

Earliest economic exploitation of chicken outside East Asia: Evidence from the Hellenistic Southern Levant

Lee Perry-Gal¹, Adi Erlich, Ayelet Gilboa, and Guy Bar-Oz

Zinman Institute of Archaeology, University of Haifa, Mount Carmel, Haifa 3498838, Israel

Edited by Melinda A. Zeder, National Museum of Natural History, Santa Fe, NM, and approved June 5, 2015 (received for review March 4, 2015)

Chicken (*Gallus gallus domesticus*) is today one of the most widespread domesticated species and is a main source of protein in the human diet. However, for thousands of years exploitation of chickens was confined to symbolic and social domains such as cockfighting. The question of when and where chickens were first used for economic purposes remains unresolved. The results of our faunal analysis demonstrate that the Hellenistic (fourth–second centuries B.C.E.) site of Maresha, Israel, is the earliest site known today where economic exploitation of chickens was widely practiced. We base our claim on the exceptionally high frequency of chicken bones at that site, the majority of which belong to adult individuals, and on the observed 2:1 ratio of female to male bones. These results are supported further by an extensive survey of faunal remains from 234 sites in the Southern Levant, spanning more than three millennia, which shows a sharp increase in the frequency of chicken during the Hellenistic period. We further argue that the earliest secure evidence for economic exploitation of chickens in Europe dates to the first century B.C.E. and therefore is predated by the finds in the Southern Levant by at least a century. We suggest that the gradual acclimatization of chickens in the Southern Levant and its gradual integration into the local economy, the latter fully accomplished in the Hellenistic period, was a crucial step in the adoption of this species in European husbandry some 100 y later.

chicken | *Gallus gallus* | zooarchaeology | Hellenistic | Levant

In the modern world, the chicken (*Gallus gallus domesticus*) is one of the most widespread livestock species and is a major source of animal protein in the human diet. The ancestor of the domestic chicken is the red jungle fowl (*Gallus gallus*), originating in Southeast Asia, with possible genetic contributions from closely related species through hybridization (1–5). Intensive hybridization between the modern chicken and its wild ancestor caused a loss of the wild progenitor genes (6, 7). Consequently, recent studies usually have focused either on the genetics of the chicken progenitor (8–12) or on zooarchaeological evidence for the domestication of chickens (13–15).

The dispersal trajectory of chickens to West Asia, to the Mediterranean, and to Europe following its initial domestication in Southeast Asia remains largely unknown. Moreover, there are only very partial data, and thus there is great uncertainty regarding the place and time of the earliest economic exploitation of chickens: When and where did chickens move from being an exotic species, used only sporadically for symbolic and ritual purposes, to an important livestock species in the Mediterranean and European economies (16, 17)? Our study of chicken remains from the Southern Levant (Israel, the Palestinian Authority, and Jordan) and particularly from the Hellenistic site of Maresha in Southern Israel sheds new light on these issues.

We define three main phases in the cultural history of chicken use, based on archaeological, historical, and iconographic evidence (Fig. 1). The early phase (Fig. 1, phase A) may have already begun around the sixth millennium B.C.E. when the chicken was initially domesticated during several independent domestication events in Southeast Asia and China (1, 2, 4, 11, 12). On the Indian subcontinent, which also constitutes a part of the natural dispersal

range of the jungle fowl, chicken remains were recorded at a few second millennium B.C.E. sites, and it is commonly assumed that domestication occurred there independently (1, 14, 15, 18, 19). The second phase took place in the third–second millennia B.C.E. and includes the dispersal of the chicken out of its natural distribution range to West Asia (Fig. 1, phase B). The earliest chicken remains in the Near East were retrieved in Iran, Anatolia, and Syria and dated to the third millennium B.C.E. or slightly earlier (20). In Egypt, the oldest known chicken remains are possibly even earlier (16). At this early phase, chicken remains in archaeological sites are very sparse and often are not associated with domestic contexts. Historical and iconographic records demonstrate an acquaintance with the chicken from the mid-second millennium B.C.E. in Egypt, Mesopotamia, and the Levant (21). All these sources relate to chickens (almost exclusively cocks) as an exotic bird, used *inter alia* for cockfighting and displayed as exotica in royal zoos. The third phase includes its introduction to Europe (Fig. 1, phase C1) and the intensification of its use mainly on this continent (Fig. 1, phase C2).

Archaeologically, chicken remains are first observed in Europe only in late ninth and eighth century B.C.E. contexts. The introduction of chickens to this region usually is attributed to the Phoenicians who brought chickens from their homeland to their colonies in the West (17, 22). This hypothesis is based on the fact that the earliest chicken remains in Europe were retrieved from Phoenician sites, mostly (although not only) in Iberia (23–25). The oldest reliable dated remains of chickens from central Europe (in the Czech Republic) are from the eighth century B.C.E. (26). The continued presence of chickens has been confirmed in Iberia (27, 28), as well as in southern France and Greece (24, 29), during the second half of the first millennium B.C.E. (Fig. 1, phase C1). However, a survey of the zooarchaeological literature of Europe demonstrates that before the first century B.C.E. the proportion

Significance

This study offers new evidence on the cultural history of the chicken, a species that until recently received limited attention compared with other domesticated animals. We provide evidence for the earliest known economic exploitation of the chicken outside its original distribution. This intensified use is first documented in the Southern Levant during the Hellenistic period (fourth–second centuries B.C.E.), at least 100 y before chickens spread widely across Europe. We explore the mechanisms for the spread of chickens as an important species in livestock economies from Asian to Mediterranean and European economies in antiquity to become one of the most widespread and dominant domesticates in the world today.

