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Quantification and Sampling of Faunal Remains in Owl Pellets

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Paleozoologists and taphonomists have long recognized various properties of quantification and sampling with respect to collections they study. Those same properties attend samples of modern owl pellets. The particular skeletal elements identified and the way in which prey remains are grouped for tallying both influence measures of relative prey abundance in a collection of 56 barn-owl (*Tyto alba*) pellets from southeastern Washington. As the number of prey and the number of pellets in a collection increases across 107 published collections of North American barn-owl pellets, the richness of mammalian genera per collection increases. As the size of the most abundant prey taxon in a pellet collection decreases, the average number of individual prey per pellet increases. Pellets with more identifiable mammalian remains contain more individual prey. Larger pellets contain more individual prey than smaller pellets. These observations indicate that the properties of quantification and sampling so well known to paleozoologists can be created during the biostratinomic phase of a taphonomic history. Modern owl pellets are an excellent educational resource for teaching principles of taphonomy and zooarchaeology.

Keywords: BARN OWL, OWL PELLET ANALYSIS, PREY RICHNESS, PREY DIVERSITY, QUANTIFICATION, SAMPLING EFFORT

Introduction

Paleontologists have long known that various nonhuman faunal agents accumulate remains of animals they have preyed upon. J. S. Mellet (1974) was explicit about the potential that mammalian carnivores often accumulate significant numbers of microvertebrate remains, and he argued that this behavior probably accounted for various fossil accumulations. A few years later, D. F. Mayhew (1977) pointed out that avian predators held the same potential and that close (microscopic) study of modern remains revealed differences in breakage patterns and digestive damage on bones and teeth accumulated by nocturnal (owl) and diurnal (falcon) avian predators. These landmark studies have subsequently been greatly expanded and supplemented such that we are now aware of interspecific differences in bone accumulation and modification behaviors of many nonhuman

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predators (e.g., Andrews, 1990; Andrews & Evans, 1983; Dodson & Wexlar, 1979; Hockett, 1995, 1996; Hoffman, 1988; Kusmer, 1990; Schmitt & Juell, 1994). In this paper we are concerned with avian predators, especially the common barn owl (*Tyto alba*).

Natural historians of various sorts and ornithologists in particular have long studied the contents of owl pellets to gain insights to owl diet and foraging behavior (Errington, 1930; Fisher, 1896) as well as to assess the taxonomic composition and structure of local faunas (Pearson & Pearson, 1947). During the course of these studies, ornithologists have grappled with many of the same issues that zooarchaeologists have, especially with respect to how to quantify the remains of vertebrate prey contained in what are variously referred to as cast or egested owl and raptor pellets in order to derive measures of the predator's diet (Marti, 1987). Thus, ornithologists define the "minimum number of animals" as "equal to the greatest number of identical bones per taxon" (Mollhagen et al., 1972:785), a definition very similar to much earlier ones by paleontologists Chester Stock (1929) and Hildegarde Howard (1930) for the familiar minimum number of individuals (MNI) of zooarchaeology (Grayson, 1984; Lyman, 1994a, b). Stock (1929:282) wrote that each taxon's abundance comprised a count "determined by the number of similar parts of the internal skeleton" and noted that the count was in many cases "probably a minimum estimate." Howard (1930:81) indicated that "the left or the right of the element occurring in greatest abundance was used to make the count."

Paleontologist Theodore White popularized the MNI quantitative unit among zooarchaeologists, defining it as "the most abundant element of the species found" once "right and left [elements are distinguished] and use the greater number as the unit of calculation" (White, 1953a:397). He made the unit especially popular when he introduced a method for converting that unit into pounds of edible meat (White, 1953a, b). The reasoning behind such a conversion was simple. A stew made from one (MNI) elephant and one (MNI) mouse is not the same as a stew made from 1 kg of elephant meat and 1 kg of mouse meat. Ornithologists independently developed nearly the same procedure several decades later for exactly the same reason (Steenhof, 1983).

