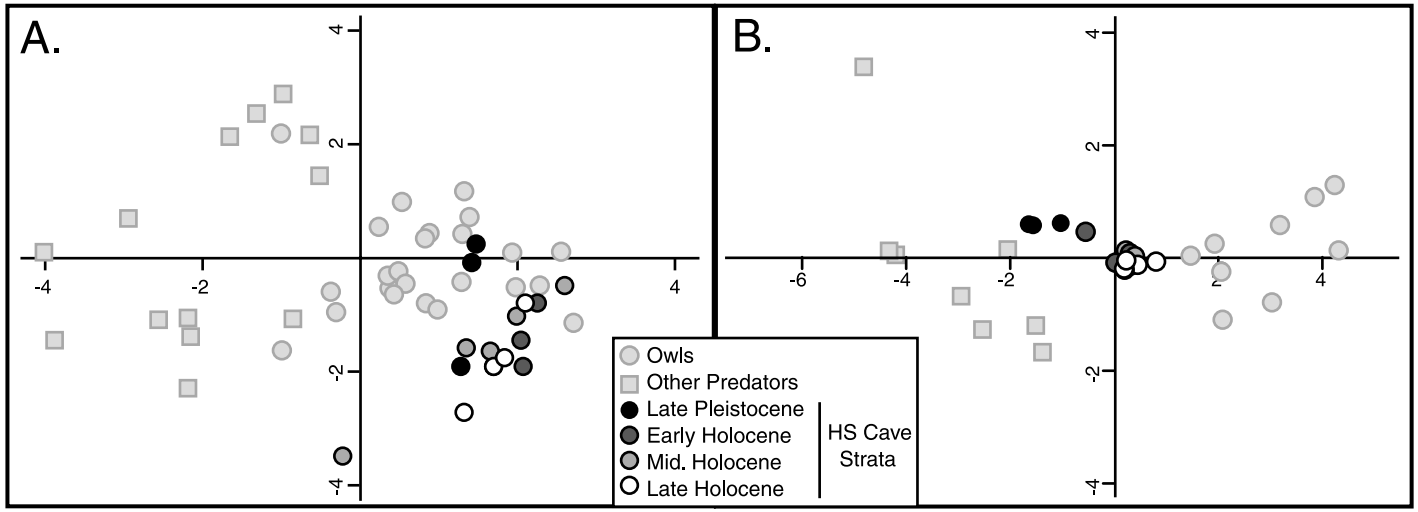


**Fig. 5.** Discriminant function analysis of Homestead Cave strata compared with modern assemblages created by different predator types. (A) Discriminant analysis based on skeletal part frequencies. No information for ribs and vertebrae was available, thus they were not included as variables in the analysis. (B) Discriminant analysis based on fragmentation patterns. Strata that show a shift towards increased breakage represent the oldest horizons in the record (late Pleistocene and early Holocene).

fragmentation, they may not have been completely lost from the record and are thus still counted in the NISP tally.

Breakage can be introduced into the record through pre-burial processes (e.g. physical weathering or trampling at the surface) or through post-burial processes (e.g. compaction). The sedimentation history of Homestead Cave is episodic (Madsen, 2000), although increased breakage does not appear to be associated with the known surfaces of non-deposition in the record, as might be expected if increased breakage were due to pre-burial processes. Compaction of older sediments due to the weight of the overlying sedimentary column, however, cannot be ruled out as a possible mechanism driving the pattern of increased breakage over time, rather than change in predator identity. If, on the other hand, predator identity had changed, one might expect that assemblages generated by diurnal raptors, for example, would also appear shifted towards increased breakage relative to their modern counterparts, thus occupying even more negative regions along the first discriminant axis. This does not appear to be the case at Homestead Cave.

