

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

## Journal of Archaeological Science

journal homepage: <http://www.elsevier.com/locate/jas>

## The urban ecology of Iron Age Tel Megiddo: using microvertebrate remains as ancient bio-indicators

L. Weissbrod<sup>a,\*</sup>, G. Bar-Oz<sup>a</sup>, T. Cucchi<sup>b,c</sup>, I. Finkelstein<sup>d</sup>

<sup>a</sup>Laboratory of Archaeozoology, Zinman Institute of Archaeology, University of Haifa, Haifa 31905, Mount Carmel, Israel

<sup>b</sup>CNRS-Muséum National d'Histoire Naturelle, UMR 7209 "Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements", Département "Ecologie et Gestion de la Biodiversité" CP 56, 75005 Paris, France

<sup>c</sup>Department of Archaeology, University of Aberdeen, Aberdeen, United Kingdom

<sup>d</sup>The Jacob M. Alkow Department of Archaeology and Ancient Near Eastern Civilizations, Tel Aviv University, Tel Aviv 69978, Israel

### ARTICLE INFO

#### Article history:

Received 23 January 2012

Received in revised form

30 June 2012

Accepted 3 July 2012

#### Keywords:

Iron Age

Tel Megiddo

Near East

Microvertebrate taphonomy

Urban ecology

Ancient bio-indicators

### ABSTRACT

The potential of microvertebrate remains for reconstructing the paleoecology of urban sites remains largely untapped except for extensive research carried out at Roman and medieval sites in Britain. We apply taphonomic and ecological approaches to analyzing an assemblage of microvertebrate remains from the Iron Age IIA of Tel Megiddo, Israel. Sampling in a dense residential area including house floors and various fills produced 1080 identifiable specimens including fish, mammal, reptile and bird remains. The mammalian remains show a number of distinct patterns pointing to accumulation from the community of small animals which lived and died on-site. These patterns include evidence for fragmentation due to trampling and presence of burned specimens. The mammalian remains also differed in their taphonomy from an assemblage from Early Bronze Age II Megiddo which originated from predator accumulation during a period of abandonment. These analyses point to an especially low taxonomic diversity in the Iron Age residential assemblage suggesting that the urban environment of Megiddo supported a unique community of small mammalian animals. This differs markedly from ecological conditions in modern day cities which in some cases show greater than background levels of diversity and suggests a dense, homogenous urban environment. We suggest that reconstructing the evolution of urban fauna in greater detail will provide a sensitive tool for tracing historical processes of growth, decline and increasing complexity of urban sites in the Near East as well as other regions of the world.

© 2012 Elsevier Ltd. All rights reserved.

"Bioindicators include biological processes, species, or communities and are used to assess the quality of the environment and how it changes over time. Changes in the environment are often attributed to anthropogenic disturbances (e.g., pollution, land use changes)..." Holt and Miller 2011.

### 1. Introduction

Research in urban ecology has shown that dense urban environments can sustain unique communities of small vertebrate animals including rodents, shrews, birds, lizards and amphibians (e.g., Dickman, 1987). Currently, little is known about the way that such ecological communities evolved in response to historical processes of urbanization in different regions of the world.

Systematic research on archaeological assemblages of microvertebrate remains from urban contexts has so far focused mainly on Roman and Medieval sites in Britain during the 1st millennium AD (e.g., Armitage, 1985; Mulkeen and O'Connor, 1997; O'Connor, 1992, 2000, 2003; Piper and O'Connor, 2001; Rackham, 1982). In this region, urbanization developed fairly late and coincided roughly with the introduction from the east of already evolved urban fauna such as house mice and rats (Armitage et al., 1984; Armitage, 1994; Audoin-Rouzeau and Vigne, 1997; Cucchi et al., 2005; Eryvynck, 2002). In this study we examine microvertebrate remains from a much earlier urban context from the Iron Age of the Near East in the beginning of the 1st millennium BC.

Research has shown that microvertebrate remains provide a rich source of information on environmental and ecological conditions in ancient urban settlements and can contribute significantly to reconstructing the living conditions at such sites and how they changed through time (see reviews in Evans, 1978; O'Connor, 2000, 2003, 2010; O'Connor and Evans, 2005; Somerville, 1999). The

\* Corresponding author. Tel.: +972 4 8240528; fax: +972 48249876.

E-mail address: [lweissbr@research.haifa.ac.il](mailto:lweissbr@research.haifa.ac.il) (L. Weissbrod).

community structure of small mammalian species, in particular, is sensitive to environmental disturbance and change. Based on ecological studies in present day urban environments we can expect high taxonomic diversity in heterogeneous sparsely populated areas with mosaics of built up and vegetated patches and low taxonomic diversity in homogenous densely built and populated areas (Castillo et al., 2003; Cavia et al., 2009; Dickman, 1987; Mahan and O'Connell, 2005). Furthermore, highly homogenized and urbanized areas are characterized by dominance of wide spread human commensals such as house mice and rats.

Studies in both archaeological and ethnographic settings provide only a handful of clues on the ecological consequences of settlement intensification such as sedentarization and urbanization during prehistoric and historic periods (Auffray et al., 1988; Bar-Yosef and Tchernov 1966; Dean, 2005, 2010; Hesse, 1979; O'Connor, 2003; Tchernov 1984, 1991; Weissbrod, 2010). The available data are widely distributed across time, space and cultural contexts and do not presently allow us to construct a full picture of the evolution of community structure of small animals in urban environments.

Here we focus on microvertebrate remains from occupation deposits in a dense residential area at the Iron Age site of Tel Megiddo, Israel. Occupation deposits include material that accumulated during the period of occupation of the given layers through two types of processes: 1) occupational accumulation resulting from the slow buildup of material in association with living surfaces containing artifacts and other remains from the period of site occupation and 2) fill which represents the relatively instantaneous formation of a deposit as a result of deliberate dumping or mixing of material, for example during construction activity and can contain remains from earlier periods. Sediment buildup within structures can, in general, occur during times when structures are abandoned. We distinguish, however, between the abandonment of specific structures and site abandonment and emphasize that the material in this study does not represent site abandonment. Occupational accumulations have received comparatively little attention in research on ancient urban environments. Rackham (1982) reported that in archaeological sites in northern Britain microvertebrate remains were scarce in most deposits except in particular features such as pits, wells and drains which acted as traps for small animals. Piper and O'Connor (2001) used the term sub-surface death assemblages to refer to remains of small animals which existed at the site, died there and eventually became incorporated into deposits such as domestic refuse. We view this mode of deposition as *in situ* accumulation of animals from the local ecological community which coexisted with the human inhabitants at the settlement. Remains which accumulated in this manner should provide direct information on the community structure of microvertebrate animals at the time of site occupation.

The goal of this study is to identify the mode of accumulation of microvertebrate remains in occupation deposits of a dense urban environment and examine their implication for reconstructing the paleoecology of the urban environment at Iron Age Megiddo. The excavation campaign included systematic collection of samples for analysis of microvertebrate remains using fine-scale recovery techniques on a large scale. The assemblage retrieved through this project presents one of the largest and earliest samples of microvertebrate remains from occupation deposits in an urban context and allows us to examine for the first time direct evidence on the ecology of an urban site, nearly 3000 years old. This study can therefore address taphonomic and paleoecological gaps in research on the evolution of urban fauna.

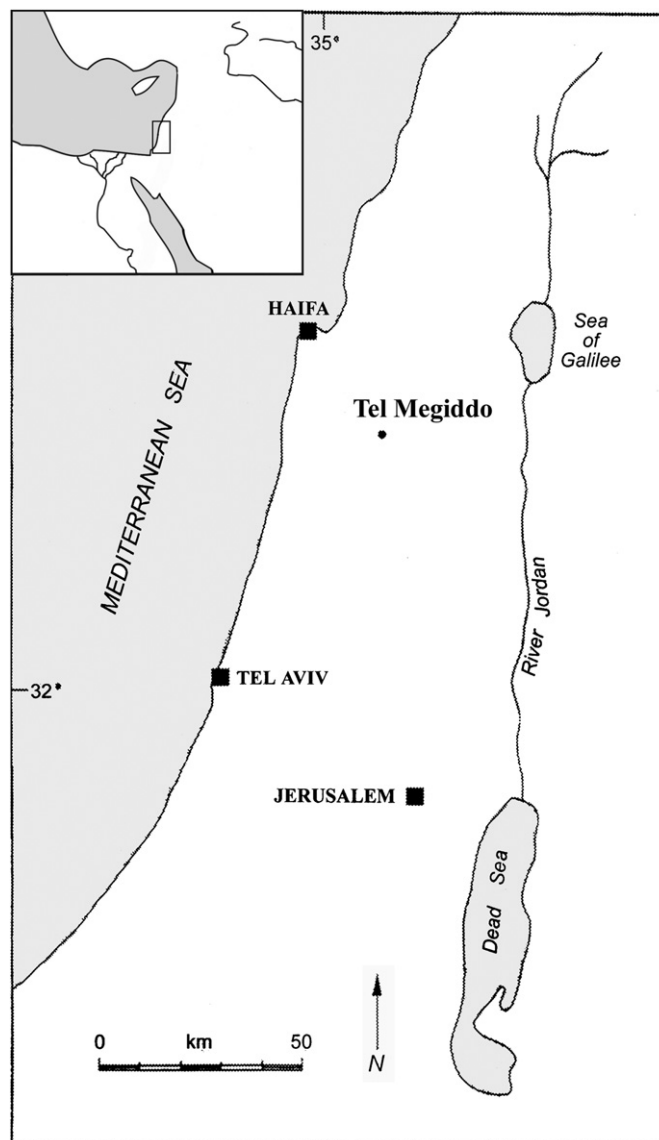


Fig. 1. Map showing the location of Tel Megiddo.