Interestingly, although paleontologists may have developed and used MNI and meat weight before biologists did, the latter share precedence in using what is today often referred to as normed or scaled minimum (number of) animal units or % MAU. Though originally introduced by C. K. Brain (1967, 1969; see Lyman, 1994b for discussion), the %MAU was popularized among zooarchaeologists by Binford (1978, 1984; Binford & Bertram, 1977; see Lyman, 1994b for discussion) in the early 1980s as a way to measure variation in frequencies of different skeletal portions. This measure was used by both Brain and Binford to help determine if variation in skeletal part frequencies was the result of differential transport and accumulation or the result of differential survival. Biologists independently developed and used this quantitative unit about the same time Brain did for very similar reasons—to assess differences and similarities in the taphonomic histories of different prey taxa—though the predator they were studying was a raptor. Mollhagen et al. (1972:789) referred to the calculated value as "percent of potential," described it as "calculated after considering which of the elements occur one per animal (cranium, sacrum) and which occur two per animal, and considering which elements potentially represent the greatest number of animals," and noted that it was "expressed [for each skeletal element] as a percentage of the element representing the greatest number of animals."

The point of the preceding is simple. Natural historians studying the contents of owl pellets and raptor nests and zooarchaeologists studying animal bones in archaeological sites have often developed similar (if not identical) analytical methods because they are all asking the same kinds of questions of the faunal remains they study. Interpretations of those remains are, however, quite another matter. For example, we attempted to

publish an analysis of two samples of owl pellets in several ornithological journals, but the manuscript was rejected because of what were thought to be serious deficiencies in our samples and our actualistic control of them. We interpret the acceptance of our manuscript by a paleozoological journal (Lyman & Lyman, 2003) as evidence of the greater sympathy for deficiencies inherent in many paleozoological samples, whether paleontological or zooarchaeological. We also attempted to publish the results presented below in several ornithological journals but again our efforts were found to be unsatisfactory. We take these rejections to signify that, although ornithologists might learn much from a greater understanding of taphonomic and paleozoological method, they seem uninterested. Given the seemingly greater flexibility and open-mindedness of paleozoologists, we offer the following as an example of how paleozoologists might use modern collections of raptor pellets to learn, or to teach students, about assessing sample adequacy and the quantification of faunal remains.

As noted above, taphonomists have now learned to recognize attributes of bone modification that serve as signatures of particular taphonomic agents. One category of such agents is birds of prey. Paleozoologists have also learned much about quantifying faunal remains and assessing the adequacy of samples of faunal remains for addressing particular questions (Grayson, 1984; Lyman, 1994a, b). So far as we are aware, no one has studied collections of faunal remains generated by birds of prey with the intention of learning about quantitative and sampling properties of those collections. That is one of our objectives here. We take our lead from basic paleozoology methods, and begin with a brief discussion of quantitative units and sampling issues in paleozoology. This is followed by a description of the materials we use to study quantification and sampling issues. Results of several kinds of analysis are then summarized and we conclude with a discussion of the taphonomic relevance of what we have learned.

Quantification and sampling in paleozoology

Two measures of taxonomic abundance are typically used in paleozoology. One is the number of identified specimens per taxon (NISP*t*), where a specimen is a single bone or tooth, or fragment thereof (Grayson, 1984; Lyman, 1994a, b). NISP*t* depends on many variables, two important ones being the degree of fragmentation of specimens (Lyman, 1994a) and whether all or only some of the skeletal specimens of a taxon in a collection are identified (Grayson, 1984). Fragmentation increases NISP*t* to a point when fragmentation is so great that specimens no longer retain taxonomically diagnostic features (Lyman, 2002); NISP*t* subsequently decreases (Marshall & Pilgram, 1993). Thus, if skeletal elements of individual taxa are differentially fragmented, NISP*t* will vary accordingly. Similarly, if only crania in one collection are identified but crania and mandibles are identified in another collection, NISP*t* values of the two collections will not be comparable.

The other measure of taxonomic abundance is the minimum number of individuals per taxon (MNI*t*), defined as the minimum number of individual animals necessary to account for the identified specimens of a taxon (Grayson, 1984; Lyman, 1994b). This measure is often used in paleozoology because NISP*t* is plagued by the problem of skeletal specimen interdependence; a left and a right mandible of a species in a collection gives an NISP*t* of 2 but the two specimens may be from the same individual animal. MNI*t* avoids this problem by tallying the most abundant skeletal element (e.g., cranium, left mandible, right femur) per taxon. MNI*t* per collection is, however, strongly influenced by how faunal specimens are aggregated. MNI*t* counts tend to be smaller when a paleozoological collection is treated as a single aggregate than when MNI*t* is derived for each stratigraphically distinct aggregate of remains and the stratum-specific MNI*t* values are summed for the collection as a whole (Grayson, 1984). This is so because different aggregates typically comprise a different skeletal element as the most abundant for a particular taxon.

