Micromammal taphonomy of el-Wad Terrace, Mount Carmel, Israel: distinguishing cultural from natural depositional agents in the Late Natufian

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“‘These are to you the unclean among the swarming things which swarm on the earth: the mole rat and the mouse…”’
(Leviticus 11:29)

Abstract

A taphonomic analysis of micromammal remains from the Late Natufian deposits of el-Wad Terrace, Mount Carmel, Israel, was conducted in order to test the long-standing premise of owl deposition as the primary accumulating agent. The inferred taphonomic sequence was modeled within an actualistic (recent) comparative framework incorporating a locally derived barn owl pellet collection and an off-site control assemblage of micromammal remains from the cliff overhanging the terrace. The sequence was reconstructed based on multiple types of recorded taphonomic data, comprising skeletal modifications (breakage, digestion, weathering, gnawing, and charring) and age structure. Evidence for post-depositional processes including fluvial transport, trampling, and weathering was isolated and consequently the typical owl imprints were traced through the two actualistic and the archaeological assemblages. Based on the extent of breakage and patterning in skeletal element frequencies it was also possible to scale the preservation potential of primary data in el-Wad Terrace as a discrete site type, intermediate between true cave and open-air depositional environments. Verifying the role of owls as principal agents of accumulation of the el-Wad Terrace micromammal remains enabled the detection of two minor superimposed cultural patterns: consumption of mole rats (Spalax sp.) by the Natufians and commensalism of mice (Mus spp.).

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1. Introduction

The complex formation history of many archaeofaunal assemblages, oftentimes comprising both natural and cultural processes of accumulation, poses a key challenge to taphonomic interpretation. The role of owls (Strigidae) as principal agents of micromammal (rodent and insectivore) accumulation in cave sites has been demonstrated repeatedly through taphonomic research on paleontological and archaeological assemblages [1,29,30,57]. Such studies have also revealed complex multiple predatory origins (nocturnal and diurnal raptors; mammalian predators) whose recognition is further complicated by the effects of secondary, attributational processes. Moreover, the possible contribution of both natural and cultural agents should always be taken into account when one deals with archaeological deposits [14,54,82] (see also Ref. [66]). Given the
prominent role played by micromammal remains in fine-tuned paleoenvironmental analyses [17,58,76–78,85], identifying agents of accumulation is of major significance to paleoecological reconstructions [1].

Micromammal accumulations from cave or cliff settings in the southern Levant are generally considered the result of deposition by owls [76]. To date this assumption remains untested, and the possible role of other agents of accumulation has likewise not been subjected to modern taphonomic study. We carried out a detailed taphonomic analysis of the micromammal assemblage of el-Wad Terrace in order to gain insight into the taphonomic imprints and to tease apart the evidence for possible agents of accumulation. Previous studies of the el-Wad Cave and Terrace micromammal assemblages [8,60,83] dealt primarily with taxonomic concerns and several paleoenvironmental inferences were drawn. However, taphonomic analyses of micromammal assemblages from the Levant are rare (e.g. Ref. [9]).

Certain owl species are micromammal specialists; they regularly inhabit caves and rocky overhangs, and inflict relatively little damage on the skeletons of their prey [13,46,52,53]. Therefore, the remarkable abundance of fossilized micromammal remains found in many prehistoric cave deposits is considered the key criterion for associating them with owls [20]. The relative scarcity of rodent remains in Levantine open-air sites suggests that owls are indeed the major micromammal accumulating agent in cave and rocky overhang settings where they are more likely to roost [79]. Nevertheless, there are other possible agents of micromammal accumulation, natural and cultural. Their identification requires detailed taphonomic scrutiny.

Certain species of diurnal raptors and mammalian carnivores also accumulate micromammal prey remains in caves [1]. Fossil assemblages produced by various predatory agents can reflect paleoenvironmental conditions differently. Remains of micromammals can also accumulate within human settlements as a result of on-site accidental mortality [89]. On-site mortality can also be envisaged for commensal rodents living in association with humans [63]. Procurement of micromammals as a food source by humans (e.g. Refs. [21,41], [44]; pp. 524–525, [59]: p. 228) is possibly consistent with a strategy termed “garden hunting” by Linares [48]. Among hunter/gatherer societies, the rationale for exploiting such small game as part of gathering activities is the high return rate it can afford relative to the low search, capture, and preparation efforts required [71]. To date, no evidence of using micromammals as a food source has been found in the Levant. Fossorial rodents can burrow their way into archaeological deposits [40,91]. A highly disruptive impact on three-dimensional artifact distribution was demonstrated for the North America pocket gopher (Thomomys bottae) [10,11,27] and also suggested for the East Mediterranean blind mole rat (Spalax eherenbergi) [15,62]. However, concurrent deposition of micromammal remains and human site occupation has been demonstrated in many instances where intrusion was patently apparent [28,65]. Moreover, Morlan [54] has suggested that skeletal remains of the burrowers themselves are not likely to be found in churned deposits.

Differentiating potentially superimposed agents of accumulation is hampered by the general lack of suitable formal taphonomic criteria for dissociating similar taphonomic imprints caused by different agents (see Ref. [72] for a discussion of problems of equifinality). Therefore, inductive pattern recognition, advocated for the science of taphonomy as a whole [49], is necessary for the analysis of this particular type of assemblage. This approach entails comprehensive reconstruction of a taphonomic history for the assemblage encompassing the range of processes beginning with deposition, through those of biostratinomy (before burial) and diagenesis (after burial), and finally, recovery through archaeological excavation. This type of inquiry necessitates using multiple lines of evidence [39] as is true for interpreting taphonomic histories of macromammal assemblages (e.g. Ref. [4]). The interpretive framework in which these objectives can be attained is that of actualistic research employing relevant experimentally derived data [49]. Nonetheless, we acknowledge that the entire range of formation intricacies and problems of equifinality associated with this taphonomically complex micromammal assemblage are not fully resolved by our study. Rather, we attempt to derive its broad formation framework upon which culturally relevant inferences can be more reliably constructed and interpreted. Although some studies of predator-derived fossil micromammal assemblages have claimed within family resolution of accumulator identification [1,29,30], in this study we analytically confine identification to family level and refer to the owl group and its common taphonomic effects in general.