Author contributions: L.P.-G., A.E., and G.B.-O. designed research; L.P.-G., A.E., A.G., and G.B.-O. performed research; A.E., A.G., and G.B.-O. contributed new reagents/analytic tools; L.P.-G. and G.B.-O. analyzed data; and L.P.-G. and G.B.-O. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. Email: leeper1980@gmail.com.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1504236112/-DCSupplemental.

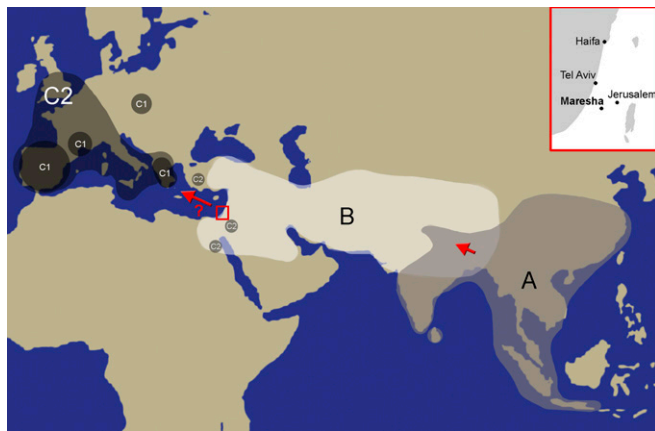


Fig. 1. The dispersal of chickens in the Old World: the area marked “A” is the geographical range of the jungle fowl in South Asia and its initial domestication, which already may have begun around the sixth millennium B.C.E. in Southeast Asia and possibly in China; The area marked “B” maps the dispersal of chickens to West Asia during the third and second millennia B.C.E. C1 represents the first wave of chicken dispersal into Europe: introduction to Europe during the eighth century B.C.E. (chicken remains have low representation in sites). C2 represents the second wave of chicken dispersal into Europe and other regions from the first century B.C.E. (chicken remains have higher representation in sites). The location of Maresha is marked in the enlarged map (*Inset*).

of chicken remains in archaeological sites was extremely low and hardly ever exceeded 3% of the total faunal remains (25, 30, 31).

The historical evidence also marks the eighth century B.C.E. (or even slightly later) as the arrival date of chickens in Europe. The arrival of chickens in Greece likely postdates Homer (around the eighth century B.C.E.), because the Greek poet does not mention this bird, but chickens are mentioned by Theognis of Megara in the sixth century (32). From the seventh century B.C.E., cocks are depicted on Greek coins and vases (28). In the fifth century B.C.E., the Greek playwright Aristophanes refers to the chicken as the “Persian bird” or “Median bird” (33), possibly indicating that in this period chickens were imported to Greece from Persia (14, 34). By the third century cocks became portrayed more frequently in Egypt (14, 22, 35 and references therein), but in Ptolemaic papyri chickens are hardly mentioned compared with other domesticated species (36). The symbolic role of cocks is well demonstrated by the Roman writer Cicero in his *De Divinatione* (37), where he mentions that cocks accompanied the Roman armies in 249 B.C.E. and that their behavior was observed carefully before battle as a sign of defeat or victory. Finally, fighting cocks are mentioned by Roman writers such as Varro (38) and Columella (39) (see also refs. 14 and 17).

Returning to faunal data, from the first century B.C.E., more sites with chicken remains are known in Europe, and the proportions of chickens at these sites are higher (Fig. 1, phase C2). This increase is apparent in Roman sites in Italy (40) and later in Southern Britain (13) and Sweden (41, 42). Significant proportions of chicken remains are observed in some first century B.C.E. locations in the Near East, such as in Sagalassos in Anatolia (43, 44) and Petra in Jordan (45, 46), and at Berenike (47) and Mons Claudianus (48) in Egypt. Indeed, the relative number of chicken remains in Berenike during Roman times is almost threefold that of the Ptolemaic period (49).

Unlike chicken bones, chicken egg shells often are overlooked during excavation (50). The first archaeological evidence for chicken eggs in the Mediterranean is from the first century B.C.E. This evidence includes some examples from Mons Claudianus and a high percentage of medullary bones from Berenike, indicative of females during laying time (47).

Although the faunal evidence points to the first century B.C.E. as a turning point in patterns of chicken exploitation in the Mediterranean, the historical and iconographic records imply a slightly earlier date for its economic utilization. For example, a Roman law in the *Lex Faunia* (161 B.C.E.) banned the consumption of more than a single chicken per meal. Other remarkable testimonies for the integration of the chicken into European livestock in the first century B.C.E. are provided by the Greek historian Diodorus Siculus, who described the sophisticated technique of artificial incubation of chicken eggs in Ptolemaic Egypt (51), and by the Roman historian Varro, who offered advice on how to treat hens during laying time (38). Subsequently, in the first century C.E. the Roman writer Columella and the Roman culinary Apicius mention chicken eggs among the ingredients in culinary recipes (39, 52).

We propose that the intensification in chicken exploitation in Europe during phase C2, as reflected by the archaeological and historical records, is related to our new data regarding chicken husbandry in the Southern Levant. The main new data we present here are from the site of Maresha, a national park situated in the Judean foothills in Southern Israel (Fig. 1 and Fig. S1) and dated to the Hellenistic period (fourth–second centuries B.C.E.). Located on an important trading route, Maresha flourished as a leading city of the region of Idumea, and its population comprised a complex ethnic mosaic (53). The town was in ruins by the late second century B.C.E. and was never resettled. In Hellenistic Maresha we note that, in addition to the symbolic cock painted in the so-called “Sidonian” tomb there (54), unisex chicken figurines are more common than any other animal figurines except for riders on horses (55, 56).