If only crania are identified, NISP*t* will correlate perfectly with MNI*t* for a collection. MNI*t* is often strongly but imperfectly correlated with the NISP*t* in paleozoological collections; correlation is imperfect because different skeletal elements are typically the most abundant for different taxa (Grayson, 1984). It has been shown that as NISP per collection (= ?NISP*t*) and MNI per collection (= ?MNI*t*) increase across a set of fossil collections, so too does taxonomic richness (number of taxa represented) per collection. Similarly, measures of taxonomic heterogeneity (e. g., Shannon index) of fossil collections sometimes correlate with measures of taxonomic abundance such as NISP and MNI (Grayson, 1984).

In paleozoology, one measure of sampling effort is the volume of sediment examined (Wolff, 1975). An equivalent measure in studies of owl diet is the number of pellets per collection. When correlations are found between a measure of sampling effort and taxonomic richness or heterogeneity in a set of collections, variation in richness and heterogeneity across those collections may be a function of sampling effort rather than a function of variation in the exploitation of prey (Grayson, 1984).

Researchers have often reported MNI*t* and Shannon indices for owl pellet collections (e.g., Clark & Bunck, 1991; Maser et al., 1970; Roth & Powers, 1979). Here we are concerned that relations similar to those between variable pairs in paleozoological collections might exist between those same variable pairs among collections of owl pellets. To determine if these relations existed, we examined the influence of (i) how prey remains are counted and how they are aggregated on measures of prey abundance, (ii) measures of prey abundance on prey richness and prey heterogeneity, (iii) the number of pellets per collection on measures of prey richness and heterogeneity, (iv) prey size on number of prey per pellet, and (v) pellet size on measures of prey richness and heterogeneity. If statistically significant correlations exist between these variable pairs among samples of modern owl pellets, then we will have strong evidence that these relations develop during the biostratinomic phase of a taphonomic history. Our second objective was to assess this possibility.

Materials and methods

We used two data sets to examine the relations between variable pairs. One data set comprised 107 published collections of barn-owl pellets. A "collection" generally comprised multiple owl pellets from a single roost or nest. Collections were selected on the basis of three criteria. First, we restricted analysis to North American collections because this is where we work and pertinent literature was readily accessible. The 107 collections are geographically distributed as follows: 3–Arizona; 10–British Columbia; 19–California; 1–Colorado; 1–District of Columbia; 1–Idaho; 2–Indiana; 2–Kansas; 3–Louisiana; 1–Massachusetts; 2–Mexico; 1–Michigan; 4–Nebraska; 1–Nevada; 11–Ohio; 1–Oklahoma; 18–Oregon; 1–Pennsylvania; 2–South Carolina; 16–Texas; 4–Utah; 1–Virginia; 2–Washington. Second, the number of pellets in a collection had to be indicated. In the collections included, the number of pellets per collection ranged from 5 to 825. Of the 107 collections, 60 had 5–100 pellets, 23 had 101–200 pellets, 12 had 201–500 pellets, and 11 had > 500 pellets. Third, the absolute abundance—the number of individual prey per taxon rather than the proportional abundance of each taxon relative to all other taxa—of total mammalian prey had to be reported. Prey could be reported as genera, species, or some combination of the two; we used genera in most analyses because of uneven reporting of species.

The second data set comprised 56 barn-owl pellets we collected in summer 1999 from a roost in southeastern Washington state, U.S.A. Size and shape (5–6 cm long, 2.5–3 cm diameter, oval) of the pellets are consistent with other reported barn-owl pellets (Moon, 1940; Wilson, 1938). The condition of the bones in the pellets (relatively complete skeletons, most long bones not fragmented or nearly complete) is also consistent with the condition of prey remains in other barn-owl pellets (Andrews, 1990; Dodson & Wexlar,

Table 1. Frequencies of mammalian crania and mandibles in 56 barn-owl pellets from southeastern Washington

Taxon	Number of of crania	Number of left mandibles	Number of right mandibles	MNI*t*
Sorex vagrans	4	4	4	4
Sylvilagus cf. *nuttallii*		1		1
Peromyscus maniculatus	155	164	166	166
Microtus montanus	46	48	47	48
Thomomys talpoides	6	6	5	6

1979; Hoffman, 1988; Kusmer, 1990). These two facts indicate this collection (LPL, hereafter) can be used to evaluate the influence of pellet size, how prey remains are grouped, and how they are counted; these variables are seldom explicitly reported among the 107 published collections.