## CONCLUSIONS

Being able to discriminate among biological agents of bone accumulation is critically important to paleoecologists, paleontologists, and zooarchaeologists alike, given that different agents of collection are likely to differ in prey selection and in the extent and style of damage that they inflict on the skeletal remains of their prey. Raptors are important concentrators of small-mammal remains, and it has long been recognized that pellets produced by owls contain qualitatively more bone and more complete skeletal specimens than assemblages produced by other predators (e.g. Mayhew, 1977), and that bones exposed to digestive processing incur distinctive patterns of etching and pitting (e.g. Rensberger and Krentz, 1988; Andrews, 1990). In contrast, this study is the first attempt to use easily quantifiable assemblage-level macroscopic damage patterns and data already available in the literature to demonstrate the possibility of determining statistically, with a high degree of confidence, whether an assemblage was primarily produced by owls, by diurnal raptors or mammalian carnivores.

Identification of predators at the species level using skeletal damage patterns appears dubious, at least given the compiled data sets used here. Thus resolving shifts in owl species occupying the same roost over time does not seem immediately possible. It must be kept in mind, however, that the data utilized in this study were not originally collected for the analyses presented here. Thus it remains unclear whether identification at the species level is ultimately impossible. However, the ability to identify the type of predator responsible for creating a scatological assemblage at a higher taxonomic level, using the data that are readily available in the literature, still carries important implications for paleoecological reconstruction, especially when dealing with deposits encompassing hundreds to thousands of years of time-summed input.

For example, the application of this method to the Holocene strata from Homestead Cave, Utah, shows that fossil assemblages yield the same patterns of damage as observed in modern (surficial) death-assemblages, and that the dominant predator type (owls) remained constant over the depositional history of the record: at Homestead Cave, up-section changes in taxon dominance are thus not taphonomic artifacts, but probably reflect a true biological signal of biotic response to environmental change.

The ability to trace the identity of biotic agents of skeletal accumulation back through

time is necessary if we are to unravel, and potentially correct for, the confounding effects of differences in predator behaviour on patterns of small-mammal community composition. Assuming post-mortem destructive processes do not significantly alter the damage patterns recorded in a death-assemblage before it becomes sealed into the permanent record, the method presented here represents a first step towards doing just that – by beginning to disentangle quantitatively the multiple potential drivers of observed small-mammal community restructuring over time.

