Owl Pellet Taphonomy: A Preliminary Study of the Post-Regurgitation Taphonomic History of Pellets in a Temperate Forest

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INTRODUCTION

Predation has long been recognized as an important mechanism leading to the concentration of small-vertebrate skeletal remains (Mellett, 1974; Dodson and Wexlar, 1979; Maas, 1985; Andrews, 1990). Modern predators include mammalian carnivores, diurnal birds of prey, and nocturnal owls (Mellett, 1974; Andrews, 1990). Although members of all raptor families produce pellets (regurgitated oblong masses of the undigested components of a bird’s food, usually consisting of fur, bones, claws, and teeth), owl pellets are characterized by survival of a higher proportion of skeletal material than pellets/scat produced by other predators (both avian and mammalian), and thus are thought to provide a more complete sample of the local fauna (Mayhew, 1977; Andrews, 1983; Hoffman 1998; Lyman, 1994). Owl pellets also can include climate indicators such as pollen (Fernandez-Jalvo et al., 1996; Scott et al., 1996; Fernandez-Jalvo et al., 1999). Because many owls show high roost fidelity (Bent, 1961; Andrews, 1990), pellet-derived accumulations also can provide a geohistorical time series for small-vertebrate communities, and thus contribute information that is critical to our ability to assess small-vertebrate community change (on seasonal to millennial scales), as well as changes in predator behavior patterns and local climate change (Avery, 1995; Hadly, 1996; Vigne and Valladas, 1996; Fernandez-Jalvo et al., 1998; Grayson, 2000; Hadly and Maurer, 2001; Avery et al., 2002).

Despite their potential as primary resources for reconstructing paleoclimates and assessing ecological and environmental change, pellet-derived small-vertebrate assemblages have been underutilized, perhaps because of uncertainty about their taphonomic history (Fernandez-Jalvo et al., 1998). The taphonomic history of a pellet consists of multiple phases, each with particular biases. First, selective hunting behavior of predators, time of predator activity, season, vulnerability of prey, and local climate conditions will introduce an initial bias into the species composition of any predator-derived accumulation (Craighead and Craighead, 1956; Andrews, 1990; Denys et al., 1996; Saavedra and Simonetti, 1998), although these same factors may permit identification of rare elements in the fauna (Avery et al., 2002). Second, the digestive process of pellet formation results in characteristic fragmentation and bone loss (Andrews, 1990). Owl pellets are formed in the stomach because a narrow pyloric opening near the entrance of the esophagus prevents large particles from entering the intestines; the undigested material travels back up the esophagus and is ejected as a pellet (Bent, 1961; Hoffman, 1988; Andrews, 1990). Third, pellet history following regurgitation (weathering, transport, disintegration, and burial) has the potential to mask original species composition and other taphonomic signatures, thus biasing the fossil record.
Of these three potential sources of bias, only raptor dietary preferences and patterns of bone destruction due to digestion have received significant attention (e.g., Craighead and Craighead, 1956; Dodson and Wexlar, 1979; Hoffman, 1988; Andrews, 1990; Denys et al., 1996; Saavedra and Simonetti, 1998; Trejo and Guthmann, 2003). Some of these studies have attempted to identify unique fragmentation and skeletal element representation signatures left by different predators (e.g., Dodson and Wexlar, 1979; Hoffman, 1988; Andrews, 1990), whereas others have investigated the microscopic effects of digestion on bones and teeth (e.g., Rensberger and Krentz, 1988; Andrews, 1990). Comprehensive study of the post-regurgitation processes acting on pellet-derived small-vertebrate assemblages is noticeably absent (but see Andrews, 1990, for limestone-cave deposits). This study presents an initial investigation into the post-regurgitation taphonomic history of owl pellets in a temperate-forest environment with a focus on: (1) the pattern of skeletal-element distribution that has developed on the forest floor below a roosting site, (2) changes in the fragmentation and relative abundance of skeletal elements, and (3) changes in the taphonomic condition of skeletal elements as pellets disintegrate and skeletal material is dispersed and incorporated into the soil.