The unprecedented amount of chicken remains revealed at Maresha, far outside the original distribution of the domestic fowl, coupled with the clear chronology of the findings and the excellent preservation of the chicken bones, render Hellenistic Maresha a key site for understanding the new role of the chicken in the Mediterranean during this period. The study of the faunal evidence at Maresha is followed by a comparative chronological and regional study, based on the frequency of chicken remains as presented in 234 faunal reports from the Southern Levant, spanning all periods until early modern times. This study provides diachronic data on the process of introduction and subsequent widespread adoption of the chicken in Levantine economies. We offer suggestions based on these data regarding the time and mode of expansion of chickens from Southwest Asia to Europe and throughout the Mediterranean.

Results

Chickens at Maresha. Radiocarbon dating of two selected chicken bones yielded uncalibrated dates of 2245 ± 45 BP (RTD-7070), 2140 ± 28 BP (RTD-7071). The calibrated ranges of both samples fall within the Hellenistic period, namely between the end of the fourth and the third century B.C.E. These results correlate well with the archaeological dating provided by the associated artifacts, both in the two loci that yielded the dated bones and in the other contexts from which chicken bones were retrieved. The high average completeness (85%) reflects the reliability of the assemblage and results from the conditions in which the bones were deposited—in chalky soil and in sealed caves and therefore largely protected from postdepositional bone attrition.

In terms of the number of identified specimens (NISP), chicken bones at Maresha (NISP = 1,092) constitute 29% of the total livestock species (including *Capra*, *Ovis*, *Bos*, *Sus*, and *Equidae*). The distribution of chicken skeletal elements shows a relatively high representation of elements from different parts of the body, including leg bones, wings, and axial parts. Cut marks were detected on 6% of the remains. Most of the butchery marks were made during dismemberment of the carcass (Fig. S2). In some cases (NISP = 4) the feet were intentionally removed from the

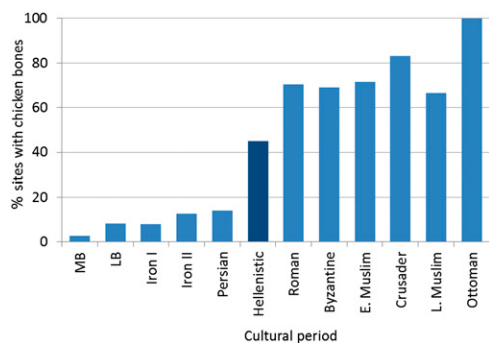


Fig. 2. Proportion of sites with chicken bones from 12 periods in the Southern Levant. General chronology following Levy 1995 (75): Middle Bronze Age II (MB) (2000–1550 B.C.E.), $n = 35$; Late Bronze Age (LB) (1550–1200 B.C.E.), $n = 24$; Iron Age I and II (1200–539 B.C.E.), $n = 80$; Persian period (539–333 B.C.E.), $n = 22$; Hellenistic period (333–63 B.C.E.), $n = 20$; Roman period (63 B.C.E.–324 C.E.), $n = 17$; Byzantine period (324–640 C.E.), $n = 12$; Early Muslim period (638–1099 C.E.), $n = 7$; Crusader period (1099–1291 C.E.), $n = 6$; Late Muslim period (1260–1517 C.E.), $n = 9$; Ottoman period (1517–1917 C.E.), $n = 2$. Data were compiled from 234 faunal reports.

carcass. On two of the tarsometatarsus bones, round and softer-edged grind marks on spurs were detected. These marks differ from butchery marks: The latter are not observed on the spurs and differ from the former in their direction, shape, and depth. Interestingly, burn marks were seen only on a single bone in the entire examined chicken assemblage, a much lower proportion than seen on bones of other livestock species at the site.

The age profile according to the ossification and porosity level of the long bones shows a high percentage of mature individuals (80.6%), implying a possible exploitation of secondary products (Fig. S3). The results of sexing according to the morphological characters of the tarsometatarsus spurs (Fig. S4A) revealed that spurs are absent from two thirds of the bones, indicating that the number of females culled is double that of males. The remaining third of the specimens have spurs at varying stages of development, representing adult, young, and castrated cocks. Sexing according to the greatest length (GL) measurement of Tarsometatarsus bones of mature individuals, combined with mixture analysis, demonstrated that females are represented more than males and constituted approximately two thirds of the culled chicken population (Fig. S4B). The results of the medullary bone analysis performed on 30 bones (10 femur, 10 tibiotarsus, and 10 tarsometatarsus bones, all from mature individuals) revealed three specimens with medullary bone in a high degree of compression (Fig. S5), indicating that some hens at Maresha produced eggs and were at some stage of the laying cycle at the time they were slaughtered. In contrast to the high presence of females, chicken egg shells have not yet been found at Maresha, nor are they reported in any of the faunal reports relating to the Hellenistic Southern Levant. This absence most likely results from the excavation methods; we note that careful and systematic sieving was not used.

Comparison of chicken bones measurements from Maresha with bones from four major Roman sites in Britain shows no significant differences in size (Table S1). The Hellenistic Levantine chickens are similar to the Roman European specimens in the length and breadth of the humerus (wing bone), coracoid (breast), and femur (leg). These results indicate that no significant change in the size of the chicken occurred during Roman times.