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## APPENDIX 1: SKELETAL PART FREQUENCY DATA SET

| Predator | Mandible | Maxilla | Incisor | Molar | Scapula | Humerus | Radius | Ulna | Rib | Vertebra | Innominate | Femur | Tlbia | CTMP | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Barn Owl | 0.996 | 0.380 | 0.033 | 0.153 | 0.409 | 0.623 | 0.678 | 0.775 | 0.192 | 0.142 | 0.522 | 0.569 | 0.757 | 0.277 | Andrews (1990) |
| Barn Owl | 1.000 | 0.489 | 0.043 | 0.043 | 0.862 | 0.989 | 0.936 | 0.979 | 0.831 | 0.444 | 0.894 | 1.000 | 0.957 | 0.385 | Andrews (1990) |
| Barn Owl | 0.992 | 0.794 | 0.183 | 0.201 | 0.841 | 0.817 | 0.698 | 0.706 | 0.638 | 0.429 | 0.897 | 0.786 | 0.841 | 0.236 | Andrews (1990) |
| Barn Owl | 0.568 | 1.000 | 0.136 | 0.072 | 0.398 | 0.545 | 0.511 | 0.500 | 0.108 | 0.211 | 0.523 | 0.580 | 0.534 | 0.084 | Andrews (1990) |
| Barn Owl | 0.717 | 0.542 | 0.208 | 0.033 | 0.583 | 0.683 | 0.500 | 0.567 | 0.142 | 0.084 | 0.908 | 1.000 | 1.000 | 0.031 | Andrews (1990) |
| Barn Owl | 1.000 | 0.800 | 0.100 | 0.028 | 0.167 | 0.367 | 0.233 | 0.300 | 0.008 | 0.033 | 0.333 | 0.367 | 0.533 | 0.013 | Andrews (1990) |
| Barn Owl | 0.983 | 0.950 | 0.483 | 0.158 | 0.517 | 0.667 | 0.550 | 0.633 | 0.218 | 0.244 | 0.667 | 0.683 | 0.700 | 0.142 | Andrews (1990) |
| Barn Owl | 1.000 | 0.606 | 0.197 | 0.228 | 0.528 | 0.725 | 0.810 | 0.577 | 0.828 | 0.076 | 0.563 | 0.718 | 1.000 | 0.175 | Andrews (1990) |
| Great Grey Owl | 0.984 | 0.859 | 0.531 | 0.203 | 0.578 | 0.875 | 0.609 | 0.719 | 0.220 | 0.047 | 0.797 | 0.828 | 0.906 | 0.045 | Andrews (1990) |
| Great Horned Owl | 1.000 | 0.300 | 0.000 | 0.000 | 0.500 | 0.800 | 0.700 | 0.700 | 0.762 | 0.286 | 0.500 | 0.400 | 0.600 | 0.479 | Terry (2004) |
| Snowy Owl | 0.714 | 0.571 | 0.286 | 0.107 | 0.679 | 0.821 | 0.714 | 0.643 | 0.824 | 0.229 | 0.929 | 0.893 | 0.964 | 0.525 | Andrews (1990) |
| Long-eared Owl | 0.991 | 0.870 | 0.204 | 0.105 | 0.361 | 0.806 | 0.481 | 0.639 | 0.098 | 0.043 | 0.880 | 0.926 | 0.889 | 0.029 | Andrews (1990) |
| Long-eared Owl | 0.873 | 0.825 | 0.103 | 0.070 | 0.659 | 0.921 | 0.905 | 0.889 | 0.551 | 0.262 | 0.873 | 0.952 | 0.992 | 0.193 | Andrews (1990) |
| Short-eared Owl | 0.833 | 0.800 | 0.133 | 0.256 | 0.467 | 0.967 | 0.833 | 0.867 | 0.303 | 0.243 | 0.733 | 0.833 | 0.900 | 0.250 | Andrews (1990) |
| Short-eared Owl | 1.000 | 0.354 | 0.875 | 0.097 | 0.146 | 0.854 | 0.479 | 0.500 | 0.050 | 0.035 | 0.375 | 0.667 | 0.604 | 0.121 | Andrews (1990) |
| Verreaux Eagle Owl | 0.891 | 1.000 | 0.152 | 0.196 | 0.565 | 0.674 | 0.587 | 0.609 | 0.316 | 0.344 | 0.348 | 0.435 | 0.500 | 0.212 | Andrews (1990) |
| Verreaux Eagle Owl | 1.000 | 0.950 | 0.270 | 0.292 | 0.630 | 0.860 | 0.910 | 0.790 | 0.294 | 0.229 | 0.560 | 0.880 | 0.850 | 0.144 | Andrews (1990) |
| Spotted Eagle Owl | 1.000 | 0.462 | 0.425 | 0.061 | 0.113 | 0.472 | 0.142 | 0.330 | 0.026 | 0.018 | 0.321 | 0.566 | 0.406 | 0.048 | Andrews (1990) |
| European Eagle Owl | 0.806 | 0.639 | 0.528 | 0.134 | 0.222 | 0.556 | 0.417 | 0.750 | 0.045 | 0.096 | 0.500 | 0.972 | 0.639 | 0.048 | Andrews (1990) |
| European Eagle Owl | 0.663 | 0.163 | 1.000 | 0.292 | 0.213 | 0.550 | 0.188 | 0.400 | 0.043 | 0.109 | 0.225 | 0.388 | 0.413 | 0.113 | Andrews (1990) |
| European Eagle Owl | 0.808 | 0.827 | 0.654 | 0.231 | 0.808 | 0.981 | 0.885 | 0.904 | 0.170 | 0.397 | 0.865 | 0.942 | 0.673 | 0.444 | Andrews (1990) |
| Tawny Owl | 0.910 | 0.821 | 0.795 | 0.071 | 0.192 | 0.603 | 0.603 | 0.538 | 0.085 | 0.016 | 0.551 | 0.949 | 0.987 | 0.047 | Andrews (1990) |
| Tawny Owl | 1.000 | 0.679 | 0.464 | 0.012 | 0.143 | 0.643 | 0.250 | 0.429 | 0.003 | 0.020 | 0.429 | 0.500 | 0.464 | 0.016 | Andrews (1990) |
| Tawny Owl | 0.964 | 0.536 | 0.536 | 0.048 | 0.214 | 0.429 | 0.393 | 0.536 | 0.071 | 0.064 | 0.500 | 0.679 | 0.536 | 0.057 | Andrews (1990) |