2. The site

El-Wad (Cave and Terrace) is situated on Mount Carmel at the opening of Nahal Me’arot (Valley of the Caves) onto the narrow Carmel coastal plain (Fig. 1). The site has been repeatedly excavated since the late 1920s [34,83,87]. A long prehistoric cultural sequence was uncovered in the cave extending from the Middle Paleolithic to the Chalcolithic. On the terrace itself the earliest and principal remains are attributed to the Natufian (Late Epipaleolithic). This culture, on the threshold of agriculture in the Levant, is that of complex hunter/gatherers. The archaeological evidence demonstrates habitation of multi-seasonal camps with permanently constructed dwellings by groups employing
economic strategies of intensified resource procurement and a broad subsistence base and practicing diverse burial customs [6,33]. A wide variety of utilitarian lithic tools as well as elaborate artistic and decorative objects of stone, bone, and shell were manufactured.

The stratigraphic subdivision of the Natufian deposits of el-Wad Terrace comprising Early (layer B2) and Late (layer B1) stages was determined principally on typological and technological aspects of the flint assemblage and associated architectural features and burials [34]. A later excavation revealed the existence of residual Final Natufian material intermixed with the disturbed overlaying historic deposits [83]. The $^{14}$C chronology of the Natufian component of el-Wad spans the period of ca. 12,950/13,000 to 10,650 YBP, covering practically the entire duration of this culture [86].

3. Materials and methods

Our working hypothesis was that owls deposited the remains of micromammals from el-Wad Terrace. This implies that the micromammal skeletal material originally accumulated at the owl roosting site, the cliff overhanging the terrace. From there, the material would have been transported to the terrace where it was subsequently buried. In order to test this hypothesis, we devised a comparative framework that includes two actualistic (recent) micromammal assemblages in addition to the prehistoric one. Together, these assemblages represent a general model of the conjectured taphonomic history denoting three idealized stages along a continuum: (1) Barn Owl – barn owl (Tyto alba) prey remains representing the assumed point of origin; (2) Niche – an off-site control from a niche in the cliff overhanging the terrace, an assumed focal location of accumulation by owls, representing an intermediate stage; and (3) Site – the fossilized material from the terrace, constituting the termination of the sequence. The Barn Owl assemblage, constituting 50 pellets collected from a roost in the rear of Isah Cave, Mount Carmel, at an aerial distance of approximately 4 km from el-Wad, includes a number of 16,545 identified specimens (NISP), the Niche assemblage 3953 NISP, and the Site assemblage 3962 NISP. Additionally, an assemblage of 283 NISP of micromammal remains from the Early Natufian layer in the interior of el-Wad Cave [60] was restudied for comparative purposes. This specific comparison is strictly qualitative owing to different mesh size used in the earlier (2 mm) as compared with the current (1 mm) excavation (for variable recovery rates associated with different mesh sizes see Ref. [68]). The el-Wad Cave site and excavation are described by Weinstein-Evron [87]. The range of extant and past taxa of the region known to constitute the prey of local owls and that fit within the zooarchaeological category of “micromammal” includes rodent and insectivore species reaching a maximum adult weight of approximately 200 g.

We selected a ca. 0.1 m$^3$ sediment sample from the Late Natufian layer of el-Wad Terrace from the recent excavation of the site. The sediments in this part of the section consist of a dark brown to grayish brown, very hard, clay loam with relatively low stoniness [88]. The sample constitutes a 0.25 m$^2$ (one horizontal excavation unit) by 0.4 m deep (seven spits ca. 5 cm each) stepped-column. It was collected from a part of the site where Late Natufian deposits were thickest and no evidence of disturbance could be detected. We wet-sieved the excavated material using screens of both 5 and 1 mm mesh, with the overwhelming majority of the micromammal remains retrieved from the fine fraction. In comparison with the scale of areal sampling in former excavations of the site extending over 270 m$^2$ [34] and 4.5 m$^2$ [83], recovery rate of micromammal remains is greater by five and three orders of magnitude, respectively. Inventory of taxa identified is also increased from four and six, respectively, to 11. Therefore, the

![Map of Israel showing the location of el-Wad Terrace.](image-url)
sample, with its dense concentration of micromammal remains (an estimated density of ca. 40,000 specimens per m²), is by far richer and thus more reliable and representative than any of the previously studied Natufian micromammal assemblages from el-Wad.

The taphonomic analysis is based on the standard counting units of zooarchaeological research: NISP, MNI, and MNE [49]. The method of recording primary skeletal specimen data is identical for all assemblages studied. We listed all identified specimens according to skeletal element and/or portion thereof (e.g., proximal or distal limb bones), body side, and taxonomic information. Taxonomic identification was feasible for molars, but only a few of the post-cranial elements. Minimum numbers of individuals and hence species frequency data (Table 1) are thus based on molar counts. We recorded skeletal element modification including breakage, digestion, weathering, gnawing, and charring and age data. We evaluated the extent of skeletal breakage based on the classification of limb and jaw specimens according to breakage schemes devised by Andrews (Ref. [1]: Figs. 3.7, 3.11, 3.12). These were expanded here in order to describe observed breakage in somewhat greater detail. To Andrews’ proximal, distal, and shaft limb breakage categories, we added a fourth category (‘other’) that comprises the smallest identifiable segments made up of detached articular portions: femur head, capitulum/trochlea of the humerus, and lunar notch of the ulna. We also recorded segments preserved with over half of the original element, and treated as complete elements by Andrews, as 2/3 portions (either proximal or distal). To Andrews’ four categories of progressive lower jaw or skull deterioration, we added two categories that correspond to the preservation of only the alveolar ridge with either two (2/3D) or one (1/3D) of the tooth alveoli remaining. We classified limb shaft fractures according to generalized formal types identified on large mammal bones: oblique, transverse, splintered, and stepped [63], which have also been detected on micromammal bones [53]. We examined digestion marks with a low vacuum scanning electron microscope (SEM; S410LV) without coating and compared these marks to types described by Andrews [1] and Fernández-Jalvo and Andrews [31]. We constructed weathering profiles by charting the frequencies of particular damage types associated with weathering stages defined by Andrews [1] for wet temperate climatic conditions. We also examined gnawing marks with SEM. We recorded only fully blackened specimens as charred to minimize possible biasing by black mineral staining of bones [69]. We used available tooth-wear schemes for reconstructing age structures of mole rats (Spalax sp.) (Ref. [36]: Fig. 334) and common mice (Mus spp.) (Ref. [47]: Fig. 9). Epiphyseal fusion data are also used to assess the age structure [57].