STUDY AREA

The Friday Harbor Laboratory of the University of Washington is situated on the eastern side of San Juan Island, Washington, and includes both coastline and temperate forest (Fig. 1). Point Caution, a headland directly north of the lab, is dominated by Western Red Cedar (Thuja plicata) and Douglas Fir (Pseudotsuga menziesii) forests that have not been logged for over 100 years (Staude, pers. comm., 2002; Guberlet, 1975). Approximately 1.6 km northwest of the lab is a 0.01 km² grove of Western Red Cedar [N48°33.615', W123°0.891']. In summer 2002, when this study was undertaken, the floor of the grove was littered with more than 1,500 small-vertebrate skeletal elements and more than 20 pellets in various stages of disintegration. The largest concentration of skeletal elements occurred around the base of one tree, but at least four other trees in the vicinity also showed separate pellet-derived bone accumulations around their bases.

The high skeletal content of the pellets as well as pellet size (average size: 5.6 cm x 3.8 cm x 2.4 cm) and the size and taxonomic composition of the prey—primarily the nocturnal Townsend’s Vole (Microtus townsendii), with a shrew (Sorex sp.) and a mole (Scapanus sp.) also present (Glass and Thies, 1997)—suggest that the pellets are from a Great Horned Owl (Bubo virginianus) (Bent, 1961; Andrews, 1990). Other large pellet-producing raptors common to San Juan Island include the diurnal Bald Eagle (Haliaeetus leucocephalus), Red-tailed Hawk (Buteo jamaicensis), Turkey Vulture (Cathartes aura), Northern Harrier (Circus cyaneus), and the nocturnal Barn Owl (Tyto alba), Western Screech Owl (Otus kennicottii), and Northern Saw-whet Owl (Aegolius acadicus). Of the nocturnal owls present on San Juan Island, Great Horned Owls are the largest, most common, are frequently found in dense forest habitat, and are the only owls to have been seen and heard around the Friday Harbor Laboratory in the last several years (Britton-Simmons, pers. comm. 2002, Smith et al., 1997).

MATERIALS AND METHODS

The analyses included in this paper are restricted to the roosting tree in the Western Red Cedar grove with the largest concentration of skeletal elements around its base. The surface distribution of skeletal elements around the roosting tree was mapped using a north/south-oriented grid, a handheld compass, tape measure, and six 0.25 m² squares (50 cm x 50 cm) subdivided into 10 cm increments.

Skeletal elements rarely were isolated, typically occurring in discrete (or semi-discrete or dispersed but still spatially definable) clusters. Spatially defined occurrences of bones typically contained at least one skull. Dodson and Wexlar (1979) reported that the mean number of pellets cast per meal is close to one for Great Horned Owls, thus, each assemblage was reasonably interpreted as a modified pellet.

Assemblages were subdivided into three categories: (1) intact pellets, (2) partially dispersed pellets, and (3) fully dispersed pellets (Fig. 2). Pellets were classified based on the presence and condition of the matted-hair matrix of the pellet. Intact pellets were unbroken and characterized by smooth, matted fur and an oblong shape. In partially dispersed pellets, the surface of the pellet was no longer smooth and matted, the pellet was broken, and/or skeletal elements had fallen loose from the pellet. In fully dispersed pellets, spatially definable assemblages of bones were characterized by the absence of matted fur. All pellet material was mapped, and skeletal elements identified when possible. Each quarter-meter quadrat on the surface map was assigned a unique coordinate and the distance from the center of the tree to the center of each quadrat was calculated. Five assemblages of each type were selected randomly and collected by hand. Before collection, the orientation of each bone with respect to the soil was marked on the exposed surface of the bone for all skeletal elements free from the matted hair of pellets.

Partial and complete pellets were hydrated overnight and picked apart with forceps under a dissecting scope (magnification 2x to 6x). All elements were identified, and...
Figure 2—Pellet classification scheme. Pellets were classified based on the presence and condition of the matted hair matrix. (A) Intact pellet. (B) Partially dispersed pellet. (C, D) Fully dispersed pellets.