Each pellet in LPL was assigned a unique number, measured (length and diameter), and then disaggregated. Materials were sorted through with a dental pick and tweezers, and all observed bones and teeth in each pellet were removed and kept separate. To determine abundances of prey taxa, mandibles, crania, and isolated maxillae were identified to the most specific level possible using comparative collections and published diagnostic criteria (Hall, 1981; Ingles, 1965; Junge & Hoffmann, 1981; Maser & Storm, 1970). The LPL collection contained crania and mandibles taxonomically distributed as indicated in Table 1. All mammal species represented in LPL have been found within a 15-km radius of the roost (Johnson & Cassidy, 1997). Based on MNI*t*, 74% of the prey are deer mice (*Peromyscus maniculatus*), 20% are montane voles (*Microtus montanus*), 3% are northern pocket gopher (*Thomomys talpoides*), 2% are vagrant shrew (*Sorex vagrans*), and 1% are Nuttall's cottontail (*Sylvilagus nuttallii*).

Results

Quantification and aggregation

Few ornithologists who study faunal remains from owl pellets discuss how and why identified remains were quantified in particular ways. Some authors are ambiguous, such as Boyd & Shriner (1954:200) who stated that "skulls were saved for identification purposes and the mandibles counted so as to obtain an estimate of the number and kind of animal prey consumed." Hawbecker (1945:161) displayed exceptional awareness of skeletal-element interdependence in his statement that "Identification in most instances was made on the basis of skulls so that there is little chance of duplicate listing of individual animals." Most analysts seem to solve the interdependence problem by treating a collection of pellets as a single aggregate and tallying the most frequent skeletal element (e.g., Cowan, 1942; Stickel & Stickel, 1948). This solution comprises the standard paleozoological definition of MNI*t* (Grayson, 1984; Lyman, 1994a, b) and contends with the fact that interdependence of prey remains can occur not only within a pellet but between pellets (e.g., Glading et al., 1943). Such interdependence was apparent in LPL. Pellet 51 contained a proximal right femur of an adult *Peromyscus* or *Microtus* that displayed an antemortem fracture and postfracture healing; pellet 54 contained the matching distal portion of that femur.

Hawbecker's (1945) solution to the interdependence problem of limiting the skeletal elements identified can underestimate prey abundance, a fact noted at least twice in the owl-pellet literature (Cowan, 1942; Epperson, 1976). For example, Epperson (1976:54) "matched each cranium with one pair of mandibles, but an extra

27 pairs of lower mandibles . . . were not used in calculating the frequency of occurrence of the [prey] species." However, counting all identifiable remains may not increase MNI*t*. LPL included 315 femora (both lefts and rights) and 283 humeri of deer mice, and 91 femora and 82 humeri of montane vole. These represent 159 individual deer mice and 47 individual montane voles. These MNI*t* values are greater than the MNI*t* indicated by crania for both taxa but lower than those values indicated by mandibles (Table 1). Identified mammalian remains that contributed to MNI*t* vary among the 107 published collections. Only crania were identified in 54 collections; crania and mandibles were identified in 7; crania, mandibles, and isolated teeth were identified in 3; only right mandibles were identified in 2; all identifiable bones were identified in 8; and all remains or bones were identified in 16 collections. It is unclear which skeletal elements were identified in the remaining 17 collections.

To avoid potential problems of skeletal-element interdependence when determining the MNI*t* in LPL, we tallied crania with both left and right maxillae, crania with either the left or right maxilla, isolated left or right maxillae, and isolated left or right mandibles per pellet. We then determined the minimum number of crania represented in each pellet based on the maximum number of left or right maxillae, isolated or not. Because each of the 56 pellets was treated as a separate and unique aggregate, frequencies of crania per pellet were summed to derive the crania counts for the entire collection (Table 1). Had we tallied the total number of left and right maxillae (isolated + part of a complete cranium) irrespective of pellet and thus treated the 56 pellets as a single aggregate, the total number of *Peromyscus* crania represented in pellets would have been 148 rather than 155. Thus, because we treated each pellet quantitatively independent of every other pellet, the total MNI*t* was inflated—the aggregation problem. Specifying more aggregates within LPL resulted in larger MNI*t* tallies whereas specifying fewer aggregates resulted in smaller MNI*t* tallies.