4. Results and comparative analysis

4.1. The basic counting units (NISP and MNI)

We initially examined the relationship between simple specimen (NISP) and MNI counts in order to assess the
potential for analytical biases [35]. Fig. 2 clearly indicates that the relationship is linear for both the Niche and Site assemblages ($r = 0.976$, $p < 0.01$; $r = 0.953$, $p < 0.01$, respectively), even including apparent outliers. According to Grayson [35], basing taxonomic identification and hence MNI derivations solely on one type of element, in this case the molars, is expected to produce a more straightforward relationship with sample sizes. Reliance on the molars is also expected to minimize effects of aggregation on MNI counts; these often result from either the partitioning or merging of faunal assemblages into arbitrary excavation units. Predictably, the MNI values tallied separately for each of the seven spits of the Site assemblage produced a higher total than those tallied for the aggregated assemblage (188 vs. 139). However, a chi-squared test of variance between the two arrays of MNI values indicates that the distributions are not significantly different ($\chi^2 = 3.9$, $p = 0.952$).

Fig. 2a reveals one outlier (mice) among the data points of the Site assemblage, exceeding two standard deviations (standardized residual = 2.74). By extrapolating on the regression line, the observed number of mouse molars is expected to yield a significantly lower number of individuals than are actually observed. Table 2 details the separate frequencies of first, second, and third molars for each species. The distribution for mice is clearly skewed towards M1. Differential loss during sieving could account for the under-representation of mouse smaller molars, M2 and M3. Notably, these teeth are among the smallest in the assemblage. Given that M1s were not as affected by this loss, we assume the observed MNI of mice approximates the actual MNI. In addition, such a sieving related bias is not expected for all larger skeletal specimens. In the Niche assemblage (Fig. 2b) the mouse datum point is also somewhat distant from the regression line but not over the two standard deviations required for a fit with the linear model.

One other analytical derivation that can elucidate the discrepancies between NISP and MNI species frequencies is the completeness of dental representation index. This index is computed by the same equation as skeletal element frequencies, except that for taxonomically identified molars the outcome is species-specific. We plotted completeness against their respective NISP values (Fig. 3) in order to evaluate potential dependence on sample size [35]. The mole rat datum signifies a high degree of completeness that does not correspond to a large sample size as for the voles (Microtus sp.) (upper right-hand corner). An inspection of relative frequencies of M1, M2, M3 (Table 2) reveals a rather uniform distribution for mole rats, with the lowest standard deviation ($s = 3.82$). Non-correspondence between the vole molar distribution and molar size indicates that for species larger than mice (including mole rats) frequencies are affected more by sample size than by molar size. Hence, recovery of teeth of these species is relatively unbiased.

### 4.2. Skeletal element frequencies

Relative skeletal element frequency ($R$) patterns for the Barn Owl, Niche, and Site assemblages (Fig. 4)
reveal a remarkable resemblance between the Niche and Site assemblages \((R = 0.841, p = 0.001)\). Data configuration in this figure is equivalent to Andrews’ [1] design of skeletal element frequency profiles also adopted by Fernández-Jalvo [29,30]. Molars and incisors are excluded from the correlation computation because their values, representing only isolated teeth, do not exclusively reflect loss as do values of all other elements, but also isolation. Taking into account in situ molars, much more prevalent in the Barn Owl than Niche and Site assemblages, increases correspondence between the three patterns. The Barn Owl pattern matches the recognized owl pattern [1,24,39,42,45] in several respects: (1) a high degree of element survival (average \(R = 73.42\)); (2) rather low frequencies of isolated teeth and of phalanges and metapodials; (3) preferential destruction of the distal limbs indicated by the calculated ratio of distal to proximal limb elements (following Ref. [1]: \(\%[\text{tibia} + \text{radius}/\text{femur} + \text{humerus}] = 95.33\)); and (4) a high proportion of isolated molars to isolated incisors. Significantly, the limb and teeth ratios are equally well defined in both the Niche and Site patterns. Teeth ratios are visually apparent in Fig. 5. Calculated limb ratios for the Niche and Site assemblages are 67.7% and 77.1%, respectively. There are also several differences between the patterns. The difference in frequencies of lower to upper jaws (Fig. 5) in the Niche and Site patterns suggests trampling by owls. Andrews [1] mentions considerable under-representation of upper jaws in recent owl trampled roost assemblages while experimental human trampling of pellet assemblages resulted in complete and rapid disintegration of all jaws. In contrast, the Barn Owl pattern, which is derived from a collection of fresh non-trampled pellets, exhibits a dominance of upper jaws.

We plotted relative reconstructed skeletal element frequencies (MNE), not scaled to MNI as above, on a log-difference scale (following Ref. [63]). This allows vertical, not just horizontal, comparisons across the graph. Fig. 5 depicts these frequencies in relation to the horizontal ‘zero’ axis, which corresponds to the standard of a complete skeleton. The patterns are relatively aligned for most skeletal elements, while for several elements noticeable gaps appear between all three assemblages. The gaps between frequencies of isolated teeth are not consistent with the vertical clustering of jaw frequencies. This implies non-correspondence between jaw destruction and tooth isolation, as suggested above. Noticeably, wide gaps also appear between frequencies of the ribs and vertebrae. Their notable under-representation in the Niche and Site patterns suggests possible effects of hydrodynamic sorting [23,42,90]. Ribs and vertebrae are among the skeletal elements most susceptible to fluvial transport and can be lost (as opposed to merely broken) early in this process. Specifically, greater under-representation of the ribs and vertebrae in the Site as compared with the Niche pattern may indicate more intensive fluvial sorting within the Site assemblage, possibly owing to its more exposed location on the terrace surface.