Chickens in the Southern Levant. A wider perspective on the integration of the chicken into the economy of the Southern Levant is provided by our survey of the relevant zooarchaeological literature for this region. The proportion of sites yielding chicken

remains rises gradually from less than 3% in the Middle Bronze Age to nearly 50% in the Hellenistic period (Fig. 2)—a dramatic increase overall. From the Hellenistic period onward, the frequency of sites with chicken remains continues to rise until it reaches 100% in the Ottoman period (16th–20th centuries C.E.) (Dataset S1). Corroborating this trend, we identified a marked threefold increase in the proportion of chicken remains relative to remains of other livestock species within sites between the pre-Hellenistic period (3% during the Persian period) and the Hellenistic period (9%) (Fig. 3). Subsequently the relative abundance of chicken remains within sites reached a zenith in the Byzantine period and then dropped. Although the sharp increase in the ratio of chicken remains is observed clearly in most of the Hellenistic Southern Levantine sites, Maresha is highly exceptional; at 29%, its proportion of chicken remains is more than threefold that at other Hellenistic sites (average, Fig. S6). Overall, the data demonstrate that before the Hellenistic period chicken exploitation was rather sporadic—the bones occur as isolated specimens in only a small number of sites—but in the Hellenistic period there is a conspicuous increase in the presence of chickens.

Discussion

The Incorporation of Chicken into the Human Diet in the Southern Levant. Archaeologically, the Southern Levant is one of the world’s most intensively studied regions. More than a 100 y of research uncovered thousands of sites, the excavation of which yielded large assemblages of animal remains spanning the entire sequence of the development of animal husbandry from late Neolithic times to the late Ottoman period. This major database allows a detailed examination of the arrival of the chicken in the region and its transformation into an established livestock species. This process was poorly known hitherto; here we are able to discuss it, for the first time to our knowledge, from a broad zooarchaeological perspective. Our results bring to the fore the Hellenistic period in the Southern Levant, and particularly the site of Maresha, as the earliest Mediterranean arena in which economic exploitation of the chicken can be demonstrated. This conclusion has important consequences for understanding the initial economic exploitation of the chicken in Europe.

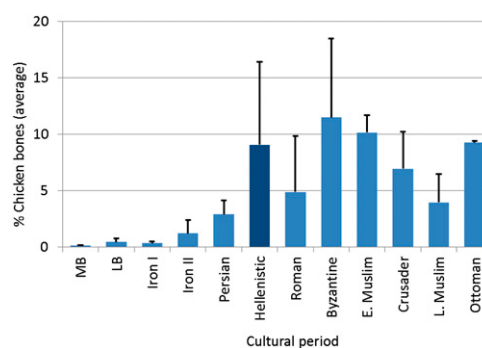


Fig. 3. Average proportion of chicken bones in total domestic bone (NISP) yield from 12 periods in Southern Levantine sites. General chronology following Levy 1995 (75): Middle Bronze Age II (2000–1550 B.C.E.), $n = 35$; Late Bronze Age (1550–1200 B.C.E.), $n = 24$; Iron Age I and II (1200–539 B.C.E.), $n = 80$; Persian period (539–333 B.C.E.), $n = 22$; Hellenistic period (333–63 B.C.E.), $n = 20$; Roman period (63 B.C.E.–324 C.E.), $n = 17$; Byzantine period (324–640 C.E.), $n = 12$; Early Muslim period (638–1099 C.E.), $n = 7$; Crusader period (1099–1291 C.E.), $n = 6$; Late Muslim period (1260–1517 C.E.), $n = 9$; Ottoman period (1517–1917 C.E.), $n = 2$. Domestic species include goat (*Capra hircus*), sheep (*Ovis aries*), cattle (*Bos taurus*), pig (*Sus scrofa*), and horse or donkey (*Equus caballus* or *Equus asinus*). Data were compiled from 234 faunal reports. Values are means + SD.

“Economic exploitation” refers to the utilization of chickens for meat and eggs, as opposed to cockfighting, sacrifice, and other purposes that do not involve large-scale consumption of chickens and chicken products. Although distinguishing between ritual and economic exploitation of chickens is crucial, this distinction often was ignored in faunal reports until recently. To date, no pre-Roman sites around the Mediterranean have yielded a proportion of chicken remains as high as that in Hellenistic Maresha. This quantity cannot indicate sporadic exploitation but rather points to intentional, large-scale breeding of this species for economic purposes. More than 80% of the chickens at Maresha reached maturity, indicating that they also may have been used for their secondary products (i.e., eggs). This observation is supported further by the twofold-higher frequency of females than males and by the medullary bones that show that some of the females were egg-laying hens. The high percentage of females in Maresha contrasts with some central Iron Age European sites, where a 3:1 ratio of cocks to hens is evident (31), and with Roman sites in the Netherlands and Britain (22). Furthermore, the presence of egg-laying hens at Maresha is thus far the earliest such evidence. Currently, similar evidence (as well as chicken egg shells) has not been observed earlier than early Roman times (47). This timing is consistent with the first appearance of chicken eggs in ancient recipes, which does not predate the first century C.E. (39, 52).

The representation of all body parts suggests that chickens were raised locally at Maresha and consumed at the site. The cut marks mainly indicate dismemberment of the body parts, and their presence on many skeletal parts also attests to exploitation as poultry. This observation differs from sites where chicken remains were found as complete articulated skeletons only (17), indicating noneconomic use such as cockfighting or some form of ritual activity. The low proportion of burnt bones implies that the cooking method did not involve direct exposure to fire.