**APPENDIX 1**—*continued*

| Predator | Mandible | Maxilla | Incisor | Molar | Scapula | Humerus | Radius | Ulna | Rib | Vertebra | Innominate | Femur | Tlbia | CTMP | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Little Owl | 0.786 | 0.214 | 0.500 | 0.298 | 0.143 | 0.786 | 0.143 | 0.500 | 0.071 | 0.054 | 0.214 | 0.857 | 1.000 | 0.108 | Andrews (1990) |
| Peregrine Falcon | 0.417 | 0.583 | 0.667 | 0.403 | 0.333 | 0.667 | 0.167 | 0.750 | 0.218 | 0.066 | 0.167 | 0.917 | 0.750 | 0.115 | Andrews (1990) |
| Peregrine Falcon | 0.571 | 0.571 | 1.000 | 0.179 | 0.000 | 0.286 | 0.071 | 0.214 | 0.000 | 0.002 | 0.071 | 0.286 | 0.286 | 0.005 | Andrews (1990) |
| Peregrine Falcon | 0.661 | 0.669 | 1.000 | 0.332 | 0.169 | 0.387 | 0.202 | 0.323 | 0.017 | 0.025 | 0.065 | 0.403 | 0.331 | 0.074 | Andrews (1990) |
| Kestrel | 0.679 | 0.343 | 1.000 | 0.284 | 0.209 | 0.500 | 0.261 | 0.366 | 0.036 | 0.033 | 0.231 | 0.381 | 0.418 | 0.054 | Andrews (1990) |
| Kestrel | 0.938 | 0.500 | 0.688 | 0.083 | 0.313 | 0.813 | 0.563 | 0.563 | 0.115 | 0.119 | 0.563 | 0.688 | 0.500 | 0.175 | Andrews (1990) |
| Hen Harrier | 0.703 | 0.688 | 1.000 | 0.198 | 0.047 | 0.359 | 0.156 | 0.141 | 0.038 | 0.006 | 0.063 | 0.156 | 0.141 | 0.038 | Andrews (1990) |
| White-tailed Mongoose | 0.357 | 0.333 | 1.000 | 0.266 | 0.119 | 0.524 | 0.095 | 0.310 | 0.112 | 0.149 | 0.167 | 0.429 | 0.190 | 0.141 | Andrews and Nesbit Evans (1983) |
| Small-spotted Genet | 0.994 | 0.460 | 0.977 | 0.114 | 0.034 | 0.511 | 0.121 | 0.161 | 0.004 | 0.061 | 0.224 | 0.598 | 0.368 | 0.013 | Andrews and Nesbit Evans (1983) |
| Bat-eared Fox | 0.765 | 0.765 | 0.971 | 0.044 | 0.118 | 0.706 | 0.176 | 0.235 | 0.059 | 0.265 | 0.324 | 0.706 | 0.176 | 0.021 | Andrews and Nesbit Evans (1983) |
| Coyote | 0.813 | 0.500 | 1.000 | 0.260 | 0.125 | 0.875 | 0.625 | 0.563 | 0.063 | 0.123 | 0.375 | 0.875 | 0.750 | 0.168 | Andrews and Nesbit Evans (1983) |
| Fox | 0.400 | 0.200 | 1.000 | 0.250 | 0.100 | 0.600 | 0.200 | 0.300 | 0.062 | 0.103 | 0.200 | 0.800 | 0.500 | 0.190 | Andrews and Nesbit Evans (1983) |
| Arctic Fox | 1.000 | 0.833 | 0.000 | 0.333 | 0.000 | 0.500 | 0.167 | 0.167 | 0.064 | 0.149 | 0.000 | 0.167 | 0.333 | 0.312 | Andrews and Nesbit Evans (1983) |
| Pine Martin | 0.400 | 0.300 | 0.900 | 0.250 | 0.200 | 0.600 | 0.100 | 0.400 | 0.046 | 0.079 | 0.100 | 0.200 | 0.100 | 0.108 | Andrews and Nesbit Evans (1983) |