In order to further explore the possible effects of fluvial transport, we examined a correlation between skeletal element frequencies and corresponding experimentally derived values of susceptibility to transport. These hydraulic equivalences, taken from Korth (Ref. [42]: Table 2), pertain to the settling velocities of micromammal skeletal elements and are also found to align generally with an actual transport sequence [42,49] determined by Dodson [23]. For the purpose of this analysis, we tallied \%MNE values strictly according to the detailed level of anatomical partitioning employed in the experiments [42], a procedure stressed by Lyman [49]. We plotted these values on a scatter diagram (Fig. 6). The resultant correlation \((r = 0.632, p < 0.01)\) is relatively strong and positive, but it appears that further information can be gleaned by probing the variation in skeletal element frequencies apparently not...
accounted for by hydrodynamic sorting. An arching cluster of four outlying data points can be detected in the lower right sector of the diagram and their removal results in a stronger correlation \((r = 0.842, p < 0.01).\) These outlying elements (jaws, proximal tibia, and complete tibia) exhibit lower than expected frequencies given their hydraulic equivalences. Preferential destruction of jaws by trampling can explain their scarcity. A rather low structural density of the proximal tibia could be responsible for its under-representation. The lower than expected frequency of the complete tibia category could reflect fragmentation prior to transport. In fact, removing all complete limb element categories from the arrays strengthens the relationship. This suggests not only that skeletal elements were broken early in the taphonomic sequence, prior to transport, but also that no significant additional breakage occurred during later stages (e.g. burial). This may explain why the correspondence between frequencies of primary breakage categories (proximal, distal, shaft) and their respective hydraulic equivalences is maintained throughout the taphonomic history.

The influence of structural density-mediated taphonomic processes such as trampling and weathering can also be assessed by examining skeletal element frequency patterns. Comparable bone density measurements are available only for marmots (genus *Marmota*; Ref. [50]: Table 2). Admittedly, these members of the order Rodentia are larger (average adult weight: 2.3–4.5 kg) than the species present in our sample (maximum average adult weight: \(\sim 200\) g). Moreover, the Niche and especially Site assemblages also comprise an amalgam of different albeit similarly small-sized (mostly rodent) species. Certain inter-taxonomic differences are expected in anatomical interrelationships of bone density estimates (e.g. [50]). Such differences could encumber attribution of causality to the relationship between skeletal element frequencies and density-mediated attrition. However, a more significant correlation was found between structural density estimates of deer (*Odocoileus* spp.) and marmot skeletons [50] than between those of similarly sized leporid (family Leporidae) and marmot skeletons [56]. The precise causes of such variation are not well understood [50]. Given these difficulties, our comparison is provisional only and aimed at exploring the possibility of structural density-mediated attrition suggested above based on patterning in frequencies of particular skeletal elements. Causality can be more confidently attributed through additional lines of evidence such as hydrodynamic sorting. We again tallied \%MNE values strictly according to the detailed level of anatomical partitioning employed in the structural density determinations. The relationship between skeletal element frequencies and their respective structural density values \((r = 0.379, p > 0.05)\) is shown in a scatter plot (Fig. 7). An outlying cluster of data points can be detected in the lower center of the diagram. As expected, removing these outliers produces a stronger correlation \((r = 0.846, p < 0.01).\) Most of the outliers (vertebrae, radius, phalanges, metapodials, pubis, and ischium) that yield a lower than expected frequency given their structural density values are also among the skeletal elements most susceptible to fluvial transport [23,42]. The one exception is the tibia shaft. A hydraulic equivalence value for this skeletal segment is lacking but its cylindrical shape should increase its susceptibility to transport [49].

A correlation coefficient was calculated between the arrays of structural density and hydraulic equivalence values, reciprocally standardized in terms of anatomical partitioning. This test produces a null outcome \((r = -0.046, p > 0.05)\) supporting the exclusiveness of the effects of fluvial transport and structural density-mediated destruction on the Site assemblage. This result can be partly explained by the fact that the respective values of the two arrays differ in their scale of measurement – whole or segments of skeletal elements in the case of hydraulic equivalence [42] and scan sites in the case of structural density [50]. Moreover, the hydrodynamic property of skeletal material combines factors other than structural density such as shape and water content [18]. We also calculated correlation

![Fig. 6. Correlation between hydraulic equivalences (Ref. [41]: Table 2) and frequencies of skeletal elements (%MNE) in the Site assemblage (empty circles represent outliers).](image)

![Fig. 7. Correlation between marmot structural densities (Ref. [49]: Table 2) and frequencies of skeletal elements (%MNE) in the Site assemblage (empty circles represent outliers).](image)
coefficients between skeletal element frequencies and both hydraulic equivalence and structural density values for the Niche assemblage. In both cases the correlations ($r = 0.433, p > 0.031$; $r = 0.31, p > 0.149$, respectively) are weaker than those obtained for the Site assemblage (by 18% and 30%, respectively) but they are distorted by outliers consisting mostly of the same skeletal elements. This result suggests a less pronounced transport impact. Undoubtedly, other processes could have contributed to some loss or destruction of different skeletal elements. However, fluvial transport and structural density-mediated processes of attrition, together, appear to account for the majority of variation in gross patterning of skeletal element frequencies.

4.3. Breakage patterns

We examined breakage patterns on all the limb bone and jaw specimens in the Barn Owl, Niche, Site, and el-Wad Cave assemblages. A most informative preliminary observation concerns the occurrence of complete elements. As is expected, these are overwhelmingly abundant in the Barn Owl assemblage (95% limb bone and 85% jaw specimens). Their frequency is markedly lower in the Niche assemblage (26% and 19%, respectively), whereas in the Site (terrace) assemblage they are absent altogether. The el-Wad Cave assemblage, on the other hand, does include complete limb bones and jaws. Similarly, 2/3 portion limb bone specimens are more abundant in the Barn Owl and Niche assemblages (6% and 9.1%, respectively) than in the Site assemblage (0.9%). Another measure of breakage is the intensity of fragmentation expressed by the index NISP/MNE or the number of fragments representing each complete element (Ref.[49] and references therein). In the Barn Owl assemblage the intensity of fragmentation of the major limb bone and jaw elements is rather low (Table 3). The intensity is mostly higher or remains the same in the Niche assemblage. It is higher still for several elements in the Site assemblage, but the proportional increase between the values of the Niche and Site assemblage is lower in this case. Moreover, it appears that for the maxilla and tibia the intensity of fragmentation in the Niche assemblage is actually higher than in the Site assemblage.