## 2. Iron Age Megiddo

Tel Megiddo is an impressive archaeological mound located on the western margin of the Jezreel Valley of inland northern Israel (Fig. 1). It is a key site for the stratigraphy and chronology of the Levant in the Bronze and Iron Ages. Settlement at the site began in the 7th millennium BC and by the late 4th millennium BC (the Early Bronze I) developed into a regionally important urban center due to its strategic position on one of the key trade routes of the ancient Near East. In the Bronze Age Megiddo was the hub of a Canaanite city–state and in the Iron Age II it served as an administrative center of the Northern Kingdom of Israel. The urban nature of the settlement is evidenced by extensive architectural remains of public buildings, elite houses and defensive structures from different periods during the long-term occupation of the site (Finkelstein et al., 2006a,b; Niemann, 2006). Though Megiddo suffered four destructions during the period of time between the late 12th and the late 8th centuries, urban life at the site continued with only short possible occupational gaps following these catastrophes. Most interpretations have suggested that these events

were human-caused destructions (summarized in Finkelstein, 2009). Material examined in this study was retrieved from deposits belonging to two layers unearthed in an area representing domestic activity in the Iron Age IIA – Levels Q-5 and Q-4, which date to the end of the 10th century and the 9th century BC.

Previous research on the faunal remains from Megiddo addressed questions of subsistence, trade and social and ethnic differentiation among the city's population (Lernau, 2000, 2006; Sasson, in press; Wapnish and Hesse, 2000). Wapnish and Hesse (2000) also described a dense concentration of microvertebrate remains from the Early Bronze Age II (ca. 3000–2700 BC) temple complex of Area J at the site. They suggested that these remains represent an accumulation by a predator, likely a nocturnal raptor, during a period of abandonment of the complex. Detailed taphonomic analysis of a portion of the remains supported this observation based on the taxonomic composition, taphonomic characteristics and spatial association of the remains (Weissbrod, in press). We employ this predator-accumulated assemblage from an abandonment period in a comparison with the Iron Age material to assess the distinctive characteristics of this occupational assemblage.

### 3. Materials and methods

To assess the mode of microvertebrate accumulation we examine three lines of evidence including taxonomic identification of the remains, bone surface modifications and the distribution of the remains in relation to different types of occupation deposits including occupational accumulations and fills.

Sampling of microvertebrate remains focused on Area Q where excavations have uncovered a dense residential quarter from the Iron Age (Fig. 2). Area Q is located toward the southeastern margins of the Tel and extends over an area of ca. 450 square meters. Samples were collected from two stratigraphic phases of the Iron Age IIA period, levels 4–5. Sample collection extended over a substantial part of the excavation area (ca. 50%).

Sampling procedure was as follows: 1) intact loci with minimal indication for disturbance were chosen for sampling, 2) in each of

the chosen loci one or more samples were collected with standard volumes of either three or five buckets of sediment (1 bucket = 10 l), 3) sediment samples were wet-sieved through 1 mm mesh screens, 4) sieved residue was carefully sorted in the laboratory by experienced students to extract all bones, and 5) the bone fraction was analyzed by one of us (L.W.) to extract all identifiable skeletal remains of microvertebrates. Altogether 19 samples were collected from 14 different loci amounting to 610 l of sediment (Table 1). In some cases 2–3 samples were collected from a locus, either from different spatial parts of the locus or from different vertical positions as in the case of locus 157. Table 1 provides information on the stratigraphic affiliation and context of the samples.

The study of the microvertebrate remains consisted of detailed taxonomic identification with the aid of the comparative collection of the Laboratory of Archaeozoology, University of Haifa. We conducted a comprehensive taxonomic analysis which included recording of all identifiable microvertebrate remains at the class level (i.e., mammals, reptiles, fish, birds and amphibians). In contrast to other microvertebrate remains, fish remains represent aquatic habitats and are not expected to be part of the terrestrial urban environment. This means that a human or other animal predator brought the remains of fish into the site and influenced their distribution. Fish remains are included in the analysis because they form an important component of the microvertebrate assemblage and can provide an interesting comparison to the remains of other microvertebrate taxa. In addition, we conducted more specific identification of the micromammalian remains to the family or genus level. Due to an overall good state of preservation it was possible to base taxonomic identifications of micromammalian remains both on cranial and post-cranial elements.

More detailed taxonomic identification focused on a key species of interest – the house mouse (*Mus musculus domesticus*) given that within the Mediterranean climate zone of Israel this species is sympatric with a wild congener (*M. macedonicus spretoides*; Auffray et al., 1990). Because conventional morphological criteria distinguishing the two species (see Gerasimov et al., 1990; Çolak et al., 2006) are not reliable in all cases we applied geometric

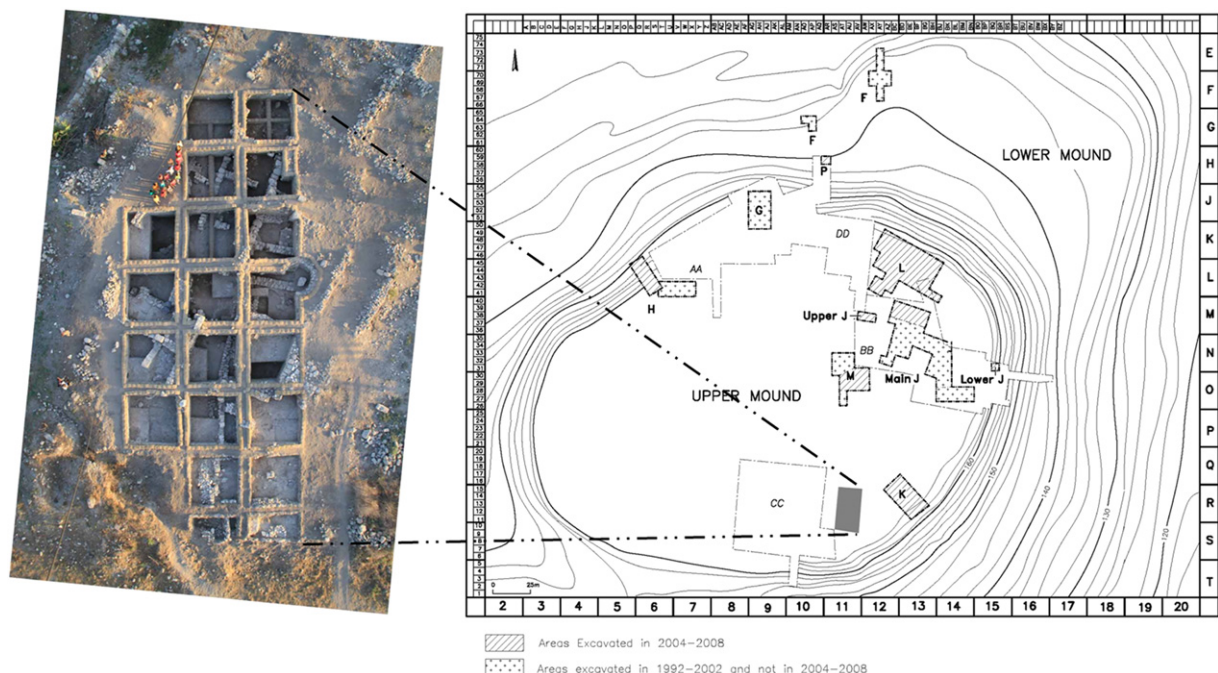


Fig. 2. Location of Area Q on the Megiddo site plan and aerial photograph showing the layout of structures exposed from the Iron Age IIA (each excavation square in grid = 5 × 5 m).

**Table 1**  
Counts of specimens and densities per sample.

Stratigraphic level	Locus/ basket	Context description	No. specimens	Sediment volume (l)	Density (No. specimens/l)
Q-4	112	Installation: oven	14	30	0.5
	33	Occupational accumulation	38	30	1.3
	46 B16	Fill	7	30	0.2
	46 B17	Fill	85	30	2.8
	55	Fill on plaster floor	43	30	1.4
	94	Fill: burned debris – ashy pit with complete vessels	36	30	1.2
	Q-5	106	Occupational accumulation	43	30
157 L1		Occupational accumulation	94	50	1.9
157 L2		Occupational accumulation	140	50	2.8
61		Fill with stone collapse	52	30	1.7
68 B4		Occupational accumulation	50	30	1.7
68 B5		Occupational accumulation	22	30	0.7
68 B9		Occupational accumulation	79	30	2.6
73 B1		Occupational accumulation	79	30	2.6
73 B2		Occupational accumulation	41	30	1.4
88		Occupational accumulation on stone floor	107	30	3.6
95		Occupational accumulation with mudbrick on floor	72	30	2.4
96		Occupational accumulation with mudbrick on floor	33	30	1.1
97		Fill: wall removal	45	30	1.5
Grand total				<b>1080</b>	<b>610</b>

morphometrics analysis to the identification of *Mus* molars. This technique has been successfully applied in species and sub-species level discrimination in the genus *Mus* in a number of recent studies from different periods across Europe (Cucchi et al., 2002, 2011; Cucchi, 2008; Valenzuela-Lamas et al., 2011).