Bone fragmentation and modification states recorded. Fragmentation is defined for this study as breakage resulting in loss of information about the function or shape of a skeletal element. The taphonomic condition of all elements from nine representative assemblages (three from each assemblage type) was assessed. Bone modification is used in this study to refer to a combination of chemical dissolution due to digestive modification and secondary weathering processes, following Behrensmeyer (1978), including the effects of contact with/burial in soil (chemical alteration, etching, and pitting) and physical weathering agents operating on the forest floor (exposure to wind, rain, temperature change). Bone modification categories used in this study are defined as follows: (1) unmodified bone—the inner cancellous bone is unexposed, protected by an intact outer layer of dense compact bone; (2) slightly modified bone—the cancellous bone is exposed; and (3) extensively modified bone—the outer compact layer is absent and the inner cancellous bone is exposed and eroded.

The slope of the forest floor was mapped using a square-meter grid and a Brunton compass. A layer of mobile conifer (cedar) detritus covers the soil. The orientations of skeletal elements from fully dispersed pellets were recorded to address the importance of hydrodynamic transport. The pH of the soil beneath the conifer detritus, as well as the phosphorus, nitrogen, and potassium (potash) content were determined using a Lammott Soil Kit. Finally, exploratory excavation of six 20-cm² sites was done using a knife and spoon. Sites were excavated in 1-cm layers to a depth of 5 to 7 cm. Each layer was collected and wet sieved (250 μm mesh).

Unless otherwise noted, statistical analysis consisted of the construction of contingency tables analyzed using Chi-square tests. Significance was established at the α = 0.05 level.

Results
Spatial Analysis

The surface of the ground surrounding the roost tree slopes ~20°–25° to the northeast. The soil beneath the conifer detritus is acidic (pH = 5) and contains trace amounts of phosphorus and nitrogen and a high amount of potassium (potash). Pellet-derived material (assemblages) is found on all sides of the roost tree. The total number of assemblages decreases with distance from the roost tree; a histogram of assemblages versus distance shows a concave, right-skewed distribution. This pattern is similar when all assemblages are pooled, as well as when assem-
Assemblages are split on the basis of type (Fig. 3). Pellet abundance peaks approximately 2 m from the tree, and intact pellets do not persist at distance from the tree, whereas partially and fully dispersed pellets do persist. The above pattern is not significant (p < 0.262; n = 52, the number of assemblages), perhaps due to the relatively small sample size for the number of quadrats; expected values of 20% of the quadrats were fewer than five, a violation of the assumptions of the Chi-square test.

The total number of bones exposed on the surface displays a bimodal distribution with distance from the tree (Fig. 4). Bones appear to be concentrated in peaks between 0 and 0.5 m from the tree, and again between 1.5 and 2.5 m from the tree. The 5-m measured distribution radius around the tree was divided at 2.5 m, creating an inner bin that contained 25% of the total area, and an outer bin that contained 75% of the total area. Skeletal elements were counted for each of the two zones, and a binomial test for proportions that took the disproportionate areas into account was performed to determine significance of the distribution. Despite the fact that the inner zone represents only 25% of the total area of the site, 59 bones (85.5% of the total number of bones) were found in the inner zone. This pattern is significantly different from what would be expected if elements were distributed randomly between the two zones at a 25:75 ratio (p < 0.0001; n = 672). Fully dispersed pellets are dominated by mandibles (18%), followed closely by vertebrae (15%), contained in pellets would increase the sample size, and would reinforce the pattern described.

Long bones were separated into two categories: (1) robust elements (humerus, pelvis, femur), and (2) fragile elements (ulna, radius, tibia). The distribution patterns of robust and fragile elements were analyzed separately using the binomial statistical method described above. Both Figure 5 and the disparate sample sizes (see below) indicate that robust elements are present in higher numbers than fragile elements throughout the entire distribution, and persist farther from the tree. The total numbers of robust and fragile skeletal elements in each area were significantly different at α = 0.05 (Robust: p < 0.0001; n = 59; Fragile: p < 0.0001; n = 10). There is no evidence (such as preferred orientations of bones or runneling of the soil surface and/or mobile conifer detritus) that would indicate hydrodynamic transport at the site.