The more specific distributions of breakage divisions for each of the major limb elements in the Site (Fig. 8a) and Niche (Fig. 8b) assemblages reveal a resemblance between the two. Rank-order correlations indicate a perfect fit (Spearman’s rho = 1; $p < 0.01$) for most limb elements besides the femur. Owl prey assemblages are typified by a pattern of limb bone breakage involving these bone segments [45]. This pattern is attributed to differential vulnerability of various bone portions to destruction effected by owls. A comparison with the distributions of breakage divisions in the Barn Owl assemblage shows the same highest rank order for these characteristic segments as in the Niche and Site assemblages (e.g., proximal femur, distal humerus). The tibia in the case of the Barn Owl assemblage – the only exception to this pattern – is represented by a higher frequency of proximal rather than distal segments. This feature has also been found in some owl prey assemblages [1,39] but not in others [45]. Nearly half of the fractures observed on the limb bone specimens in the Niche and Site assemblages (50.2% and 49.2%, respectively) are attributed to the oblique or transverse (either regular or irregular) fracture type. This type of fracture can be generated by various possible agents during earlier stages of weathering and fossilization as a result of dynamic loading impact [49]. Trampling of

<table>
<thead>
<tr>
<th>Element</th>
<th>Site Niche</th>
<th>Barn Owl</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandible</td>
<td>1.82</td>
<td>1.52</td>
</tr>
<tr>
<td>Maxilla</td>
<td>0.92</td>
<td>1.00</td>
</tr>
<tr>
<td>Femur</td>
<td>1.60</td>
<td>1.00</td>
</tr>
<tr>
<td>Tibia</td>
<td>1.48</td>
<td>1.00</td>
</tr>
<tr>
<td>Humerus</td>
<td>1.41</td>
<td>1.00</td>
</tr>
<tr>
<td>Radius</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Ulna</td>
<td>1.40</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Fig. 8. Distributions of breakage divisions (following Ref. [1]: Fig. 3.7) for the major limb elements in the (a) Site and (b) Niche assemblages (based on NISP; totals include complete elements and/or 2/3 segments, not shown here; numbers represent sample sizes).
micromammal bones by owls in their roost prior to transport is a conceivable source of such impact.

Examination of change in jaw breakage patterns from the Barn Owl to the Niche and Site assemblages demonstrates the expected dynamics of skeletal breakage. From right to left, Fig. 9 reveals a shift in concentration of both mandible (Fig. 9a) and maxilla (Fig. 9b) specimens from the categories of least breakage (A, B) to those of greatest breakage (1/3D, 2/3D) with a leveling off of the distribution in the middle Niche assemblage. Two useful indices that measure the degree of jaw breakage are: (1) percent molar loss – the proportion of empty to total number of alveolar spaces [1]; and (2) percent alveolar space survival – the proportion of observed to expected alveolar spaces given the number of molars present. The latter index is equivalent in its implication for jaw breakage to Andrews’ [1] index – % isolated molars – but is calculated differently and produces outcomes of a much lower order of magnitude. The first index predictably produces the lowest outcome for the Barn Owl assemblage, in which most of the molars are still in situ (Table 4). More surprisingly, the highest outcome is that of the Niche assemblage, probably because of isolation of molars prior to actual disintegration of the alveoli. This is especially relevant in the case of the unrooted vole molars. Alveolar loss increases in the Site assemblage, resulting in a lower “percent molar loss”. Species-specific data for computing the second index are available for both the Niche and Site assemblages. Such interspecific comparisons can highlight taphonomic biases [90]. For the shrews (Soricidae) the outcome is higher than the expected value (100) and testifies to a deficit in the number of molars needed to account for all the alveolar spaces present (Table 4). These molars, the smallest in the assemblage, could possibly have been lost during sieving. The lowest outcome in the Site assemblage is that of mole rats, indicating significant jaw breakage.

### 4.4. Digestion marks

Chemical corrosion through digestion is the most diagnostic imprint of predatory owls on skeletal material [1]. Furthermore, vole molars are known as one of the most suitable skeletal elements for registering these marks owing to their mineralogical composition. However, inter-assemblage comparisons based on vole molars are hindered in this case by the low frequency of this species in the Barn Owl assemblage. Digestion marks were recorded on the left and right vole M1 samples from the Site assemblage. Maintaining separate samples in data recording prevents potential bias related to anatomical interconnectedness. The right M1 sample produced the maximum extent of digestion where 41.3% of the molars are affected to some degree. The degree of digestion in both samples is restricted to light and moderate grades. Following Fernández-Jalvo and Andrews’ [31] terminology and classification, these encompass: (1) rounding and enamel loss at the edges of occlusal surfaces (Fig. 10a); (2) removal of enamel along the salient angles (Fig. 10b). In addition, we observed equivalent grades of digestion on murid molars in the form of surface pitting and in situ breakage.

We also inspected limb bone extremities from the Barn Owl, Niche, and Site assemblages for digestion marks (Fig. 10c–e). Intrusive localized corrosion of the more vulnerable articular surfaces characterizes predatory assemblages [22]. We restricted this analysis to the early fusing distal humerus and proximal femur specimens to avert the potential biasing associated with the less resistant juvenile elements. The frequency of digested femur heads is consistently higher than that of

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**Table 4**

Indices of jaw breakage in the Site, Niche, and Barn Owl assemblages

<table>
<thead>
<tr>
<th>Index</th>
<th>Site</th>
<th>Niche</th>
<th>Barn Owl</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Isolated molars</td>
<td>28.57</td>
<td>50.42</td>
<td>19.68</td>
</tr>
<tr>
<td>% Alveolar space survival</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spalax sp.</td>
<td>17.54</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mus spp.</td>
<td>50.41</td>
<td>74.47</td>
<td>–</td>
</tr>
<tr>
<td>Soricidae</td>
<td>140.00</td>
<td>109.38</td>
<td>–</td>
</tr>
</tbody>
</table>

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digested distal humerus joints in the three assemblages (Table 5). This disproportion possibly reflects the differential susceptibility of the two limb extremities to digestive corrosion. The significance of this pattern is emphasized by the pronounced increase of the discrepancy in the time-averaged Site assemblage, which shows a strong relative predominance of digested femur heads. Moreover, the change in digestion ratio of these two articular portions between the three assemblages does not correspond to the shifts in general proportions of the respective limb elements (Table 5). We graded degrees of digestive effects on the limb bones in the three assemblages as light to moderate following Andrews’ [1] criteria.