Following the protocol of previous studies, two-dimensional Cartesian coordinates were digitized on the external outline of *Mus* lower first molars (m1) in occlusal view. One landmark was positioned on the apex of the m1 and the rest of the outline was captured with 63 semi-landmarks using the image analyzer tpsDig (Ver.2.16; Rohlf, 2010a). Data from all specimens were standardized through a Generalized Procrustes Analysis (GPA, Bookstein, 1991) with the program Relative warps (Ver.1.49; Rohlf, 2010b) to remove all non-shape information (i.e., position, scale, orientation). To identify the Megiddo specimens we used modern samples of house mouse ( $N = 25$ ) and wild short-tailed mice ( $N = 14$ ) from Israel, curated at the Institut des Sciences de l'Évolution, Montpellier, France. The sub-specific attribution of the archaeological specimens to either of these taxa has been performed with probabilistic prediction using a Linear Discriminant Analysis (LDA). The level of discrimination of the reference groups was assessed using the leave-one-out cross validation procedure (Ripley, 1996) on a reduced set of shape variables using a Principal Component Analysis approach (Baylac and Friess, 2005). Assignment of the

archaeological specimens to the reference taxa was assessed by the probabilities associated with the prediction. Allocation below a probability of 0.9 is rejected and the archaeological specimen remains undetermined. Predictive LDA used the R language (R Development Core Team, 2011) and the Rmorph package (Baylac, 2007).

We also recorded taphonomic observations on the micro-mammalian remains including the composition of skeletal elements and various modifications of the skeletal elements such as fragmentation patterns and burning. These taphonomic observations can provide important clues on the mode of accumulation of the remains. Because little research has so far focused on the taphonomy of microvertebrate accumulations in ancient urban environments (e.g., Piper and O'Connor, 2001) and none has considered occupational accumulations, we focus on contrasting taphonomic patterns in the Iron Age occupational assemblage with the Megiddo Early Bronze Age predator-accumulated assemblage. A wide range of distinctive taphonomic patterns involving differential survivorship of skeletal elements, fragmentation and digestion had been identified in predator-accumulated micro-mammalian remains (Andrews, 1990; Stahl, 1996). Such assemblages are characterized typically by a preponderance of young individuals which are the preferred prey of many predators (Andrews, 1990; Weissbrod et al., 2005). We may also expect absence or low impact of burning associated with predation. In contrast, occupational accumulations may be associated with greater representation of adult or old individuals due to better survivorship in anthropogenic environments (e.g., Courtney and Fenton, 1976). We can also expect some degree of burning in such contexts.

To assess differential preservation of skeletal elements we examined the frequencies of skeletal elements based on the proportion of specimens of each element from the total number of specimens. To account for the fact that the numbers of different elements within the complete skeleton are variable, we divided the raw frequency of specimens from each element by the number of times that element occurs in the complete skeleton. For example, the number of humeri was divided by two, the number of molars by twelve and the number of vertebrae (spinal and caudal) by twenty seven. To further assess the effects of specific taphonomic processes such as the effect of digestion by predators and physical effects such as trampling, we also used two indices of skeletal proportions. These include an index of post-cranial to cranial specimens ( $[(\text{femura} + \text{humeri})/(\text{mandibles} + \text{maxillae})]$  multiplied by 100, Andrews, 1990: Table 3.2) and an index of proximal to distal limb elements ( $[(\text{tibiae} + \text{radii})/(\text{femura} + \text{humeri})]$  multiplied by 100, Andrews, 1990: Table 3.2).

Patterns of fragmentation were recorded based on the frequencies of complete cranial and post-cranial elements in the assemblage. In addition, we used an index of breakage of the jaws which is the proportion of teeth isolated from the jaws. The index is calculated as the number of isolated teeth, either molars or incisors, divided by the number of empty alveolar spaces within the jaws multiplied by 100 (Andrews, 1990: Table 6.1). Additional observations were noted on aging of the material based on the presence of unfused epiphysal parts of the long bones and on evidence for chemical corrosion of the remains which may result from predator digestion or post-depositional processes such as root etching.

Finally, we examine the distribution of the remains in relation to the different archaeological contexts which were sampled. In particular, we assess whether different types of contexts including occupational accumulations and fills are associated with varying composition of the microvertebrate assemblage. We use the ordination technique of correspondence analysis to examine patterns of similarity in taxonomic composition among samples from different

types of contexts. The analysis is based on the raw abundances organized in a matrix of samples by taxa and is conducted using the program for paleontological statistics PAST (Ver.1.81; Hammer et al., 2008). This analysis can further shed light on the mode of accumulation of the remains and whether and how they may reflect aspects of human occupation behavior at the site.

To reconstruct aspects of community structure from the micromammalian assemblage, we consider the composition and diversity of taxa. We use two common measures of taxonomic diversity: the number of taxa also referred to as richness and the Shannon–Wiener index of heterogeneity which combines richness with an assessment of the evenness in distribution of individuals among taxonomic categories (see Krebs, 1989). We estimated richness with the sample-based rarefaction method in program PAST. To determine the Shannon–Wiener index we used the minimum numbers of individuals from each of the micromammalian taxa. These minimum numbers are drawn from the element with the most abundant number of specimens in each of the samples taking into account side in the body (left or right) and part of the element represented (proximal, distal or shaft) in long bones and for molar teeth also placement within the jaws (M1–M3).

## 4. Results

### 4.1. Taxonomy

A total of 1080 identifiable specimens were retrieved from the 19 samples (see Inline Supplementary Table S1). This material includes remains from four major groups of microvertebrate species: mammals, reptiles (Squamata, mainly snakes and lizards), bony fish (Osteichthyes) and birds. The data in Table 1 shows that numbers of specimens are generally low and widely distributed among the samples indicating dispersion rather than concentration of the remains. Using Green's coefficient of dispersion (see Krebs, 1989: Equation (4.25)) shows values of 0.09 in Level Q-4 and 0.02 in Level Q-5 which indicate random rather than aggregated or uniform distribution of the remains among the samples.

Inline Supplementary Table S1 can be found online at <http://dx.doi.org/10.1016/j.jas.2012.07.001>.

The average number of specimens per liter of sediment (i.e., density) across the 19 samples is 1.7 with a standard deviation of 0.9 (see densities in Table 1). High density of 3.6 specimens/l was recorded in Locus 10/Q/88 which is an occupational accumulation overlying a stone floor and low density of <1 specimens/l can be seen in samples from Loci 10/Q/112, 10/Q/46 and 10/Q/68 from various context types. Fig. 3 presents a distribution of densities across the 14 loci for each of the microvertebrate classes. This shows low densities of reptile and bird remains (<0.5 specimens/l) and comparatively high densities of mammal and fish remains. Fish remains show the greatest average density (0.8 specimens/l; sd = 0.4). Mammal remains show somewhat lower densities and are also less evenly distributed among the loci than the fish remains (average = 0.7 specimens/l; sd = 0.5).

The microvertebrate assemblage includes 435 remains of micromammals of which 214 could be identified to family or genus. We identified five different genera of small rodents and a single family of white-toothed shrews (Soricidae). The rodent genera in order of abundance include common mouse (*Mus* spp.), jird (*Meriones tristrami*), mole rat (*Spalax ehrenbergi*), gerbil (*Gerbillus dasyurus*) and field vole (*Microtus guentheri*). The 12 *Mus* lower first molars have been assigned to *M. musculus domesticus* with posterior probabilities of 1 based on highly significant discrimination of the reference specimens (MANOVA, Wilk's Lambda = 0.087,  $df_1 = 13$ ,  $df_2 = 26$ ,  $F = 20.78$ ,  $P < 0.0001$ ).