The exceptional case study of Maresha is part of a wider regional trajectory in the cultural history of chicken exploitation, which is evident in the Hellenistic Southern Levant in general from the fourth to the second centuries B.C.E. At that period, this region exhibited a striking increase in the proportion of sites with chicken remains and a corresponding increase in the abundance of chicken remains relative to those of other livestock. These patterns strongly support the assumption that chickens were incorporated into the subsistence economies of the region during the Hellenistic period. Importantly, this increase marks a trend that intensifies in later periods.

The Southern Levant Provides a Springboard for the Global Spread of the Chicken. We distinguished between two phases of the presence of chickens in Europe and the Mediterranean, C1 and C2 in Fig. 1. The first phase, C1, began around the eighth century B.C.E. and continued until the end of the second century B.C.E. During this stage the proportions of chicken remains in European sites are especially low [$<3.5\%$ in the Iberian assemblages (25) and $<0.5\%$ in central European ones (31)]. In our opinion, the low ratios of chicken remains during this time-span cannot be related to economic utilization but rather indicate several other uses, such as cockfighting and various ritual protocols. The second phase, C2, defines the earliest period when chickens gradually became abundant in Europe and in some parts of the Near East, i.e., not before the first century B.C.E. according to the archaeological evidence. For example, the average proportion of chicken remains in Roman Britain (beginning in the first century C.E.) is $<6\%$ (13; full data are given in ref. 57). Similar frequencies are evident in Roman sites of the Southern Levant surveyed here and by others (16, 46). The incorporation of chickens as a livestock in Europe thus occurred around the first century B.C.E. Interestingly, our results show that the incorporation of the chicken as a local livestock species in the

Southern Levant occurred at least 100 y earlier. These observations provide new insights regarding the trajectory through which the chicken became an important economic species in Europe and the Mediterranean. We argue that the Hellenistic Southern Levant was a crucial intermediate region in this process.

Environmental and Anthropogenic Conditions for the Economic Exploitation of Chickens. Functioning as a bridge between Asia and Europe, the Southern Levant was the stage for an intermediary phase in the dispersal of the chicken between its initial domestication in Southeast Asia and its adoption to the European economy during the mid-second and first centuries B.C.E. After its first introduction to the Southern Levant in the second millennium B.C.E., chickens became acclimatized to nontropical conditions and gradually adapted to the relatively dry Mediterranean environment. This adaption consequently led to various morphological changes over time (58).

Redding (16) has suggested that in the Levant chickens came to replace pigs as an important economic species in the first millennium B.C.E. In contrast to large herd animals, both taxa could be reared on a smaller household scale, engendering relatively little interest from central authorities, artists, or historians. Both taxa would have exerted similar demands (food and labor) on the household economy, thereby likely competing for these resources (16). However, as opposed to the low mobility and high water consumption of pigs, chickens provided an easy-to-grow, compact, and highly portable package of meat and a more efficient source of protein through both its eggs and meat (16, 59). A critical factor contributing to tipping the balance in favor of chickens over pigs would have been the harvesting of eggs, which were a new, accessible source of protein. The conditions for developing a flourishing chicken economy seem to have been well met at Maresha.

By the Hellenistic period, the inhabitants of Maresha fully realized the advantages of a chicken economy. Over a period of roughly 200 y the exploitation of chickens was intensified, perhaps involving the maintenance of chickens in stressful conditions of crowded hutches or coops [as turkeys were kept in North America (60)]. Under the conditions of a firm management regime, appreciable behavioral changes and morphological modifications could have occurred. These modifications possibly include increased tolerance for penning, reduced aggression, and increased sexual precocity. This scenario is made likely by the relatively short generation span of chickens, resulting from the short time between hatching to full maturity. Such combined, fairly rapid behavioral and morphological changes are observed widely in other livestock species (61–63, and see ref. 64 for farm fox taming). Our study shows that the Hellenistic chickens of Levantine Maresha did not differ in their wing, breast, and leg dimensions from those of European chicken breeds in the Roman period. This observation challenges the hypothesis that selective breeding in Roman times caused a substantial size increase in chickens (65, 66). Our data suggest that this change already is evident in the Hellenistic Southern Levant.

Historical evidence suggests that before the Hellenistic period consumption of chickens was tabooed in various parts of the world, either culturally or legally (17 and references therein). The emergence of the Hellenistic koine (Greek cultural and linguistic uniformity) generated an ambience of globalization in which science and philosophy flourished and which conceivably encouraged the abandonment of old taboos and the adoption of new traditions. In this atmosphere, the Ptolemaic rulers of Egypt introduced new exotic animal breeds to their kingdom. The Zenon papyri from the mid-third century B.C.E. highlight the southern Levant as the origin of various new animal breeds (e.g., certain sheep breeds and crossbred wild asses and donkeys imported to Egypt) (36). Our data show that, for the first time in

the history of the Middle East, chickens were seen not only as exotic animals but also as an important source of food.

The acceleration of cross-Mediterranean economic interconnections in Roman times, beginning in the first century B.C.E., would have provided the conditions for intensifying chicken exploitation in Europe as well. The Romans introduced to Europe a variety of plant and animal species [e.g., domestic guinea fowl (*Numida Meleagris*) (66), pheasant (*Phasianus colchicus*) (22), and rabbit (*Oryctolagus cuniculus*) (67)], and we argue that they also were responsible for the introduction of the chickens from the Southern Levant. The mechanism behind the initial introduction of the Southern Levantine chicken may have been the supply of novel foods to urban markets, satisfying a need created by feasts, both public and private (68, 69). Their small size and relative ease of transport and management meant that chicks and chicken eggs were exchanged easily between areas of agricultural production (*pastio villatica*) and urban centers, as described in several literary sources (70). In Roman Britain, higher proportions of chicken remains were uncovered in urban than in other types of sites (13). It has been suggested that chicken was, at least in the beginning, a luxury food, consumed by the Roman upper classes (23).