4.5. Weathering

Documenting the frequencies of various modifications of skeletal material ascribed to weathering can yield an estimate of the relative extent of their aerial exposure [49]. The actual exposure duration cannot be ascertained with confidence owing to the high temporal variability that characterizes the progression of weathering processes under different environmental conditions [42]. Cracking, chipping, and splitting of micromammal
bones and teeth are ordinarily recognized as weathering effects [1]. We examined these damage types on vole and mouse molar samples from the Niche (right M1 of voles and right M1 of mice) and Site (left and right M1 of voles and all M1s of mice) assemblages. The separate samples from the Site assemblage demonstrated no significant differences within each species (voles: $\chi^2 = 0.392$, $p = 0.822$; mice: $\chi^2 = 9.07$, $p = 0.17$) despite relatively small sample sizes. The two weathering profiles of the Site assemblage (Fig. 11a) are generated by summing the figures for the separate samples. For both voles and mice, the profiles indicate a lesser degree of exposure in the Niche assemblage (Fig. 11b) than in the Site assemblage. The bar representing advanced weathering ('splitting') is greatly diminished in the Niche assemblage profiles in comparison to the Site assemblage profiles. Splitting of skeletal elements is associated with later stages of weathering [1]. Similarly, stepped and splintered type fractures associated with more advanced weathering appear on nearly half of the limb bone specimens in the Niche and Site assemblages.

4.6. Gnawing

We detected conspicuous, exceptionally smooth and parallel grooves on two of the mole rat femur heads from the Site assemblage (Fig. 10f). These grooves approximate in width that of the sharpened edge of a mouse size incisor (<1 mm). A few of the other larger femur heads were missing substantial chunks of bone, some on opposite sides of the head, yielding an appearance unlike that of a typical fracture. Given that large mammal bones from el-Wad Terrace also exhibit rodent gnawing marks [5], we identify this atypical damage pattern as such.

4.7. Charring

Patterning in the anatomical association of burned micromammal remains has been used as a signature for human consumption [37,84]. We recorded a total of 45 blackened limb bone specimens in the Site assemblage, constituting approximately 8% of all the limb bone specimens (humerus, radius, ulna, femur, and tibia). Of these charred specimens, 17 are remains of mole rats. These account for 26.2% of the 65 mole rat limb bone specimens present in the assemblage. Thus, mole rat bone charring is significantly greater than that for all other species together ($\chi^2 = 14.76, p < 0.0001$). Despite the relatively small sample size, this considerable difference rules out incidental charring (e.g. Ref. [73]) of mole rat bones.

We further examined the occurrence of charred limb bone specimens, separating those of mole rats from the others, by inspecting their distribution among the various limb bone breakage segments (Fig. 12). Notably, the two distributions differ ($\chi^2 = 15.33, p = 0.001$). Over 70% of the mole rat specimens are in the category of smallest identifiable limb bone segments. It can be expected that an increased exposure to fire would induce a greater degree of fragmentation [73]. In contrast, the frequencies of charred specimens are nearly evenly distributed across limb bone elements. Deliberate roasting by humans as part of food preparation practices is a conceivable cause for these divergent patterns. The economic significance of mole rats could be accounted for by their large size (average adult weight: ~200 g) and by the fact that these exclusively fossorial animals are conspicuous above ground by the mounds created by their extensive tunnel digging activity.
4.8. Age structure

Certain agents of accumulation, such as nocturnal raptors, are associated with particular prey age profiles. The standard basic patterns for catastrophic (L-shaped) and attritional (U-shaped) mortality, documented for larger fauna, have also been recognized in micromammal assemblages [43]. We independently classified the four samples of M1 mouse molars from the Site assemblage into formal tooth-wear stages [47]. The patterns obtained do not significantly differ ($\chi^2 = 17.59$, $p = 0.285$). Although tooth-wear patterns can sometimes reflect intraspecific dietary variation [16], this correspondence suggests that the patterns are age-related. We thus tallied these frequencies into one array according to MNI per age cohort by deriving the highest count from each. Incorporating the age criteria into the mouse MNI enlarges this figure from 30 to 34 individuals. We aged right M1 samples in the same manner for the Niche and Barn Owl assemblages.

The Barn Owl and Niche age structures (Fig. 13) do not significantly differ ($\chi^2 = 0.41$, $p = 0.815$), and display a markedly different range than that of the Site assemblage, which includes individuals from additional older cohorts. If these cohorts (age categories 6–8) are excluded, the three mortality profiles, exhibiting a dominance of juvenile to sub-adult age groups, are characteristic of recent as well as fossilized Barn Owl prey assemblages [57] and reflect greater vulnerability of younger individuals to owl predation. The Site assemblage age structure may reflect superposition of two distinct mouse assemblages with different depositional origins.

The presence of juveniles in substantial frequencies in the Barn Owl, Niche, and Site assemblages is supported by epiphyseal fusion data, although the exact age correspondence with tooth-wear data is not fully understood. We tallied these data according to frequencies of either the unfused limb bone extremities or epiphyseal plates, whichever were more abundant. Proportions of unfused specimens in relation to frequencies (actual or reconstructed) of complete skeletal elements produce the number of juvenile individuals. These are highest in the Barn Owl assemblage for all four articular regions inspected (Table 6), with a maximum of 87.8%. Excluding the proximal femur, proportions are lower in the Niche assemblage (maximum of 66.7%) and still lower in the Site assemblage (maximum of 41.6%). These lower percentages of juvenile individuals could result from selective loss of their skeletal elements, which are more susceptible to the various taphonomic processes of destruction [61]. Inconsistency in rank order of articular regions within assemblages indicates that the pattern does not primarily reflect a preservation bias.