The composition of micromammalian taxa is presented in Fig. 4 based on proportions of specimens from each taxon. House mice dominate the assemblage and their remains account for over 80% of the micromammalian remains in all loci except for Locus 10/Q/94 which contains only specimens of shrews. The shrews are the second most common taxa occurring in six of the 14 loci. Other taxa occur only sporadically in one or two of the loci. The numbers of individuals which can be reconstructed from the skeletal specimens are generally low in correspondence with the low numbers of specimens across samples (see Inline Supplementary Table S2). In

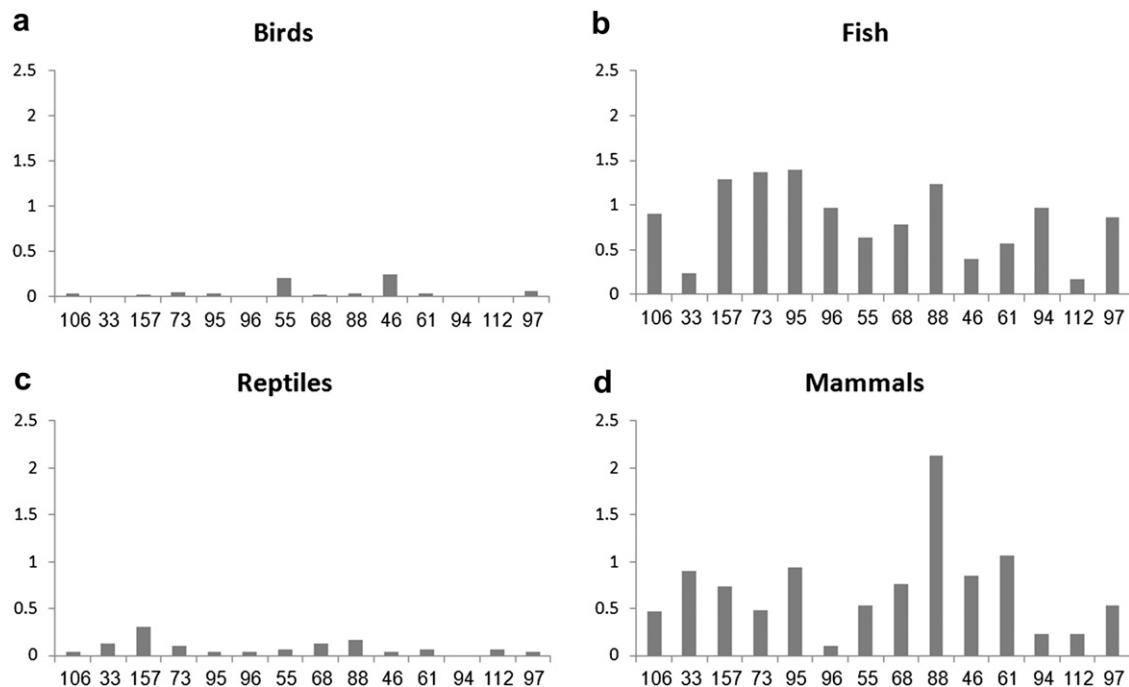


Fig. 3. Density of specimens (specimens/l sediment) per locus for each of the vertebrate classes.

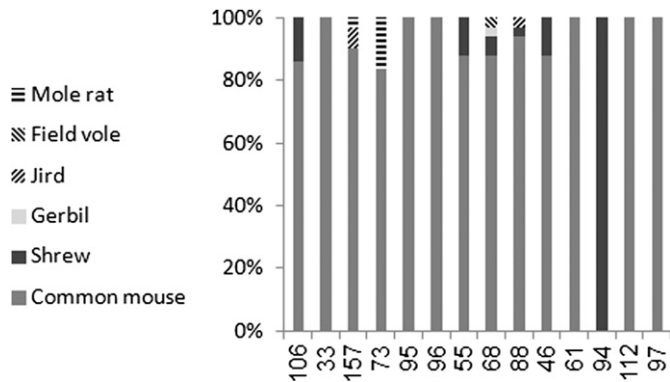


Fig. 4. Composition of micromammalian taxa per locus based on proportions of specimens.

three of the samples with the largest number of specimens including Loci 10/Q/46 (B17), 10/Q/88 and 10/Q/157 (sample 157 L2) we counted between three and four individuals of common mouse.

Inline Supplementary Table S2 can be found online at <http://dx.doi.org/10.1016/j.jas.2012.07.001>.

#### 4.2. Taphonomy

The assemblage includes 427 remains of micromammals which could be identified to skeletal element. The numbers of specimens from each of the separate samples (see Inline Supplementary Table S3) are too low and variable to allow meaningful quantification of per-sample skeletal element composition. The overall skeletal element composition for the assemblage is presented in Fig. 5. The graph shows that nearly all of the major elements of the skeleton are represented in the assemblage although in markedly varying frequencies.

Inline Supplementary Table S3 can be found online at <http://dx.doi.org/10.1016/j.jas.2012.07.001>.

Fig. 5 shows relatively high representation of certain elements including the tibia, humerus and ulna. These elements in the skeleton of small mammals are characterized by high levels of structural density (Lyman et al., 1992: Table 1; Pavao and Stahl, 1999: Table 1). This may explain their higher rates of survival in comparison to less dense elements such as the scapula. Other elements with relatively high structural densities such as the mandible and pelvis are not as well represented in the assemblage,

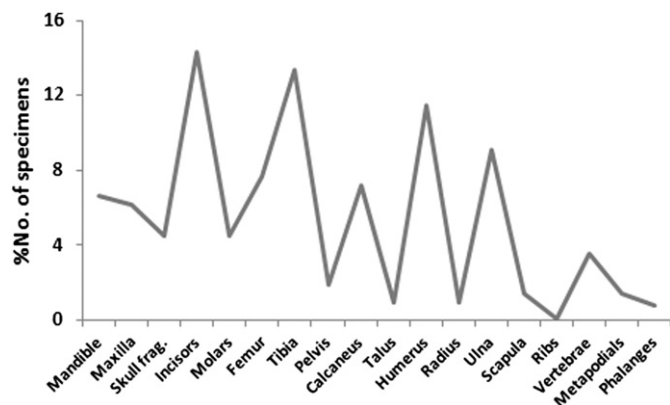


Fig. 5. Composition of skeletal elements in the micromammalian remains based on proportions of specimens.

however. This effect may be due to trampling. Experimental trampling of micromammalian remains has shown that this can lead to preferential preservation of limb elements such as the tibia and humerus and destruction of elements such as the mandible, maxilla and pelvis (see Andrews, 1990: 7–10). An index of fragmentation based on the proportion of post-cranial to cranial elements shows a relatively high value of 148 compared to the standard in a complete skeleton which is 100. This indicates underrepresentation of the cranial elements and further stresses the effect of trampling. An additional index of the proportion of proximal to distal limb elements shows a value of 78, indicating some destruction of distal elements. This may be due to predation but other potential causes such as trampling cannot be ruled out.

The frequencies of complete or nearly complete specimens retaining >80% of the original element are fairly low: mandibles – 14%, maxillas – 23%, femora – 6% and humeri – 4%. An index of jaw breakage based on the extent of isolation of teeth shows an especially high value of 1350 for the incisors. This indicates high levels of breakage of the mandibles and maxillas leading to especially high abundance of isolated incisors. The isolation of molars is, however, much less pronounced with an index value of 113.

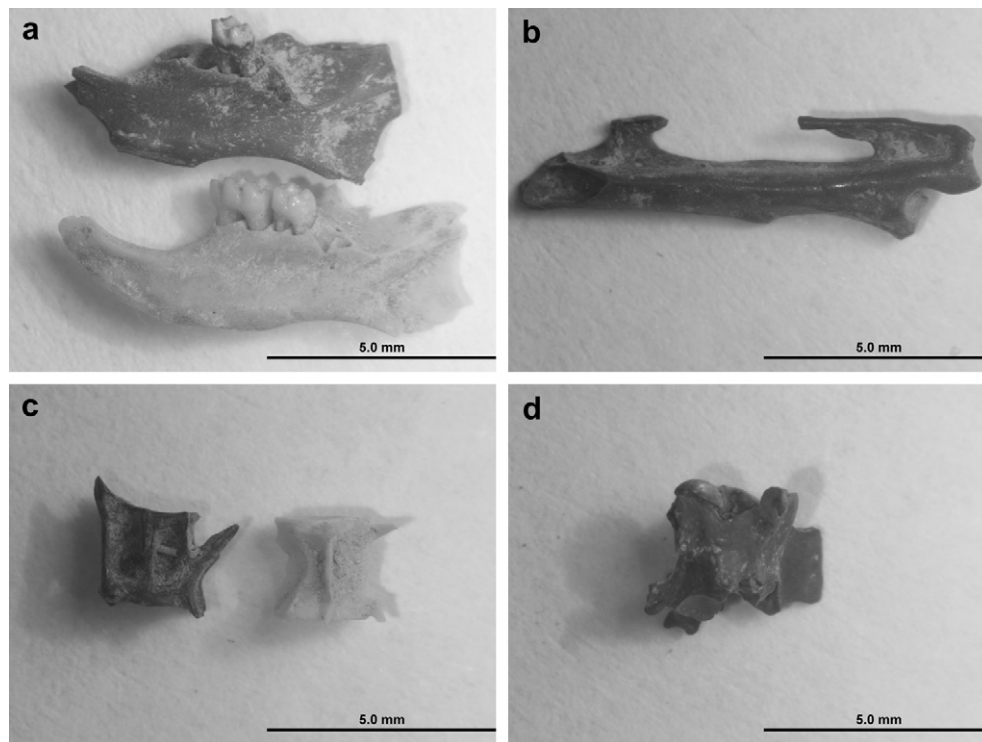
There are 17 burned remains of micromammals in the Iron Age assemblage (Fig. 6). The material contains an additional 13 burned remains from other microvertebrate classes including birds, reptiles and fish (Table 2). Table 2 shows that the burned microvertebrate remains are widely distributed among the sampled loci with low numbers of burned specimens per locus. It is interesting to note that there are greater proportions of burned remains of mammals, birds and reptiles (3–8%) than of fish (2%). These low proportions of burning which could have resulted from intentional or incidental exposure to fire indicate overall low rates of exposure. It is difficult to determine based on the available evidence the reasons for these low exposure rates although some clues may be provided by the variation in exposure rates among different microvertebrate groups. Fish remains were undoubtedly introduced from outside the site whereas the mammal, bird and reptile remains may have been part of the local living community of the settlement. Differing accumulation pathways may also entail differing locations of accumulation and sets of post-depositional processes affecting the remains such as occasional tossing of carcasses into the fire, incidental occurrence of scattered remains in sediments underlying fire places and the sweeping of living surfaces.