Left and right mandibles in LPL were each tallied separately irrespective of pellet; tallies for both are greater than the result of either counting maxillae as from a single aggregate or from 56 aggregates for 3 of 5 taxa (Table 1). We derived the MNI*t* for LPL by determining whether crania, left mandibles, or right mandibles produced the largest number across the complete collection of pellets (collection treated as a single aggregate). Had we used only crania, our tallies of deer mice and montane voles would have been lower by 11 and 2 respectively. That no remains of Nuttall's cottontail would have been tallied had we tallied only crania and ignored mandibles (Table 1) indicates how choice in which skeletal elements are identified can influence measures of prey abundance, a point noted by Marti (1987) in his synopsis of methods used by ornithologists to study the prey remains deposited by owls and raptors.

Studies of paleozoological collections (Grayson, 1984) across which grouping and counting vary indicate taxonomic abundances measured with MNI*t* are best treated as ordinal-scale measures rather than as interval-scale measures precisely because of the problems of skeletal element interdependence and aggregation. Other studies indicate that differential fragmentation renders NISP*t* measures of taxonomic abundances ordinal scale at best. Our analysis thus far indicates exactly the same conclusions apply to collections of faunal remains from modern owl pellets. That is, the ordinal scale nature of taxonomic abundance data can be created during the biostratinomic phase of a taphonomic history.

Prey abundance, prey richness, and prey heterogeneity

NISP is not reported among the published collections. To determine if NISP is correlated with MNI in collections of barn owl pellets, we summed the number of crania, isolated single maxillae, and isolated mandibles per pellet (= NISP) and determined the MNI per pellet in LPL.

As shown in Figure 1, the correlation between MNI and NISP in LPL is strong, positive,

and significant (r = 0.96, P < 0.001). We assume this relation holds across each of the 107 published collections and use MNI per collection as a measure of prey abundance.

As MNI increases across the 107 published collections, so too should taxonomic richness of mammalian prey. However, following Marti (1987), we suspect that richness will not increase indefinitely. North American barn owls prey on a wide variety of mammalian taxa, most with body sizes < 300 g (Clark & Bunck, 1991; Marti, 1988). Thus taxonomic richness of prey will be limited because some taxa exceed the maximum size of barn-owl prey. As well, individuals of appropriate size representing other taxa within foraging areas may be diurnal whereas barn owls are largely nocturnal foragers (e.g., Dice, 1947; Konishi, 1973; Payne, 1962; Payne & Drury, 1958). As a result of these factors the richness of prey taxa should level off at some MNI value. We therefore hypothesized that as MNI increases, taxonomic richness will first increase and then stabilize despite further increases in MNI. A bivariate scatterplot of these two variables suggests our hypothesis is correct (Figure 2; r = 0.48, P < 0.001) (one collection in which only 984 individuals [= MNI] of a single taxon were found [Jemison & Chabreck, 1962] disregarded; conversion of MNI to log10 makes the point scatter more linear and improves the correlation to r = 0.58). These results suggest that the taxonomic richness of prey in a collection of barn-owl pellets may be influenced by the abundance of prey in the collection.

Sampling effort, prey richness, and prey heterogeneity

We hypothesized that as sampling effort measured as the number of pellets in a collection increased, so too would the taxonomic richness of prey until all prey taxa were represented, after which richness would cease to increase for the same reasons that richness eventually levels off relative to MNI. The number of pellets comprising each of the 107 published collections and the richness of mammalian genera per collection are correlated (Figure 3; r = 0.50, P < 0.001), and the scatterplot suggests our hypothesis is correct (one collection of 804 pellets that contained remains of a single taxon omitted; conversion of the number of pellets to log10 makes the point scatter more linear but improves the correlation to only r = 0.52). To ensure that a particular collection is representative of taxonomic richness of prey, one could treat each

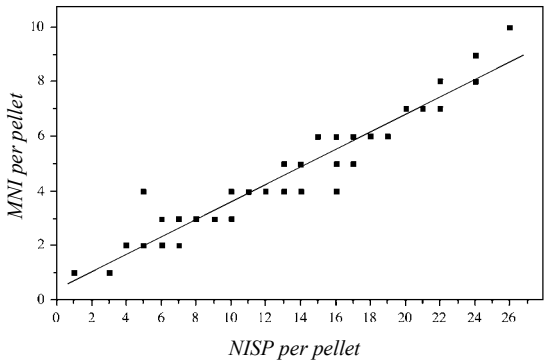

Figure 1. Relation between the mammalian NISP per pellet and the mammalian MNI per pellet in LPL collection of 56 barn-owl pellets from southeastern Washington (r = 0.96, P < 0.001). Note that a dozen points represent multiple pellets. Simple best-fit regression line shown for reference.