We classified three of the mole rat M1 samples from the Site assemblage according to tooth-wear stages representing broad age groups [36]. An inverted L-shaped age structure results (Fig. 14). This structure is diametrically opposed to that of a recent sample of mole rat remains from barn owl pellets collected in Israel. The recent age structure is explained by the increased above-ground activity of juvenile to sub-adult mole rat individuals as a consequence of their exclusion by adults through territorial aggression [38]. In the Barn Owl and Niche assemblages the frequencies of mole rat molars are too low for us to reconstruct the age structures.

5. The taphonomic history of el-Wad Terrace micromammal assemblage

We identified significant taphonomic patterns in the el-Wad Terrace micromammal assemblage through its

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Table 6

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Site No.</th>
<th>Site %</th>
<th>Niche No.</th>
<th>Niche %</th>
<th>Barn Owl No.</th>
<th>Barn Owl %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proximal femur</td>
<td>30</td>
<td>33.71</td>
<td>22</td>
<td>31.43</td>
<td>118</td>
<td>43.70</td>
</tr>
<tr>
<td>Distal femur</td>
<td>37</td>
<td>41.57</td>
<td>32</td>
<td>45.71</td>
<td>237</td>
<td>87.78</td>
</tr>
<tr>
<td>Proximal humerus</td>
<td>33</td>
<td>36.67</td>
<td>40</td>
<td>45.45</td>
<td>171</td>
<td>64.53</td>
</tr>
<tr>
<td>Proximal tibia</td>
<td>19</td>
<td>22.35</td>
<td>40</td>
<td>66.67</td>
<td>195</td>
<td>73.31</td>
</tr>
</tbody>
</table>

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Fig. 13. Age structures of mice in the Site, Niche, and Barn Owl assemblages (numbers represent sample sizes).

Fig. 14. Age structures of mole rats in the el-Wad Terrace assemblage and recent barn owl pellet collections (recent data taken from Ref. [38]; numbers represent sample sizes).
analysis within an actualistic and controlled comparative framework. The multiple types of data reveal traces of the major depositional and secondary stages along the taphonomic sequence. The working hypothesis represented by our model of the taphonomic history posits the accumulation of the micromammal remains by owls roosting in the cliff overhanging el-Wad Terrace and their subsequent transport to the site (Fig. 15). A synthesis of the data enables the detailed reconstruction of the taphonomic sequence as discussed below.

5.1. Deposition

We identified several distinct features of the taphonomic signature of owls in the Barn Owl assemblage and then traced them through the Niche and Site assemblages. Most significantly, we found digestion marks on both molars and post-cranial elements which are generally compatible in frequency and degree with those recorded in either recent or paleontological owl prey assemblages [1,29–31]. This is also the case for the higher proportion of digested femur heads relative to digested distal humeri occurring in the three assemblages. Low to moderate degrees of digestion persist through all the specimens examined and correspond well to the low digestive impact associated with owls [1].

Patterns of skeletal element representation also revealed some distinct features of the taphonomic signature of owls. These mainly include a higher proportion of isolated molars relative to isolated incisors, which is unique to the actualistic pattern of barn owls studied by Andrews [1], and a slight to moderate loss of distal limb elements, which is a general owl pattern feature [1]. The distributions of limb element breakage divisions in the three assemblages are also similar to those found in actualistic owl prey assemblages [45]. Attaining within family level identification of the strigid accumulating agent can be problematic. Variation in taphonomic signatures of owls has been observed geographically [64] and between different age groups [61]. However, barn owls are the most likely candidate because of their ubiquity in this region, especially among the cave-dwelling nocturnal raptors [3,80].

Several lines of evidence disclose the minor superimposed contributions of two other agents of accumulation. The mole rat remains consistently exhibit taphonomic patterning that deviates from the generally observed or expected owl imprint. These consist of the age distributions, extent of charring, rodent gnaw marks, completeness of dentary representation, and breakage patterns. Furthermore, the relative abundance of mole rats in the Site assemblage (10.8%) significantly exceeds those in the Niche and Barn Owl assemblages (1.4% and 0.7%, respectively). The typical frequency of mole rat prey in recent barn owl pellet collections from Israel does not exceed 2% [25]. Cumulatively, this evidence suggests consumption of mole rats by the Late Natufians of el-Wad Terrace. Consumption of micromammals from the high end of the body-size scale, also associated with increased levels of charring, was archaeologically recorded at two rockshelter sites of central Chile [70]. Procurement of other fossorial species such as the South African dune mole rat (*Bathergus suillus*) [37] and the North American pocket gopher (Ref. [44: p. 448; 67]) is also documented ethnographically and archaeologically. Conspicuousness, which is suggested as an important aspect of the desirability of such small animals [70], may also be bolstered by the mound-building habits of underground rodents. The potential economic significance of microvertebrates in Levantine prehistoric periods has previously been ruled out specifically because taphonomic data demonstrating modes of accumulation were lacking [26,55]. Changes in small-game use patterns during the Epipaleolithic of the Levant indicate a shift in exploitation strategies associated with the broad spectrum revolution [74]. Specialization implied by intensified procurement of other harder-to-catch species as hares and partridges could have extended to relatively large rodents such as the fossorial mole rats.

Representation of older mouse individuals in the Site age structure, as compared with their absence in the Niche and Barn Owl profiles, together with evidence of gnawing indicates the presence of live mice in the Natufian settlement. Gnawing marks were also found on macromammal remains from the site [5]. The earliest known specimens of the commensal mouse (*Mus musculus domesticus*) were identified in the Natufian layer of Hayonim Cave, northern Israel [2]. Reduced mobility and prolonged site occupation resulted in newly created anthropogenic habitats [74] that may
have allowed the house mouse to colonize regions formerly dominated by the local wild mouse (Mus macedonicus) [12]. Therefore, house mouse remains in Natufian sites serve as a key indicator for one of the pivotal cultural processes of this time period [7]. Protection from predators is one advantage afforded to micromammal species that colonize the human environment [79]. Thus, remains of commensal mice with a longer life-span may eventually accumulate in situ. This alternate mode of deposition can resolve the problematic issue of whether owl prey assemblages accurately reflect the phenomenon of commensalism [75,81]. We thus propose controlled comparative analysis of age structures as an additional indicator of micromammal commensalism. This approach provides further support for the well-established argument of a marked increase in the visibility of this phenomenon associated with the Levantine Natufian culture [79,80].