Data on the age composition of the micromammalian remains are scant because of relatively low numbers of ageable specimens. The long bone specimens include two fused and four unfused proximal femura with a 67% of unfused specimens. Other long bone elements with unfused specimens including the proximal humerus and tibia and the distal femur each number fewer than four specimens.

The assemblage also contains six specimens with indication for chemical corrosion including 4 M, one incisor and a femur bone (Fig. 7). Potential causes of this low level of corrosive effect may include digestive effects due to predation, for example, by a domestic cat or post-depositional processes such as root etching. Clear evidence of root etching was not observed on any of the specimens.

#### 4.3. Spatial analysis

We examine patterns in the distribution of microvertebrate remains which may be related to differences among context types. For the purpose of this analysis we use the raw abundances of specimens from the four different microvertebrate classes which exhibited the most variation among samples. A correspondence



**Fig. 6.** Burned remains of microvertebrates: (a) rodent mandible with unburned specimen below, (b) bird carpometacarpus, (c) fish vertebra with unburned specimen on right and (d) reptile vertebra.

analysis of these abundances produces a coordinate system summarizing 88% of the similarity in taxonomic composition among samples: Axis 1 = 55.6% and Axis 2 = 32.4%.

The results of the correspondence analysis are shown in Fig. 8. The graph shows broadly a single cluster of samples without separate associations of samples with any of the microvertebrate taxa. An examination of the raw abundances and densities shows that samples falling on the left side of Axis 1 contain greater proportions of fish remains whereas samples on the right mostly contain greater proportions of mammal remains. Some of the samples on the right including Loci 10/Q/46 and 10/Q/55 also have somewhat greater proportions of bird remains although the absolute numbers of specimens are rather low (<15). Fig. 8 also shows that samples from the same locus are generally more similar to each other than to the majority of other samples. This suggests that

the similarities or differences among loci in taxonomic composition are not random.

To highlight different aspects of the variation among the samples, Fig. 8 also includes different symbols designating samples from occupational accumulation and fill contexts. Samples from the two context types do not reveal any clear difference in distribution. Some samples from fills such as Loci 10/Q/46 and 10/Q/55 have somewhat greater proportions of mammal and/or bird remains but the numbers of specimens, particularly those of bird remains are low in these cases. This indicates general similarity in composition of microvertebrate groups between occupational accumulations and fills and that the observed variation in numbers of fish versus mammalian specimens is not related to context type.

#### 4.4. Intra-site taphonomic comparisons

A comparison of the Iron Age IIA microvertebrate assemblage of Megiddo with a previously analyzed assemblage from the Early Bronze Age II at the site (Weissbrod, in press) is especially enlightening from a taphonomic perspective. In comparing the two assemblages it should be borne in mind that systematic fine-sieving was applied only in the collection of the Iron Age material. In spite of this difficulty, a number of clear differences can be noted. It is particularly interesting to note the absence of burned specimens in the Early Bronze Age assemblage in contrast to their presence in the Iron Age assemblage, albeit in fairly low frequencies. Furthermore, the Early Bronze Age fragmentation index with a value of only 33 indicates marked under-representation of post-cranial elements whereas these specimens are over-represented among the Iron Age remains (Tables 3 and 4). We should not expect a systematic bias in recovery of cranial versus post-cranial elements due to method of recovery. This is because complete post-cranial elements such as the major limb bones in the skeleton of small mammals are roughly similar in size to cranial elements

**Table 2**  
Counts and proportions of burned specimens according to vertebrate classes.

Locus	Bird	Mammal	Fish	Reptile	Grand total	Total no. of specimens	% Burned
106						43	
112	1			1	2	14	14
157	4		4	2	10	234	4
33	1				1	38	3
46						92	
55	1				1	43	2
61						52	
68	2				2	151	1
73	2				2	120	2
88	1	4		3	8	107	7
94			1		1	36	3
95		1	2		3	72	4
96			1		1	33	1
97		1	1		2	45	4
Grand total	1	17	9	6	33	1080	–

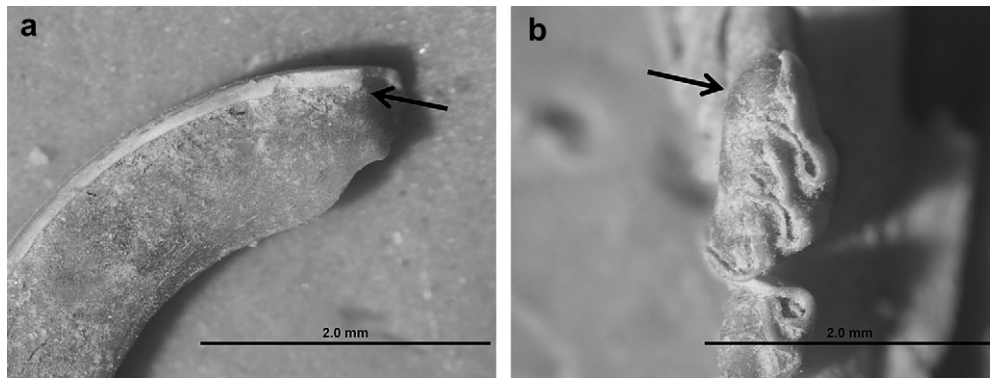


Fig. 7. Specimens with signs of chemical corrosion: (a) rodent incisor and (b) rodent molar showing partial removal of enamel. Arrows indicate the location of enamel removal.

such as mandibles or isolated maxillas. It appears that preferential destruction of cranial elements in the Iron Age material which may be related to extensive trampling is not evident in the Early Bronze Age material.

Similarly, the index of proximal to distal limb elements in the Iron Age assemblage (78) is higher than the Early Bronze Age index value (54). These differences may indicate the effect of predation in the Early Bronze Age assemblage. According to Andrews (1990), high survivorship of cranial elements and underrepresentation of distal limbs characterize the prey remains of certain species of predators which through their feeding manner and digestive system tend to damage certain skeletal elements more than others. In particular, the low proportion of distal limb elements corresponds with figures given by Andrews (1990: Table 3.2) for certain diurnal raptors such as the hawk or small carnivores as the fox.

Additional differences between the two assemblages can be observed in the condition of the specimens. Among the Early Bronze Age remains of jaws and limb bones there is a high frequency of complete specimens. The frequencies of complete specimens of mandibles, maxillas and femora are between 25 and 58% (Table 4). Table 4 shows that these frequencies are greater than in the Iron Age assemblage for all the elements examined. Similar results are obtained by using the index of fragmentation of the jaws. The numbers of isolated teeth in the Early Bronze Age material are rather low, especially when compared with the Iron Age indices. This could be due in part to the lack of fine-sieving rather than merely good preservation of the jaws, however. The 33% of unfused femura is considerably lower than in the Iron Age assemblage. However, data on fusion of other elements including

the proximal tibia and distal femur show much greater proportions of >80% of unfused specimens. Hence, the difference among the two assemblages in age composition is unclear. In addition, clear signs from digestion by predators were not identified in either the Iron Age or Early Bronze Age assemblages.

An especially pronounced difference can be observed in taxonomic composition of micromammalian remains between the Early Bronze Age and Iron Age assemblages. Fig. 9 shows that whereas the Iron Age assemblage is dominated by common mouse the Early Bronze Age assemblage is dominated by voles and is more heterogeneous. The Early Bronze Age assemblage includes two taxa which are not present in the Iron Age – spiny mouse (*Acomys cahirinus*) and golden hamster (*Mesocricetus auratus*) – and is missing two of the Iron Age taxa – gerbil and mole rat. Only the shrews occur in both of the assemblages in similar proportions (ca. 5%). The marked differences in taxonomic composition between the two assemblages cannot be accounted for by recovery bias. This is especially true as voles with larger body size than common mice are very rare and additional larger taxa as spiny mice and hamsters are altogether absent in the Iron Age assemblage where fine-sieving was applied.

## 5. Discussion

The analysis shows that microvertebrate remains are widely distributed within the occupation deposits of Area Q of Iron Age Megiddo although they occur in generally low densities. The assemblage includes the remains of small mammals, reptiles, birds and fish and reveals comparatively high abundances of mammal and fish remains and low abundances of reptile and bird remains. The mammalian component is dominated by common mice. Geometric morphometrics analysis of common mouse molars shows that all of the examined specimens belong to the house mouse rather than the local wild congener. Taphonomic analysis of the micromammalian remains revealed some evidence of trampling. Evidence for burning was observed mainly among the mammal and reptile remains and less frequently among the fish remains.