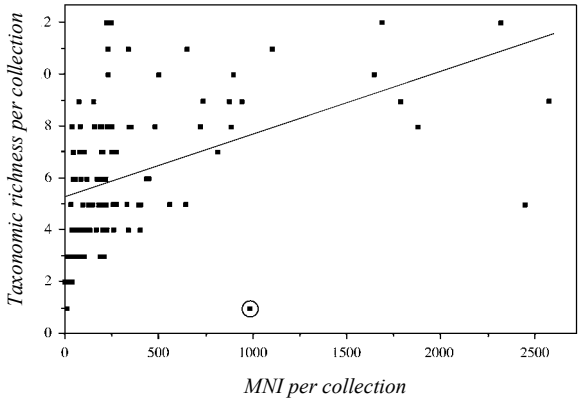

Figure 2. Relation between the MNI in a collection and the number of mammalian genera represented in 107 published collections of barn-owl pellets (r = 0.48, P < 0.001). Circled point is not included in correlation because it represents a collection in which 984 individuals (= MNI) of a single taxon were found. Simple best-fit regression line shown for reference.

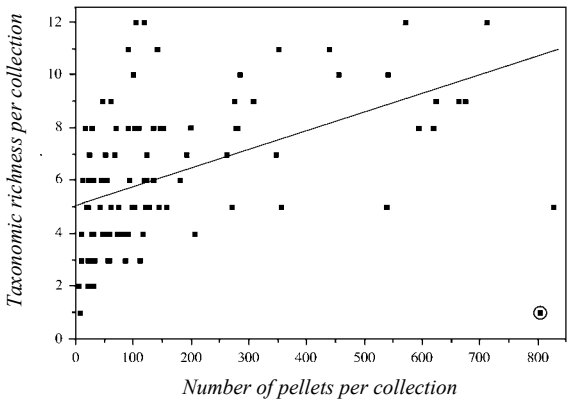

Figure 3. Relation between the number of pellets in a collection and the number of mammalian genera represented in 107 published collections of barn-owl pellets (r = 0.50, P < 0.001). Circled point is not included in correlation because it represents a collection of 804 pellets in which remains of a single taxon were found. Simple best-fit regression line shown for reference.

individual pellet as a new sample and plot richness against number of samples (as in Figure 3) until the addition of new pellets fails to add new prey taxa (see also Marti, 1987, figure 5.1).

We hypothesized that dietary heterogeneity would also correlate with the number of pellets per collection. We used the Shannon index to measure prey heterogeneity per collection because this is the index used in many of the published studies we examined (see Marti, 1987 for discussion of this and related measures in ornithology). The heterogeneities of mammalian genera in 103 of the published collections of barn-owl pellets (diversities of 4 collections were not included for various reasons) are not correlated with the number of pellets per sample (r = 0.07, P = 0.49), suggesting sampling effort is not influencing measures of barn-owl dietary heterogeneity among these collections.

Prey size and MNI per pellet

In the 107 published collections, the mean MNI per pellet ranges from 0.6 to 5.8; the grand mean (mean of the means) for these samples is 2.28 (SD = 1.05). The MNI per pellet in LPL ranged from 1 to 10 and averaged 4.41 (SD = 1.93). The mean MNI per pellet in LPL is significantly larger than the grand mean for the published collections (Student's t = –2.019, P < 0.025). The frequency distribution of classes of mean MNI per pellet among the published collections (Figure 4) suggests some collections will have many MNI per pellet but most will have few MNI per pellet. To determine why this is so, we first evaluated the relation between the number of pellets per collection and the average MNI per pellet in a collection and found none (r = 0.01; P > 0.5). Furthermore, LPL (not plotted in Figure 4) falls in class 4.1–4.5 MNI per pellet, a high abundance of prey per pellet relative to the published collections, and we suspected this was so because many of the prey in LPL are juvenile and subadult deer mice that weighed = 20 g when captured (Lyman et al., 2001). Many published samples of barn-owl pellets are dominated by various species of *Microtus*, the adults of which weigh > 40 g. Finally, we noted that several studies indicate mean barn-owl prey size falls between 30 g and 65 g but prey can be larger or smaller (Colvin & McLean, 1986; Janes & Barss, 1985). These observations suggested the hypothesis that the MNI per pellet would vary inversely with the size of prey such that if prey of large body size were most often exploited then the mean MNI per pellet would be