Taphonomic Analysis

Relative proportions of all skeletal elements from 15 assemblages were calculated for each assemblage type (intact pellets, partially dispersed pellets, fully dispersed pellets; Fig. 6). The relative proportions of different skeletal elements differ significantly between assemblage types (P < 0.0001, n = 672). Fully dispersed pellets are dominated by mandibles (18%), followed closely by vertebrae (15%),
FIGURE 6—Relative proportions of skeletal elements with assemblage type; proportions differ significantly among assemblage types ($p < 0.0001; n = 672$); Sk = skull; Ma = mandible; Sc = scapula; V = vertebra; H = humerus; U = ulna; Ra = radius; P = pelvis; F = femur; T = tibia/fibula; Ri = rib; CTP = manus and pes elements. (A) Intact pellets. (B) Partially dispersed pellets. Note (A) and (B) are dominated by vertebrae, ribs, and manus and pes elements. (C) Fully dispersed pellets, which are dominated by more robust skeletal elements.

FIGURE 7—Fragmentation frequency with assemblage type. Fully dispersed pellets contain the highest proportion of fragmented elements. Results are significant ($p < 0.0001; n = 351$).

Different types of skeletal elements display unique breakage patterns. Skulls, for example, exhibit a characteristic breakage pattern of the cranium in which the posterior half of the skull is completely absent (Fig. 8A, B). Skulls that exhibit this type of breakage are found most frequently in fully dispersed pellets (23%) and partially dispersed pellets (30%; Fig. 8C). All skulls found in intact pellets were unbroken. While results were found to be significant ($p < 0.0151; n = 13$), the small sample size violates assumptions of the test, making statistical analysis inconclusive but consistent with the observed pattern.

The epiphyseal ends of long bones, which represent growth centers that become fused during the adult life of an animal (Swindler, 1998), can provide clues about the age structure of a prey assemblage. Approximately 63% of all long bones (humerus, femur, tibia) from 15 assemblages are missing epiphyses (Fig. 9). Significance of this pattern was established using an unpaired $t$-test ($p < 0.0098; n = 46$). This suggests a potential age bias towards youn-
FIGURE 8—Fragmentation patterns of skulls; scale bar in millimeters. (A) Dorsal view of three skulls (*Microtus townsendii*). Two exhibit a common posterior breakage pattern. (B) Ventral view of the same skulls. (C) Frequency of posterior skull breakage. All skulls recovered from intact pellets were unbroken. Results are significant ($p < 0.0151$; $n = 13$), however, small sample size violates the assumptions of the Chi-square test.

FIGURE 9—Epiphyseal presence and absence in humeri and femora of *Microtus townsendii*; scale bar in millimeters. (A) Humerus with proximal epiphysis missing. (B) Humerus with proximal epiphysis present. (C) Femur with distal epiphysis missing. (D) Femur with distal epiphysis present.

...ger individuals in the prey assemblage. No significant difference was found for the frequency of epiphysis loss between the different types of skeletal elements ($p < 0.0758$).

Bone-modification results pooled for all elements by assemblage type are presented in Figure 10. The differences are significant ($p < 0.0116$; $n = 191$) and suggest that for fully dispersed pellets, more than 60% of the bones exhibit no bone modification, whereas for intact pellets, only about 45% of the bones show no bone modification. Conversely, about 25% of skeletal elements from fully dispersed pellets and almost 20% of skeletal elements from intact pellets show evidence of extensive bone modification.

Bone modification results for skeletal elements found in fully dispersed pellets were compared with results for the same skeletal elements from intact pellets. Results were not significant ($p < 0.2022$; $n = 101$), indicating no difference in terms of bone modification between elements present in both assemblage types.

Different skeletal elements show different degrees of modification, as do the shaft and ends of a single long bone. For all long bones (with and without epiphyses) for all assemblage types pooled together, the ends of long bones show a significantly higher degree of bone modification than the shafts ($p < 0.0001$; $n = 43$; Fig. 11).