The Iron Age assemblage of Megiddo reveals markedly contrasting taxonomic and taphonomic patterns from an Early Bronze Age assemblage from the same site. The stark difference in taxonomic composition of the micromammalian component certainly cannot be accounted for by climate induced environmental change. This is because the magnitude of the change required for explaining the observed difference would be extreme. An alternative explanation is that the observed differences are due to differing modes of accumulation of the remains.

The Iron Age assemblage was retrieved from occupation deposits in a dense residential area mainly from house floors and

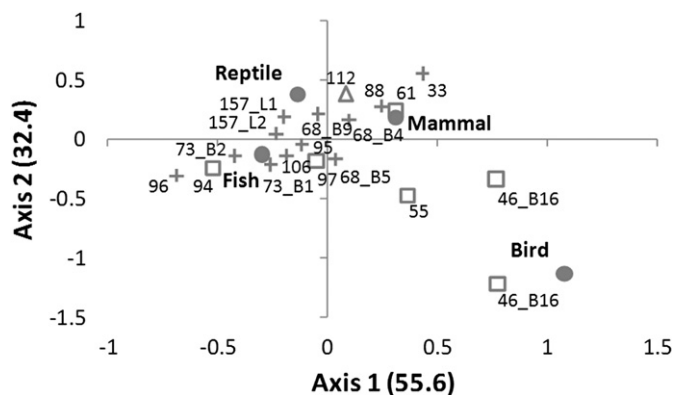


Fig. 8. Correspondence analysis results plot of samples and microvertebrate classes (circles). Sample symbols designate occupational accumulation (+), fill (square) and other (triangle).



**Table 3**

Counts of specimens used in calculating indices of skeletal completeness.

	Mandible		Maxilla		Incisors			Molars		
	Total	#Complete (>80%)	Total	#Complete (>80%)	<i>In situ</i>	Isolated	Empty sockets	<i>In situ</i>	Isolated	Empty sockets
Iron Age IIA	14	2	13	3	6	54	4	35	19	16
Early Bronze Age II	24	10	16	4	17	9	8	41	5	33

	Femur		Tibia	Humerus		Radius
	Total	#Complete (>80%)		Total	#Complete (>80%)	
Iron Age IIA	16	1	29	24	1	2
Early Bronze Age II	12	7	7	1	1	0

various fills. In comparison to the Early Bronze Age assemblage, the Iron Age micromammalian assemblage is remarkably species-poor and reveals evidence of modifications of the remains which are directly related to human occupation including trampling and burning. In contrast, the Early Bronze Age assemblage which accumulated during a period of abandonment did not reveal evidence of either trampling or burning and indicated the impact of predation. These observations suggest that the Iron Age remains of mammals, reptiles and birds represent part of the urban community of small fauna. We suggest that these animals died on-site and the remains were incorporated into the deposits with other occupation debris from daily life. Given the low density and random dispersion of the remains it is likely that the rate of accumulation is comparatively slow. This *in situ* mode of accumulation can be contrasted with other modes of accumulation of microvertebrate remains in ancient urban settings including accumulation due to pitfalls in various sunken features (Armitage and West, 1985; Whyte, 1991; Stahl, 2000; Piper and O'Connor, 2001) and accumulation by small predators (Rackham, 1982; Bar-Oz and Dayan, 2001; De Cupere et al., 2009; Weissbrod, in press) which can lead to dense concentrations of the remains at isolated find spots within the site.

The especially stark contrast in taxonomic composition between the Iron Age and Early Bronze Age assemblages from Megiddo throws further light on the distinctive characteristics of *in situ* accumulated remains of small urban fauna in occupational deposits. The preponderance of voles in the Early Bronze Age accumulation suggests that this material was collected mainly from open grass fields and possibly agricultural plots surrounding the site rather than within the confines of the site. Together with common mice and jirds, voles are among the most common species in present day agricultural fields in the valleys of northern Israel based on analysis of the prey of barn owls (*Tyto alba*; Tores et al., 2005; Charter et al., 2009). Hamsters are an additional representative of open grass field biotopes whereas spiny mice inhabit mostly rocky slopes (Harrison and Bates, 1991). The heterogeneous composition of this assemblage is another indication that it was concentrated at the site by a predator which collected the animals from areas adjacent to the site. The rarity of voles and jirds and absence of hamsters and spiny mice from the Iron Age occupational assemblage emphasize the uniqueness of this accumulation and supports our conclusion that it represents distinctive and isolated communities of small animals inhabiting the urban environment.

**Table 4**

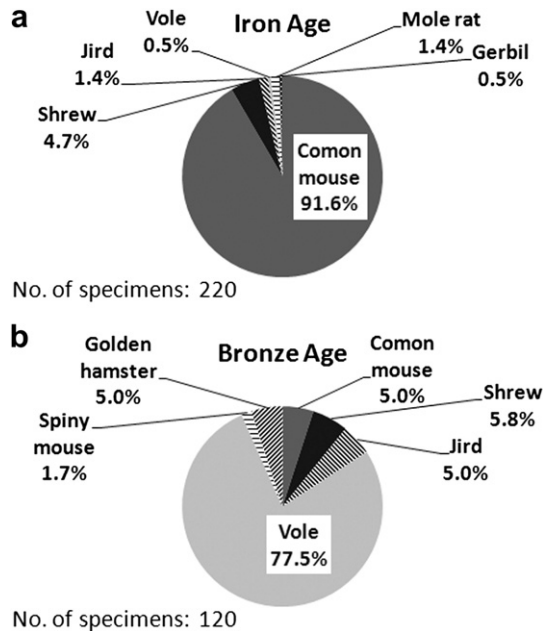
Indices of skeletal completeness (formulas shown in text).

	% Post-cranial specimens	% Distal limb specimens	% Complete				% Isolated	
			Mandible	Maxilla	Femur	Humerus	Molars	Incisors
Iron Age IIA	148	78	14	23	6	4	119	1350
Early Bronze Age II	33	54	42	25	58	100	15	113

Additional analysis of the composition of microvertebrate groups among samples from different types of contexts in the Iron Age assemblage shows little variation which can be related to context type. Fish remains which represent accumulation from exogenous sources and potentially part of the small-grained garbage and mammal remains originating mainly from small house fauna and *in situ* accumulation are similarly distributed among samples from occupational accumulations and fills. Although occupational accumulations and fills undoubtedly were deposited in distinctly different ways there appears to be general similarity in the manner that microvertebrate remains accumulated within them. This could imply that the remains were incorporated into the fills either following their deposition and in a similar manner to their incorporation into occupational accumulations at the same location or more likely that fills represent re-deposited occupational accumulations. Additional more detailed research on the taphonomy and distribution patterns of microvertebrate remains in occupation deposits of dense residential areas is needed to clarify the processes of formation of such accumulations and to assess implications for micro-stratigraphic studies of occupation deposits.

The suggested mode of accumulation of the remains allows us to characterize the community structure of the urban small fauna of the Iron Age settlement of Megiddo. The micromammalian component of this fauna shows very low heterogeneity of species with extreme dominance of the house mouse which accounts for over 80% of the remains in the majority of samples. Shrews are fairly common among the samples and are likely an additional component of the urban faunal community. Other rodent taxa including jird, gerbil, mole rat and field vole occur only sporadically and may even represent post-depositional intrusive components. This suggestion is based on the tendency of these species to rely extensively on tunnel digging. Isolated finds of jird and mole rat remains showing little fossilization and suggesting recent intrusion were uncovered in several locations at the site (see Weissbrod, in press).

Species richness in the Iron Age assemblage amounts to only two if we disregard the rare species also suspected as intrusive. Sample-based rarefaction analysis of the data shows that species saturation is reached with 13 of the 19 samples used in the study with an especially small standard deviation of  $2 \pm 0.0003$  taxa (analysis conducted with PAST program). A measure of taxonomic heterogeneity based on the Shannon–Wiener index and drawn from minimum numbers of individuals (see Inline Supplementary Table S2) shows an especially low value of 0.44 for the Iron Age



**Fig. 9.** Composition of micromammalian taxa in Iron Age (a) and Early Bronze Age (b) assemblages from Tel Megiddo based on numbers of specimens.

assemblage when excluding the suspected intrusive species. This can be compared to heterogeneity values from a number of medieval sites in Britain. These figures are based on micromammalian remains retrieved from densely built up sections of the ancient towns. The heterogeneity range for three such sites was between 0.42 and 1.02 (Armitage, 1985: Table 1). In three additional sites from more peripheral locations of urban settlements the heterogeneity range was between 1.09 and 2.09. According to these figures, the taxonomic diversity at Iron Age Megiddo is especially low. The significance of this finding is further emphasized if we consider that potential diversity of small rodents and shrews in the inner valleys of the Mediterranean climate zone of Israel (15 taxa) is only two species short of their diversity in Britain as a whole (17 taxa).