*Note*: CTMP represents the grouping of carpals, tarsals, metapodials, and phalanges.

## APPENDIX 2: FRAGMENTATION FREQUENCY DATA SET

*Note*: CTMP represents the grouping of carpals, tarsals, metapodials, and phalanges.

| Predator | H complete | H broken | U complete | U broken | F complete | F broken | T complete | T broken | Source |
|---|---|---|---|---|---|---|---|---|---|
| Barn Owl | 0.775 | 0.225 | 0.853 | 0.147 | 0.955 | 0.045 | 0.882 | 0.118 | Andrews (1990) |
| Barn Owl | 0.874 | 0.126 | 0.988 | 0.012 | 0.833 | 0.167 | 0.908 | 0.092 | Andrews (1990) |
| Barn Owl | 0.710 | 0.290 | 0.985 | 0.015 | 0.627 | 0.373 | 0.783 | 0.217 | Andrews (1990) |
| Barn Owl | 0.949 | 0.051 | 0.957 | 0.043 | 0.989 | 0.011 | 0.931 | 0.069 | Hoffman (1988) |
| Barn Owl | 0.893 | 0.107 | 0.654 | 0.346 | 1.000 | 0.000 | 0.773 | 0.227 | Dodson and Wexlar (1979) |
| Barred Owl | 0.667 | 0.333 | 0.696 | 0.304 | 0.734 | 0.266 | 0.760 | 0.240 | Hoffman (1988) |
| Great Horned Owl | 0.870 | 0.130 | 0.790 | 0.210 | 0.838 | 0.162 | 0.919 | 0.081 | Hoffman (1988) |
| Great Horned Owl | 0.623 | 0.377 | 0.580 | 0.420 | 0.718 | 0.282 | 0.444 | 0.556 | Dodson and Wexlar (1979) |
| Great Horned Owl | 0.615 | 0.385 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | Terry (2004) |
| Red-tailed Hawk | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | Hoffman (1988) |
| Rough-legged Hawk | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 1.000 | 0.000 | 1.000 | Hoffman (1988) |
| Kestrel | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | Hoffman (1988) |
| White-tailed Mongoose | 0.300 | 0.700 | 0.080 | 0.920 | 0.250 | 0.750 | 0.370 | 0.630 | Andrews and Nesbit Evans (1983) |
| Small-spotted Genet | 0.430 | 0.570 | 0.540 | 0.460 | 0.170 | 0.830 | 0.570 | 0.430 | Andrews and Nesbit Evans (1983) |
| Bat-eared Fox | 0.260 | 0.740 | 0.570 | 0.430 | 0.030 | 0.970 | 0.100 | 0.900 | Andrews and Nesbit Evans (1983) |
| Coyote | 0.070 | 0.930 | 0.250 | 0.750 | 0.000 | 1.000 | 0.000 | 1.000 | Andrews and Nesbit Evans (1983) |
| Fox | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | Andrews and Nesbit Evans (1983) |
| Pine Martin | 0.000 | 1.000 | 0.250 | 0.750 | 0.000 | 1.000 | 0.000 | 1.000 | Andrews and Nesbit Evans (1983) |

*Note*: H = humerus, U = ulna, F = femur, T = tibia.