Chickens were not the only exotic birds brought from afar to be served as culinary delicacies in banquets during Roman Republican times. Other avian species such as the peacock (*Pavo cristatus*) and flamingo (*Phoenicopterus* spp.), which initially were kept for their ornamental qualities and symbolic characteristics, were beginning to be regarded as a delicacy under the Late Republic when Quintus Hortensius introduced them to the Roman table (71, 72). However, unlike other exotic birds, the chicken spread quickly in Europe and rapidly became a common domestic fowl.

Materials and Methods

The chicken bones from Maresha were retrieved from five subterranean complexes hewn below the dwellings of the lower city (Fig. S1); therefore the original context of the remains is assumed to be domestic (53). It is unclear whether the bones accumulated gradually from the residential contexts of the lower city into the subterranean complexes or resulted from a single destructive event during the Hasmonean conquest of the city. This uncertainty notwithstanding, the attribution of the bones to the Hellenistic period cannot be doubted, because of the sheer quantities of bones in contexts where the accompanying artifacts (mainly ceramics and coins) date only to the Hellenistic period, no later than ca. 100 B.C.E., with no later finds. This dating has been verified by radiocarbon dating of the two bones retrieved from sealed loci in different areas.

Identification as to taxon and skeletal element was carried out using the comparative collection of the Laboratory of Archaeozoology at the University of Haifa, and the distribution of skeletal elements has been recorded. Following Serjeantson (22), we studied bone attrition and surface modification, including butchery and burn marks. Age at death was determined based on the state of ossification and level of porosity of the long bones, based, among other long bones, on the proximal tarsometatarsus which is fully

ossified around 19–27 wk (22). The chicken bones were sexed by a combination of three methods. The first was a biometric method, using the measurements of the tarsometatarsus bones (73, 74). For this analysis we used the GL measurement of the chicken tarsometatarsus bones. Fused specimens were measured to the nearest 0.1 mm using Vernier calipers. We implemented a statistical analysis of the sexes and presented it by mixture analysis modeling. The second was examination of the presence or absence of medullary bone in femur, tibiotarsus, and tarsometatarsus bones of adult chickens (47). The third was morphological observations of the developmental stage of the leg spur in cocks (22). The rationale for combining those methods derives from possible inaccuracies in them, particularly in the third: In general, adult males have a developed spur (used for combat between males), spur cores, or spur scars attached to the tarsometatarsus, whereas females rarely do. However, because spurs may become fused to the diaphysis of the tarsometatarsus rather late, and spurs or spur scars occasionally occur also among female chickens, additional methods are needed to examine the sexual dimorphism among ancient chicken populations. Bone measurements of Hellenistic chicken remains from Maresha were compared with those of chicken remains from several European Roman sites (four sites in Britain) (Table S1). Student's *t*-test was used to compare the average GL and distal breadth (Bd) of the humerus, coracoid, and femur.

To provide a long-term perspective of the change in the social and economic role of the chicken in the Southern Levant, we reviewed the appearance and the dispersal of chickens in this region through time. We used data on the occurrence and frequency of chicken remains from 234 published zooarchaeological reports spanning more than three millennia—from Middle Bronze Age II (the first half of the second millennium B.C.E.) to the end of the Ottoman period (the early 20th century C.E.). Before the Middle Bronze Age wild and domestic chickens were completely absent from the region. We included in our survey of the literature nearly all published faunal assemblages. We excluded from the analysis only assemblages that are not well dated and those with a very low number of faunal remains (<10 specimens in total). For each period, we present the percentage of sites with chicken remains and the average percentage of chicken remains relative to the remains of all other domesticates in these sites. For all these analyses we used the NISP to compute the frequency of chicken remains. The minimum number of individuals could not be calculated because many reports lack the appropriate data. Finally, to put the Maresha findings into a wider temporal and regional context, we compared the proportion of chicken remains at Maresha with those at contemporary Hellenistic sites in the Southern Levant, the only region from which sufficient data are available.

ACKNOWLEDGMENTS. We thank Ian Stern for inviting us to work on the faunal material from Maresha and for his assistance; Ofer Bar-Yosef, Laszlo Bartosiewicz, Simon Davis, Greger Larson, Nimrod Marom, Arturo Morales, Joris Peters, Ruth Shahack-Gross, Naomi Sykes, Jean-Denis Vigne, Lior Weissbrod, Reuven Yeshurun, and Melinda Zeder for their constructive comments and stimulating discussions; Elisabetta Boaretto for the radiocarbon dating performed in the Dangoor-Research Accelerator Mass Spectrometry Radiocarbon Laboratory at the Weizmann Institute of Science; and Anat Regev-Gisis for preparing the graphics and drawings. This study was supported in part by Israel Science Foundation Grant 340/14 (to G.B.-O.). The research was carried out when L.P.-G. was a Rotenreich Doctoral Fellow. This paper was originally presented at the Archaeozoology of Southwestern Asia and Adjacent Areas meeting at the University of Haifa, Haifa, Israel, June 23–28, 2013.