The distinctive taxonomic composition of the Megiddo Iron Age assemblage including an extremely low number and diversity of species strongly suggests that the ancient urban environment functioned as a unique type of habitat. This point comes to light particularly when we compare the Iron Age fauna from a dense residential area to the Early Bronze Age predator-accumulated fauna from an abandonment period in a temple context. This comparison highlights the fact that a wider range of species existed in the vicinity of the site that were not part of the urban dwelling fauna. This finding strongly suggests that the Iron Age settlement was ecologically isolated from its surroundings and fits with early conceptions of the urban environment as a 'biological desert' (cf. Elton, 1966). Such conceptions were common among ecologists until the 1970's and account for the general lack of research interest in urban environments seen as biologically sterile (see Armitage, 1985). Extensive research in modern day urban environments has demonstrated that such conceptions are grossly inaccurate. Today's urban ecosystems often support especially complex faunal associations in certain cases revealing greater levels of biological diversity than outside environments (Czamani et al., 2008; Dickman, 1987; Pickett et al., 2008). This phenomenon can be attributed in part to the fact that modern day urban environments are composed of complex mosaics of built up and densely vegetated areas. The metaphor of the biological urban desert may, however, fit more closely the ecological conditions in ancient urban sites such as at Iron Age Megiddo.

The paleoecological signal of Iron Age Megiddo paints a picture of a homogenous, relatively densely built and populated environment. In light of the ecological record from modern cities and the paleoecology of medieval sites in Britain the low biological diversity of the Iron Age settlement coupled with extreme dominance of commensal common mice are unprecedented. The evidence from Megiddo reveals critical information on the path of evolution of the urban fauna at the beginning of the first millennium BC in the Near East. We know from archaeological surveys and excavations that the Iron Age II period in the Near East saw major changes in demography, settlement patterns and social and political organization with the emergence of early centralized state societies (Broshi and Finkelstein, 1992). In particular, Broshi and Finkelstein (1992) have shown based on regional paleo-demographic analysis that during this period there was a greater concentration of the population within rural areas of settlement compared to preceding periods. In the western part of the Jezreel Valley this involved increase in the number of sites and overall extent of the built up area suggesting steady population growth during the Iron Age I and II (Finkelstein et al., 2006a,b). Very little is known, however, about change in the organization of urban sites and how they transformed in response to such critical processes. Undoubtedly, additional data are needed on the microvertebrate faunas of both earlier and later periods to reconstruct the full picture of the evolution of urban dwelling fauna and use it to trace the history of urban development.

#### Acknowledgments

The research at Tel Megiddo was funded by a post-doctoral grant awarded to L.W. from the European Research Council under the European Community's Seventh Framework Program (FP7/2007–2013)/ERC grant agreement number 229418. The laboratory work was also supported by funding by the Israel Science Foundation (Grant 52/10). We especially thank Dr. Norma Franklin, supervisor of excavations at Area Q of Tel Megiddo for her efforts in securing the samples for this study.

#### References

- Andrews, P., 1990. *Owls, Caves, and Fossils*. University of Chicago Press, Chicago.
- Armitage, P.L., 1985. Small mammal faunas in later mediaeval towns. *Biologist* 32, 65–71.
- Armitage, P.L., 1994. Unwelcome companions: ancient rats reviewed. *Antiquity* 68, 231–240.
- Armitage, P.L., West, B., 1985. Faunal evidence from a Late Medieval garden well of the Greyfriars, London. *Transact. Lond.* 36, 107–136.
- Armitage, P., West, B., Steedman, K., 1984. New evidence of the black rat in Roman London. *Lond. Archaeol.* 4, 375–383.
- Audoine-Rouzeau, F., Vigne, J.D., 1997. Le rat noir (*Rattus rattus*) en Europe antique et medievale: Les voies du commerce et l'expansion de la peste. *Anthropozoologica* 25–26, 399–404.
- Auffray, J.-C., Tchernov, E., Nevo, E., 1988. Origine du commensalisme de la souris domestique (*Mus musculus domesticus*) vis-à-vis de l'homme. *Compt. Rend. Acad. Sci.* 307, 517–522.
- Auffray, J.-C., Tchernov, E., Bonhomme, F., Heth, G., Simson, S., Nevo, E., 1990. Presence and ecological distribution of *Mus musculus domesticus* and *Mus spretoides* in Israel. Circum-mediterranean vicariance in the genus *Mus*. *Z. Säugetierkunde* 55, 1–10.
- Bar-Oz, G., Dayan, T., 2001. Weasels from the Hellenistic period of Israel. *Isr. J. Zool.* 47, 271–273.
- Bar-Yosef, O., Tchernov, E., 1966. Archaeological finds and the fossil faunas of the Natufian and microlithic industries at Hayonim Cave (western Galilee, Israel). *Isr. J. Zool.* 15, 121–140.
- Baylac, M., 2007. *Rmorph: A R geometric and Multivariate Morphometrics Library*. Available from the author: baylac@mnhn.fr.
- Baylac, M., Friess, M., 2005. Fourier descriptors, procrustes superimposition, and data dimensionality: an example of cranial shape analysis in modern human populations. In: Slice, D.E. (Ed.), *Modern Morphometrics in Physical Anthropology*. University of Chicago, Chicago, pp. 145–166.
- Bookstein, F.L., 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press, New York.