Skeletal elements from fully dispersed pellets are scattered on the forest floor, with one side of the bone exposed to air, and the other side exposed to twig litter or soil. Bone modification for each surface of all bones derived from fully dispersed pellets is shown in Figure 12. Seventy percent of surfaces exposed to the air showed little to no bone modification, whereas only 50% of surfaces exposed to the soil showed little to no bone modification. However, almost 20% of surfaces exposed to the soil show extensive bone modification, while only 5% of surfaces exposed to the air show extensive bone modification ($p < 0.0449$; $n = 241$).

Excavation Results

Preliminary excavation of three 20-cm squares to depths of 5 to 7 cm yielded skeletal elements incorporated...
into the soil to a depth of 2 cm below the soil surface (2 skulls, 4 mandibles, 1 pelvis, 1 femur, 1 tibia, 1 vertebra; Fig. 13). All skeletal elements recovered from the soil show extensive bone modification.

**DISCUSSION**

Skeletal material can be concentrated by both physical (fluvial sorting, wind deflation) and biological (predation) processes. These different concentrating mechanisms have the potential to introduce different biases into an assemblage, which should then affect paleoecological interpretation (Behrensmeyer, 1993). Thus, before a pellet-derived small-vertebrate assemblage can be used for paleoecological reconstruction, there must be a reliable way to recognize that it is indeed pellet-derived. Previous studies, primarily conducted in laboratory settings, have focused on fragmentation patterns as the means of identifying pellet-derived assemblages (Dodson and Wexlar, 1979; Hoffman, 1988; Andrews, 1990; Kusmer, 1990). Relative abundance of skeletal material and characteristic breakage patterns produced in laboratory settings also have been proposed as methods to facilitate predator identification from field assemblages (Dodson and Wexlar, 1979; Hoffman, 1988; Andrews, 1990). In his paper on pellet-derived fragmentation patterns, Hoffman (1988) briefly acknowledged that post-pellet diagenetic processes might confound the taphonomic signatures of small-vertebrate assemblages, making definitive predator identification difficult. However, the number of actiological studies of the post-regurgitation history of pellets is limited (but see Andrews, 1990). The results from this study illustrate the importance of understanding how post-regurgitation processes can bias small-vertebrate assemblages over time in a temperate-forest environment. Once a pellet has been regurgitated and is exposed to physical and chemical weathering processes on the forest...
floor, the matted hair in the pellet protects the skeletal elements contained inside (Andrews, 1990). Assuming the different pellet types designated in this study (intact pellets, partially dispersed pellets, and fully dispersed pellets) represent steps in the disintegration process over time, both the relative proportion of skeletal elements present in an assemblage and the degree of fragmentation changed as a result of time exposed on the forest floor. As the pellets broke down, bones became dispersed, and fragmentation increased (Fig. 7). Evidence for transport and dispersal by hydrodynamic processes is lacking, thus, the increased dispersal and fragmentation of skeletal material must be due to other factors, such as scavenging.

Dodson and Wexlar (1979) observed a high frequency of posterior breakage in skulls recovered from Great Horned Owl pellets in a laboratory setting and presented this as a possible predator identification tool. However, they also reported feeding observations for Great Horned Owls, in which the owls swallow mice whole and headfirst, making no attempt to extract the brain of the animal. In comparison, the skulls recovered from intact pellets in this study primarily were unbroken, consistent with the feeding observations of Dodson and Wexlar (1979), while broken skulls were found in partially dispersed pellets and fully dispersed pellets on the forest floor (Fig. 8). This suggests that skulls become fragmented more frequently during post-regurgitation processes such as scavenging; and that caution should be used if employing skull breakage as a tool for predator identification.