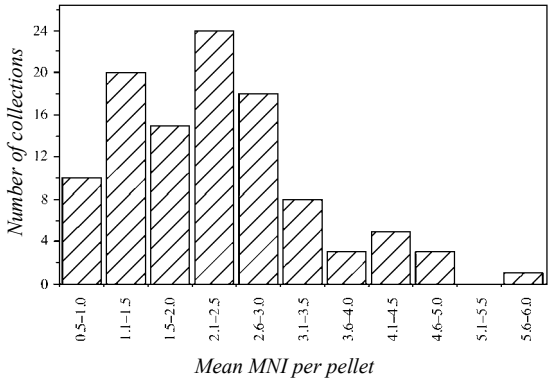

Figure 4. Frequencies of barn-owl pellet collections with different mean MNI per pellet.

Table 2. Size classes (g) of most abundant prey species in 78 samples of barn-owl pellets relative to the grand mean number of prey per pellet per prey size class

Size class	Number of pellet samples	Grand mean of prey per pellet	Standard deviation	Range
8–25	15	3.68	1.14	2.05–5.82
30–45	8	2.75	0.70	2.05–4.09
50–55	31	2.29	0.68	1.14–3.58
135–155	24	1.26	0.41	0.60–2.22

small whereas if prey of small body size were most often exploited then the mean MNI per pellet would be large.

To test our hypothesis, we noted the species that was most abundant in each published collection. For the 77 collections for which such data were available, plus our sample, the average adult size of each species was determined from mammalogy literature local to the area of the pellet sample. Among the four size classes of prey we specified (Table 2), there tends to be more prey MNI per pellet in pellets cast by barn owls that were exploiting mostly small prey, and progressively fewer prey per pellet in pellets cast by barn owls that were mostly exploiting progressively larger prey. The two variables are inversely correlated (Figure 5; $r = -0.72$, $P < 0.001$), with nearly 52% of the variation in MNI per pellet explained by the size of the most abundant prey taxon. Mean MNI per pellet for a collection is often reported in the literature we examined, although it has seldom been used for analytical purposes. Our analysis indicates that more MNI of small prey are included in a pellet than are MNI of large prey, but this relationship breaks down if juveniles of large taxa comprise the major prey. The MNI-per-pellet index may help detect such covariation in prey taxonomy, abundance, and ontogeny.

Pellet volume and prey frequency

Pellets in LPL varied greatly in size, and some were obviously partially disaggregated and incomplete. We hypothesized that larger, more complete pellets would contain more individual prey than would smaller, less complete pellets. Pellet volume was calculated as if each pellet comprised a cylinder, and although this overestimates individual pellet volume, it suffices for our purposes. Larger pellets in LPL generally contained remains of more individual prey than did smaller pellets (Figure 6, $r = 0.71$, $P < 0.001$), supporting our hypothesis. Pellet volume is not correlated with taxonomic richness within a pellet ($r = 0.247$, $P = 0.07$).

Do small pellets contain different relative abundances of taxa than large pellets? Frequencies of individuals of the two most abundant taxa (Table 1) in LPL are 166 *Peromyscus* and 48 *Microtus,* or 74% and 21% respectively of all prey. Those abundances in the smallest 28 pellets are 45 *Peromyscus* (66%) and 20 *Microtus* (29%). The

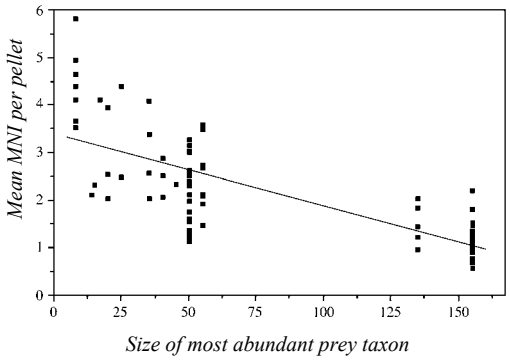

Figure 5. Relation between size of most abundant prey taxon and mean MNI of prey per pellet in 78 collections of barn-owl pellets ($r = -0.72$, $P < 0.001$). Simple best-fit regression line shown for reference.