- Broshi, M., Finkelstein, I., 1992. The population of Palestine in Iron Age II. *Bull. Am. Sch. Orient. Res.* 287, 47–60.
- Castillo, E., Priotti, R., Ambrosio, A.M., Provencal, M.C., Pini, N., Morales, M.A., Steinmann, A., Polop, J.J., 2003. Commensal and wild rodents in an urban area of Argentina. *Int. Biodeter. Biodegr.* 52, 135–141.
- Cavia, R., Cueto, G.R., Suárez, O.V., 2009. Changes in rodent communities according to the landscape structure in an urban ecosystem. *Landscape Urban Plan.* 90, 11–19.
- Charter, M., Izhaki, I., Meyrom, K., Motro, Y., Leshem, Y., 2009. Diets of barn owls differ in the same agricultural region. *Wilson J. Ornithol.* 121, 378–383.
- Çolak, E., Yiğit, N., Sözen, M., Çolak, R., Özkurt, Ş., Kanklıç, T., Kanklıç, T., 2006. The morphological analysis of *Mus musculus* and *Mus macedonicus* (Mammalia: Rodentia) in Turkey. *Turk. J. Zool.* 30, 309–317.
- Courtney, P.A., Fenton, M.B., 1976. The effects of a small rural garbage dump on populations of *Peromyscus leucopus rafinesque* and other small mammals. *J. Appl. Biol.* 13, 413–422.
- Cucchi, T., 2008. Uluburun shipwreck stowaway house mouse: molar shape analysis and indirect clues about the vessel's last journey. *J. Archaeol. Sci.* 35, 2953–2959.
- Cucchi, T., Vigne, J.-D., Auffray, J.-C., Croft, P., Peltenburg, E., 2002. Passive transport of the house mouse (*Mus musculus domesticus*) to Cyprus at the Early Pre-ceramic Neolithic (late 9th and 8th millennia cal. BC). *Compt. Rend. Palevol.* 1, 235–241.
- Cucchi, T., Vigne, J.-D., Auffray, J.-C., 2005. First occurrence of the house mouse (*Mus musculus domesticus* Schwarz & Schwarz, 1943) in the Western Mediterranean: a zooarchaeological revision of fossorial occurrences. *Biol. J. Linn. Soc.* 84, 429–445.
- Cucchi, T., Balasescu, A., Bern, C., Radu, V., Vigne, J.-D., Tresset, A., 2011. New insights into the invasive process of the eastern house mouse (*Mus musculus musculus*): evidence from the burnt houses of Chalcolithic Romania. *Holocene* 21, 1195–1202.
- Czamanski, D., Benenson, I., Malkinson, D., Marinov, M., Roth, R., Wittenberg, L., 2008. Urban sprawl and ecosystems—can nature survive? *Int. Rev. Environ. Resour. Econ.* 2, 1–45.
- De Cupere, B., Thys, S., Van Neer, W., Ervynck, A., Corremans, M., Waelkens, M., 2009. Eagle owl (*Bubo bubo*) pellets from Roman Sagalassos (SW Turkey). Distinguishing the prey remains from nest and roost sites. *Int. J. Osteoarchaeol.* 19, 1–22.
- Dean, R.M., 2005. Site-use intensity, cultural modification of the environment, and the development of agricultural communities in Southern Arizona. *Am. Antiq.* 70, 403–431.
- Dean, R.M., 2010. The effect of cultivation techniques on small-game population: an archaeological example of the Hohokam region. In: Dean, R.M. (Ed.), *The Archaeology of Anthropogenic Environments*. Occasional Papers No. 37. Center for Archaeological Investigations, Carbondale, pp. 250–265.
- Dickman, C.R., 1987. Habitat fragmentation and vertebrate species richness in an urban environment. *J. Appl. Ecol.* 24, 337–351.
- Elton, C.S., 1966. *The Pattern of Animal Communities*. Methuen, London.
- Ervynck, A., 2002. Sedentism or urbanism? On the origin of the commensal black rat (*Rattus rattus*). In: Dobney, K., O'Connor, T.P. (Eds.), *Bones and the Man: Studies in Honour of Don Brothwell*. Oxbow Books, Oxford, pp. 95–109.
- Evans, J.G., 1978. *An Introduction to Environmental Archaeology*. Paul Elek, London.
- Finkelstein, I., 2009. Destructions: Megiddo as a case study. In: Schleon, D.J. (Ed.), *Exploring the Longue Duree, Essays in Honor of Lawrence E. Stager*. Eisenbrauns, Winona Lake, pp. 113–126.
- Finkelstein, I., Halpern, B., Lehmann, G., Niemann, H.M., 2006a. The Megiddo Hinterland project. In: Finkelstein, I., Ussishkin, D., Halpern, B. (Eds.), *Megiddo IV: the 1998–2002 Seasons*. Emery and Claire Yass Publications in Archaeology, Tel Aviv, pp. 705–776.
- Finkelstein, I., Ussishkin, D., Halpern, B., 2006b. Archaeological and historical conclusions. In: Finkelstein, I., Ussishkin, D., Halpern, B. (Eds.), *Megiddo IV: the 1998–2002 Seasons*. Emery and Claire Yass Publications in Archaeology, Tel Aviv, pp. 821–842.
- Gerasimov, S., Nikolov, H., Mihailova, V., Auffray, J.-C., Bonhomme, F., 1990. Morphometric stepwise discriminant analysis of the five genetically determined European taxa of the genus *Mus*. *Biol. J. Linn. Soc.* 41, 47–64.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2008. *PAST – Palaeontological Statistics, Version 1.81*. University of Oslo, Oslo, Norway.
- Harrison, D.L., Bates, P.J.J., 1991. *The Mammals of Arabia*. Zoological Museum Publications, Kent.
- Hesse, B., 1979. Rodent remains and sedentism in the Neolithic: evidence from Tepe Ganj Dareh, western Iran. *J. Mammal.* 60, 856–857.
- Holt, E.A., Miller, S.W., 2011. Bioindicators: using organisms to measure environmental impacts. *Nat. Educ. Knowl.* 2, 8.
- Krebs, C.J., 1989. *Ecological Methodology*. Benjamin/Cummings, Menlo Park.
- Lernau, O., 2000. Fish bones. In: Finkelstein, I., Ussishkin, D., Halpern, B. (Eds.), *Megiddo III – the 1992–1996 Seasons*. Emery and Claire Yass Publications in Archaeology, Tel Aviv, pp. 463–477.
- Lernau, O., 2006. Fish remains. In: Finkelstein, I., Ussishkin, D., Halpern, B. (Eds.), *Megiddo IV: the 1998–2002 Seasons*. Emery and Claire Yass Publications in Archaeology, Tel Aviv, pp. 474–496.
- Lyman, R.L., Houghton, L.E., Chambers, A.L., 1992. The effect of structural density on marmot skeletal part representation in archaeological sites. *J. Archaeol. Sci.* 19, 557–573.
- Mahan, C.G., O'Connell, T.J., 2005. Small mammal use of suburban and urban parks in central Pennsylvania. *Northeast. Nat.* 12, 307–314.
- Mulkeen, S., O'Connor, T.P., 1997. Raptors in towns: towards an ecological model. *Int. J. Osteoarchaeol.* 7, 440–449.
- Niemann, H.M., 2006. Core Israel in the highlands and its periphery: Megiddo, the Jezreel Valley and the Galilee in the 11th to 8th centuries BCE. In: Finkelstein, I., Ussishkin, D., Halpern, B. (Eds.), *Megiddo IV: the 1998–2002 Seasons*. Emery and Claire Yass Publications in Archaeology, Tel Aviv, pp. 821–842.
- O'Connor, T.P., 1992. Pets and pests in Roman and medieval Britain. *Mammal Rev.* 22, 107–113.
- O'Connor, T.P., 2000. Human refuse as a major ecological factor in medieval urban vertebrate communities. In: Bailey, G., Charles, R., Winder, N. (Eds.), *Human Ecodynamics*. Symposia of the Association for Environmental Archaeology 19. Oxbow Books, Oxford, pp. 15–20.
- O'Connor, T.P., 2003. *The Analysis of Urban Animal Bone Assemblages: A Handbook for Archaeologists*. The Council for British Archaeology, York.
- O'Connor, T.P., 2010. Making themselves at home: the archaeology of commensal vertebrates. In: Campana, D., Crabtree, P., de France, S.D., Lev-Tov, J., Choyke, A. (Eds.), *Anthropological Approaches to Zooarchaeology*. Oxbow Books, Oxford, pp. 270–274.
- O'Connor, T.P., Evans, J.G., 2005. *Environmental Archaeology: Principles and Methods*. Sutton Publishing, Gloucestershire.
- Pavao, B., Stahl, P.W., 1999. Structural density assays of leporid skeletal elements with implications for taphonomic, actualistic, and archaeological research. *J. Archaeol. Sci.* 26, 53–67.
- Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Groffman, P.M., Band, L.E., Boone, C.G., Burch, W.R., Grimmond, C.S.B., Hom, J., Jenkins, J.C., Law, N., Nilon, C.H., Pouyat, R.V., Szlavecz, K., Warren, P.S., Wilson, M.A., 2008. Beyond urban legends: emerging framework of urban ecology, as illustrated by the Baltimore Ecosystem Study. *BioScience* 58, 141–152.
- Piper, P.J., O'Connor, T.P., 2001. Urban small vertebrate taphonomy: a case study from Anglo-Scandinavian York. *Int. J. Osteoarchaeol.* 11, 336–344.
- R Development Core Team, 2011. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rackham, D.J., 1982. The smaller mammals in the urban environment: their recovery and interpretation from archaeological deposits. In: Hall, A.R., Kenward, H.K. (Eds.), *Environmental Archaeology in the Urban Context*. The Council for British Archaeology, London, pp. 86–93.
- Ripley, B.D., 1996. *Pattern Recognition and Neural Networks*. Cambridge University Press, New York.
- Rohlf, F.J., 2010a. *TpsDig – Thin Plate Spline Digitizer, Version 2.16*. State University of New York at Stony Brook, New York.
- Rohlf, F.J., 2010b. *TpsRelw – Thin Plate Spline Relative Warp Analysis, Version 1.49*. State University of New York at Stony Brook, New York.
- Sasson, A. The faunal remains. In: Finkelstein, I., Ussishkin, D., Cline, E.H. (Eds.), *Megiddo V: the 2000–2008 Seasons*. Emery and Claire Yass Publications in Archaeology, Tel Aviv, in press.
- Somerville, E.M., 1999. Some aspects of the palaeoecology of commensals. *Quat. Proc.* 7, 605–613.
- Stahl, P.W., 1996. The recovery and interpretation of microvertebrate bone assemblages from archaeological contexts. *J. Archaeol. Method Theory* 3, 31–75.
- Stahl, P.W., 2000. Archaeofaunal accumulation, fragmented forests, and anthropogenic landscape mosaics in the tropical lowlands of prehispanic Ecuador. *Lat. Am. Antiq.* 11, 241–257.
- Tchernov, E., 1984. Commensal animals and human sedentism in the Middle East. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology*, 3: Early Herders and Their Flocks. *British Archaeological Reports*, Oxford, pp. 91–115.
- Tchernov, E., 1991. Biological evidence for human sedentism in Southwest Asia during the Natufian. In: Bar-Yosef, O., Valla, F.R. (Eds.), *The Natufian Culture in the Levant*. *International Monographs in Prehistory*, Ann Arbor, pp. 315–340.
- Tores, M., Motro, Y., Motro, U., Yom-Tov, Y., 2005. The barn owl – a selective opportunist predator. *Isr. J. Zool.* 51, 349–360.
- Valenzuela-Lamas, S., Baylac, M., Cucchi, T., Vigne, J.-D., 2011. House mouse dispersal in Iron Age Spain: a geometric morphometrics appraisal. *Biol. J. Linn. Soc.* 102, 483–497.
- Wapnish, P., Hesse, B., 2000. Mammal remains from the Early Bronze Sacred Compound. In: Finkelstein, I., Ussishkin, D., Halpern, B. (Eds.), *Megiddo III: the 1992–1996 Seasons*. Emery and Claire Yass Publications in Archaeology, Tel Aviv, pp. 429–462.
- Weissbrod, L., 2010. Biological indicators of occupation intensity: an environmental ethnoarchaeology of Maasai settlements. In: Dean, R.M. (Ed.), *The Archaeology of Anthropogenic Environments*. Center for Archaeological Investigations, Carbondale, pp. 295–320.
- Weissbrod, L., Dayan, T., Kaufman, D., Weinstein-Evron, M., 2005. Micromammal taphonomy of el-Wad Terrace, Mount Carmel, Israel: distinguishing natural from cultural depositional agents in the Late Natufian. *J. Archaeol. Sci.* 32, 1–17.
- Weissbrod, L. The micromammalian remains. In: Finkelstein, I., Ussishkin, D., Cline, E.H. (Eds.), *Megiddo V: the 2000–2008 Seasons*. Emery and Claire Yass Publications in Archaeology, Tel Aviv, in press.
- Whyte, T.R., 1991. Small-animal remains in archaeological pit features. In: Purdue, J.R., Klippel, W.E., Styles, B.W. (Eds.), *Beamers, Bobwhites, and Blue-points. Tributes to the Career of Paul W. Parmalee*. Illinois State Museum, Springfield, pp. 163–176.