Based on this study, as pellets disintegrate, the skeletal composition of the assemblage shifts from a high proportion of small, fragile elements to a high proportion of larger, more robust elements, because the fragile elements are preferentially lost (Figs. 5, 6). Skeletal elements from fully dispersed pellets (which potentially have spent the most time in contact with the forest floor) show the highest frequency of no bone modification. Elements from intact pellets, however, show lower proportions of no modification than bones from dispersed pellets and high frequencies of both slight and extensive bone modification (Fig. 10). A possible explanation is that the matted hair in a pellet initially shields the smaller and fragile bone fractions (which are perhaps more intensely modified by digestion). Upon pellet disintegration, these smaller, fragile, extensively

FIGURE 13—Skeletal elements (*Microtus townsendii*) recovered from the subsurface; scale in millimeters. (A) Skull from 1 cm below the soil surface. (B) Mandible from 2 cm below the soil surface. (C) Mandible and pelvis from 1 cm below the soil surface. (D) Mandibles from the top of the soil surface below the leaf litter.
modified elements then become exposed to physical- and chemical-weathering processes on the forest floor. Armour-Chelu and Andrews (1994) documented significant burial and lateral transport of small skeletal elements due to earthworm bioturbation. This, coupled with potential effects of preferential destruction due to higher modification, would result in a residual concentration of the larger, robust, skeletal elements that were less extensively modified by digestion. Of the bones that do remain on the forest floor, it should be noted that the surface in contact with the soil shows a higher degree of bone modification than the surface that is exposed to the air (Fig. 12). This preferential damage is consistent with a variety of actualistic studies of weathering of larger bones (e.g., Behrensmeyer and Hill, 1980).

The distinctive characteristics of fragmentation and skeletal element representation thus change over time. This presents a problem if these characteristics are to be used to determine whether an assemblage is predator-derived, and to identify the predator. Alternate methods for identifying an assemblage as pellet-derived deserve more attention. As expected, in this study, the density of skeletal element decreases with distance from the tree. The right-skewed, bimodal distribution of skeletal elements seen below the roost site, with a distribution radius of intact pellets approximately 2 m from the tree (Figs. 3, 4), is most likely the result of a reflecting boundary (the tree trunk) and preferred roosting position of the owl. As pellets are regurgitated and tumble through the dense branches to the ground below, scattering off the branches and the trunk would yield a peak in abundance at a moderate distance from the trunk. If surface patterns also are preserved at depth (especially in environments more conducive to preservation than acidic, moist, coastal-forest soils), they could be powerful indicators that an assemblage is pellet-derived. Alternative techniques for identifying whether an assemblage is predator-derived that deserve further study include microscopic investigation of chemical etching, pitting, and dissolution that occurs with digestion (and taxonomic differences in preservation potential). Microscopic analyses also are needed to distinguish the effects of digestion from secondary chemical dissolution that occurs as bones come in contact with the soil. Finally, actualistic and microscopic studies also are needed to better understand the confounding effects of scavenging on dispersal, skeletal-element representation, and fragmentation patterns. These analyses are beyond the scope of this work.

CONCLUSIONS

(1) Pellets and skeletal elements become dispersed with distance from the tree. The pattern of dispersal of skeletal elements follows a right-skewed bimodal distribution.

(2) The relative proportions of skeletal elements change as pellets disintegrate, thus this is not a reliable criterion for identifying the pellet origin of and predator responsible for subfossil assemblages. Intact pellets are dominated by small fragile elements, which are preferentially lost with pellet disintegration over time.

(3) Frequency of fragmentation increases as pellets become dispersed, and individual breakage patterns (such as loss of the cranium in skulls) can be incurred due to post-regurgitation processes such as scavenging. Thus, fragmentation is not a reliable indicator for predator identification.

(4) The frequency of intense bone modification is highest in pellets and lowest in dispersed assemblages. This likely reflects preferential destruction of smaller, more fragile skeletal elements, which may be modified more intensely due to digestive processes, upon being released from the pellet.

(5) The taphonomic history of pellet-derived small-vertebrate assemblages is more complex than commonly acknowledged. Since post-regurgitation processes distort the original skeletal composition of pellet-derived assemblages, actualistic studies are necessary in order to understand and correct for this bias, leading to more accurate assessments of small-vertebrate community change and paleoenvironmental reconstruction.

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