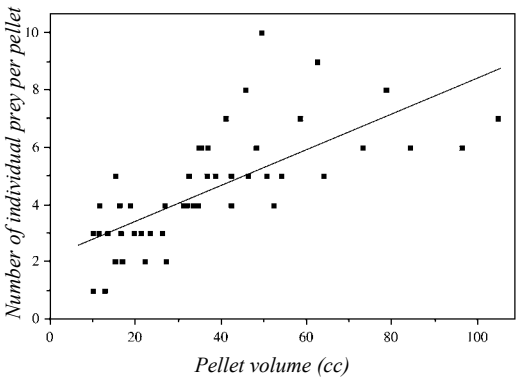

Figure 6. Relation between individual pellet volume and the number of individual prey represented in a pellet in LPL collection of 56 barn-owl pellets from southeastern Washington ($r = 0.71$, $P < 0.001$). Simple best-fit regression line shown for reference.

smallest 37 pellets (67% of the total) yield abundances of 79 *Peromyscus* (72%) and 24 *Microtus* (22%). The largest 19 pellets (33% of the total) yield abundances of 87 *Peromyscus* (76%) and 24 *Microtus* (21%). None of these differences in proportional abundance are statistically significant (arcsin t, $P > 0.1$ in all comparisons).

Discussion

Like many of those whose work he references, in his overview of the study and interpretation of microvertebrate remains, including those accumulated by avian predators, Stahl (1996) considers problems with the recovery of microvertebrate remains but does not consider issues of taxonomic quantification or sample adequacy. The data and analyses we have presented here comprise the only study of which we are aware that focuses directly on these issues with respect to collections of raptor and/or owl pellets. What, then, have we learned?

Paleozoologists have long known that taxonomic richness is often directly correlated with sample size. We show here that taxonomic richness is influenced by sampling effort measured as the number of owl pellets. Paleozoologists also have long realized that the manner in which prey remains are aggregated influences measures of prey abundance such as MNI*t*. Our analysis shows that taxonomic abundances in a collection will be influenced by how pellets comprising that collection are aggregated. We have also shown that fragmentation (of crania into isolated maxillae) and the combination of skeletal elements identified (crania, maxillae, mandibles) influence not only NISP*t* but also MNI*t*. Our analyses indicate that as MNI increases, so to does taxonomic richness, but the latter levels off given constraints on the predator's capabilities. And, we have shown that larger pellets contain the remains of more individual prey than small pellets. So far, this all sounds fairly commensensical, and with the exception that these conclusions originate in collections of modern owl pellets, they comprise general knowledge among paleozoologists. But we have also identified what seems to be a unique feature of the prey content of owl pellets. Ornithologists seem to have been aware that the MNI of prey per pellet is influenced by the size of prey, but our analysis shows that the MNI per pellet is also influenced by the ontogenic age of prey. If prey are young and not full grown, the tendency is for the MNI per pellet to be higher than if prey were full-grown adults.

What, one might ask, do any of these findings have to do with taphonomy? We think the significance of these observations for taphonomy reside in two areas. First, our analysis is the first (so far as we are aware) to show that several properties of quantification and sampling applicable to paleozoogical collections of microvertebrates also apply to modern collections of owl pellets. This means that these particular properties can be created during the biostratinomic phase of a taphonomic history. The second significant aspect of our analysis resides in the fact that modern owl pellets provide a rich pedagogical resource. Many biologists use them to teach students various aspects of biology because they are readily available in many locations, and in fact some biological suppliers sell them; putting "owl pellet" into a web-based search engine should produce a list of over a dozen commercial suppliers of owl pellets. Students can learn about

taphonomic signature criteria, how to identify microvertebrate remains to skeletal element and taxon, and how to quantify faunal remains for various sorts of analyses. Requisite storage space is minimal, and such teaching collections are not irreplaceable. We have found that the only possible problem is no real problem, unless you cannot handle the quizzical looks you receive when you say that you are studying owl puke.

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