- West B, Zhou B-X (1988) Did chickens go North? New evidence for domestication. *J Archaeol Sci* 15:515–533.
- Crawford RD (1990) *Poultry Breeding and Genetics* (Elsevier Ltd., Amsterdam).
- Hillel J, et al. (2003) Biodiversity of 52 chicken populations assessed by microsatellite typing of DNA pools. *Genet Sel Evol* 35(5):533–557.
- Eriksson J, et al. (2008) Identification of the yellow skin gene reveals a hybrid origin of the domestic chicken. *PLoS Genet* 4(2):e1000010.
- Kanginakudru S, Metta M, Jakati RD, Nagaraju J (2008) Genetic evidence from Indian red jungle fowl corroborates multiple domestication of modern day chicken. *BMC Evol Biol* 8:174–197.
- Brisbin IL (1995) Conservation of the wild ancestors of domestic animals. *Conserv Biol* 9(5):1327–1328.
- Peterson AT, Brisbin IL (1998) Genetic endangerment of wild Red Junglefowl *Gallus gallus*? *Bird Conserv Int* 8(04):387–394.
- Liu Y-P, et al. (2006) Multiple maternal origins of chickens: Out of the Asian jungles. *Mol Phylogenet Evol* 38(1):12–19.
- Gongora J, et al. (2008) Indo-European and Asian origins for Chilean and Pacific chickens revealed by mtDNA. *Proc Natl Acad Sci USA* 105(30):10308–10313.
- Fuller DQ, Boivin N, Hoogervorst T, Allaby R (2011) Across the Indian Ocean: The prehistoric movement of plants and animals. *Antiquity* 85(328):544–558.
- Xiang H, et al. (2014) Early Holocene chicken domestication in northern China. *Proc Natl Acad Sci USA* 111(49):17564–17569.
- Storey AA, et al. (2012) Investigating the global dispersal of chickens in prehistory using ancient mitochondrial DNA signatures. *PLoS ONE* 7(7):e39171.
- Maltby M (1997) Domestic fowl on Romano-British sites: Inter-site comparisons of abundance. *Int J Osteoarchaeol* 7(4):402–414.
- Potts A (2012) *Chicken* (Reaktion Books, London).
- Badam GL (1984) Holocene faunal material from India with special reference to domesticated animals in *Animals and Archaeology: Early Herders and Their Flocks*. BAR International Series 202, eds Clutton-Brock J, Grigson C (Archaeopress, Oxford, UK), pp 339–353.
- Redding RW (2015) The pig and the chicken in the Middle East: Modeling human subsistence behavior in the archaeological record using historical and animal husbandry data. *J Archaeol Res* 23:163–213.
- Sykes N (2012) A social perspective on the introduction of exotic animals: The case of the chicken. *World Archaeol* 44(1):158–169.