5.2. Biostratinomic stage

Most skeletal material loss from the Site assemblage seems to have resulted from trampling, weathering, and fluvial transport, which generally follow deposition. This is evident from the comparison of skeletal element representation patterns for the Barn Owl, Niche, and Site assemblages (Fig. 4). The patterns reveal a wide gap between the former “depositional” assemblage and the latter two “post-depositional” assemblages which exhibit considerable overlapping. Hydrodynamic sorting appears to account for a substantial degree of the variation in skeletal element frequencies in the Niche and Site assemblages. Evidently, this process is principally responsible for the highly significant correlation between the two patterns, both representing lag deposits. Several discrepancies that were repeatedly detected by various analyses suggest the recognized effects of owls trampling prey remains in their roosts, as determined by Andrews [1]. Predictably, weathering is less pronounced in the Niche than in the Site assemblage, probably due to further aerial exposure of the skeletal material during transport and prior to burial. In addition, structural density of skeletal elements may explain partially and independently their observed frequencies in the Niche and Site assemblages. Fluvial transport, as well as, trampling and weathering are all structural density-mediated processes [49]. Nonetheless, it would have been preferable to compare observed skeletal element frequencies with structural density estimates derived from equivalent species to those present in the Niche and Site assemblages (see Refs. [56,66]).

Predictably, the various measures of skeletal breakage recorded indicate that, in general, breakage is less extensive in the Niche than in the Site assemblage. However, the more quantitative measure of intensity of fragmentation yields a higher proportional increase from the Barn Owl to the Niche assemblages than from the latter to the Site assemblage. Measures of breakage record patterns in the surviving portion of faunal assemblages and are therefore not indicators of the loss that has accrued, as are the reconstructed relative element frequencies. Patterns of skeletal element frequencies, however, can reflect loss that is in part due to breakage (destruction to below the visibility threshold), through trampling, for example. Breakage initially results in increasing numbers of skeletal specimens, while during later taphonomic stages, loss is manifested by fragmentation of elements into unidentifiable specimens [51]. These facts can explain the considerable overlap in skeletal element frequency patterns of the Niche and Site assemblages and suggest that the observed degree of breakage is largely related to the biostratigraphic rather than diageneric (burial) stage. Most breakage could thus have resulted from initial processes of trampling and weathering that together with hydrodynamic sorting seem to have determined the Niche and Site patterns of skeletal element representation.

Evidently, the intensity of the taphonomic processes that followed deposition of the micromammal remains was moderate enough to allow the preservation of primary data in the Site assemblage, consisting of the signatures of natural as well as cultural agents of accumulation. The lower extent of breakage observed in the el-Wad Cave Natufian assemblage, however, suggests better conditions of preservation prevailing inside this more protected environment. On the other hand, open-air sites such as the multi-seasonal camp of Ohalo II [9] and others from widely separate geographical, temporal, and contextual settings (e.g. Refs. [19,32,42,90]) exhibit an exceptionally low representation of skeletal elements. This pattern differs markedly from the typically high representation of skeletal elements generally recorded for cave assemblages (e.g. Refs. [1,29,30,57]) and that also characterizes the Site assemblage pattern (Fig. 4). The preservation potential of primary data in el-Wad Terrace, representing a discrete site type, is thus scaled intermediate between cave and open-air depositional environments.

5.3. Burial stage

A relatively rapid rate of burial of the Site assemblage is suggested by the good preservation of evidence for the earlier stages of the taphonomic sequence – biostratigraphic and especially depositional processes. Micromorphology and FTIR analyses of the Late Natufian sediments indicate a burial environment supporting a relatively low extent of post-depositional biological and chemical reworking of skeletal elements [88]. Hence,
diagenetic processes (e.g. soil compaction) would have had relatively little impact on the state of preservation of the assemblage. The colluvial sedimentation of locally derived terra rossa soils [88] is also consistent with migration of micromammal remains from the cliff to the terrace. As shown above, the pattern of skeletal element representation was largely imprinted prior to burial. Burial of micromammal skeletal material effectively protects it from most of the damage and loss caused by above-ground taphonomic processes [1]. However, the somewhat higher extent of breakage generally recorded for the Site assemblage as compared with the Niche assemblage suggests some impact of diagenetic processes.

5.4. Excavation methods

The marked resemblance between skeletal element representation patterns of the Niche and Site assemblages suggests that damage and loss attributed to post-biostratigraphic stages, including excavation procedures, is minimal. The under-representation of shrew molars and of mouse second and third molars hints at restricted differential loss caused by the mesh size (1 mm) employed in the sieving of the el-Wad Terrace deposits. Both mice and shrews occupy the lower end of the micromammal species size range represented in the Site assemblage. The use of 1 mm mesh screens is standard practice in prehistoric excavations in Israel, although smaller mesh sizes of 0.5 mm [30] and even 0.25 mm [58] have been used elsewhere. Our results underscore the vital importance of implementing fine screening as a standard component of excavation procedures in circumstances where recovery of micromammal remains is expected.

6. Conclusions

In this study we establish taphonomically the predominant contribution of owls to the formation of fossilized micromammal assemblages at el-Wad Terrace and by inference at other sites in similar settings. Our results provide a baseline for comparative research of micromammal taphonomy in Levantine sites. Owing to the detailed and comprehensive taphonomic analysis carried out in an actualistic and controlled comparative framework, we were able to distinguish cultural vestiges that have survived in the el-Wad Terrace faunal record. Consumption and commensalism of micromammal species – mole rats and mice, respectively – demonstrated as agents of accumulation in and of themselves, bear significant consequences for the economy and settlement pattern of the Levantine Natufian culture.

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