18. Pawankar SJ, Thomas PK (1997) Fauna and subsistence pattern in the Chalcolithic culture of Western India, with special reference to Inamgaon: Postpaleolithic Europe II, Asia, Africa. *Anthropozoologica* 25-26:737-746.
19. Fuller DQ (2006) Agricultural origins and frontiers in South Asia: A working synthesis. *J World Prehist* 20(1):1-86.
20. Benecke N (1994) *Der Mensch und Seine Haustiere: Die Geschichte Einer Jahrtausendalten Beziehung* (Theiss, Stuttgart).
21. Egger J (2010) Iconography of deities and demons: Electronic pre-publication: Rooster. Available at: www.religionswissenschaft.uzh.ch/idd/. Accessed May 10, 2015.
22. Serjeantson D (2009) *Birds* (Cambridge Univ Press, New York).
23. Garcia Petit L (2005) Recent studies on prehistoric to Medieval bird bone remains from Catalonia and Southeast France in International Council for Archaeozoology Bird Working Group, *Feathers, Grit and Symbolism: Birds and Humans in the Ancient Old and New Worlds*, eds Grupe G, Peters J (Verlag Marie Leidorf GmbH, Rahden/Westf, Germany), pp 147-163.
24. Garcia Petit L (2002) La migration du coq: De l'Extreme-Orient a la Mediterranee in *Mouvements ou Déplacements de Populations Animales en Méditerranée au Cours de l'Holocène*, BAR International Series, ed Gardeisen A (Archaeopress, Oxford, UK), pp 73-82.
25. Hernandez-Carrasquilla F (1992) Some comments on the introduction of domestic fowl in Iberia. *Archaeofauna* 1:45-53.
26. Kysely R (2010) Review of the oldest evidence of domestic fowl *Gallus gallus* f. domestica from the Czech Republic in its European context. *Acta Zool Cracoviensia* 53(1):9-34.
27. Davis SJM (2006) *Faunal Remains from Alcáçova de Santarém, Portugal*, Trabalhos de Arqueologia 43 (Instituto Português de Arqueologia, Lisboa).
28. Davis SJM (2007a) *Mammal and Bird Remains from the Iron Age and Roman periods at Castro Marim, Algarve* (International Committee for Architectural Photogrammetry, Lisbon).
29. Prummel W (2005) The avifauna of the Hellenistic town of New Halos, Thessaly, Greece in International Council for Archaeozoology Bird Working Group, *Feathers, Grit and Symbolism: Birds and Humans in the Ancient Old and New Worlds*, eds Grupe G, Peters J (Marie Leidorf GmbH, Rahden/Westfalen, Germany), pp 350-360.
30. Davis SJM, Moreno-Garcia M (2007b) Of metapodials, measurements and music: Eight years of miscellaneous zooarchaeological discoveries at the IPA, Lisbon. *O Arqueólogo Português IV* 25:9-165.
31. Benecke N (1993) On the utilization of the domestic fowl in central Europe from the Iron Age up to the Middle Ages. *Archaeofauna* 2:21-31.
32. Figueira TJ, Nagy G (1985) *Theognis of Megara: Poetry and the Polis* (Johns Hopkins Univ Press, Baltimore).
33. Aristophanes (1995). *The Birds*, trans Dunbar N (Oxford Univ Press, Oxford, UK).
34. Toussaint-Samat M (2009) *A History of Food* (Wiley-Blackwell, UK).
35. Houlihan PF, Goodman SM (1986) *The Birds of Ancient Egypt* (Aris & Phillips, Warminster, UK).
36. Rostovtzeff M (1967) *A Large estate in Egypt in the Third Century B.C.*, Studia Historica 52 (L'Erma di Bretschneider, Roma).
37. Cicero MT, Wardle D (2006) *Cicero on Divination, Book 1*, ed Wardle D (Oxford Univ Press, Oxford, UK).
38. Hooper WD, Ash HB (1954) *Cato and Varro on Agriculture* (Harvard Univ Press, Cambridge, MA).
39. Columella LJM (1745) Of Husbandry in Twelve Books: And His Book Concerning Trees (A Millar, London).
40. De Grossi Mazzorin J (2000) Introduzione e diffusione del pollame in Italia ed evoluzione delle sue forme di allevamento fino al Medioevo. *Atti del 3° Convegno nazionale di archeozoologia* (Istituto poligrafico e zecca dello Stato, Roma), pp 351-361.
41. Tyrberg T (2002) The archaeological record of domesticated and tamed birds in Sweden. *Acta Zool Cracoviensia* 45:215-231.
42. Ericson P, Tyrberg T (2004) *The Early History of the Swedish Avifauna: A Review of the Subfossil Record and Early Written Sources* (Kungl, Stockholm), Vol 4.
43. De Cupere B (2001) *Animals at Ancient Sagalassos: Evidence of the Faunal Remains* (Brepols, Turnhout, Belgium).
44. Fuller BT, et al. (2012) Isotopic reconstruction of human diet and animal husbandry practices during the Classical-Hellenistic, imperial, and Byzantine periods at Sagalassos, Turkey. *Am J Phys Anthropol* 149(2):157-171.
45. Studer J, Frösén J, Tomasz FZ (2002) City and monastery: Animals raised and consumed in the Petra area in Petra: *A City Forgotten and Rediscovered* (Amos Andersen Art Museum, Helsinki), pp 167-172.
46. Studer J (2002) Dietary differences at Ez Zantur Petra, Jordan (1st century BC-AD 5th century) in *Archaeozoology of the Near East V*, eds Buitenhuis H, Choyke AM, Mashkour M, Al-Shiyab AH (Archaeological Research and Consultancy, Groningen, The Netherlands), pp 273-281.
47. Van Neer W, Noyen K, De Cupere B, Beuls I (2002) On the use of endosteal layers and medullary bone from domestic fowl in archaeozoological studies. *J Archaeol Sci* 29(2): 123-134.
48. Hamilton-Dyer S (1997) The domestic fowl and other birds from the Roman site of Mons Claudianus. *Int J Osteoarchaeol* 7(4):326-329.
49. Sidebotham SE, Wendrich W, Aldsworth F (1999) *Berenike 1997: Report of the 1997 Excavations at Berenike and the Survey of the Eastern Desert, including Excavations at Shenshef* (Leiden University, Leiden, The Netherlands).
50. Stewart JRM, Allen RB, Jones AKG, Penkman KEH, Collins MJ (2013) ZooMS: Making eggshell visible in the archaeological record. *J Archaeol Sci* 40(4):1797-1804.
51. Diodorus (1933) *Diodorus of Sicily*, trans Oldfather CH (Heinemann, London) Vol 1.
52. Apicius EJ (1984) *The Roman Cookery of Apicius: A Treasury of Gourmet Recipes and Herbal Cookery* (Hartley & Marks, Point Roberts, WA).
53. Kloner A, Eshel E, Finkielstejn G, Korzakova HB (2010) *Maresha Excavations Final Report III. Epigraphic Finds from the 1989-2000 Seasons* (Israel Antiquities Authority, Jerusalem).
54. Peters JP, Thiersch H (1905) *Painted Tombs in the Necropolis of Marissa* (Committee of the Palestine Exploration Fund, London).
55. Erlich A, Kloner A (2008) *Maresha Excavations Final Report II: Hellenistic Terracotta Figurines from the 1989-1996 Seasons* (Israel Antiquities Authority, Jerusalem).
56. Erlich A (2014) *Terracotta Figurines. The Excavations of Maresha Subterranean Complex 57: The "Heliodoros" Cave*. BAR International Series 2652, eds Stern I, Alpert B (Archaeopress, Oxford, UK), pp 39-71.
57. Allen MG (2011) *Animalscapes and Empire: New Perspectives on the Iron Age/Romano British Transition*. Thesis (University of Nottingham, Nottingham, UK).
58. Girdland Flink L, et al. (2014) Establishing the validity of domestication genes using DNA from ancient chickens. *Proc Natl Acad Sci USA* 111(17):6184-6189.
59. Storey AA, et al. (2008) Counting your chickens: Density and distribution of chicken remains in archaeological sites of Oceania. *Int J Osteoarchaeol* 18(3):240-261.
60. Munro ND (2011) Domestication of the turkey in the American Southwest in *The Subsistence Economies of Indigenous North American Societies: A Handbook*, ed Smith BD (Smithsonian Institution, Washington, DC), pp 543-555.
61. Zeder MA, Emshwiller E, Smith BD, Bradley DG (2006) Documenting domestication: The intersection of genetics and archaeology. *Trends Genet* 22(3):139-155.
62. Zeder MA (2015) Core questions in domestication research. *Proc Natl Acad Sci USA* 112(11):3191-3198.
63. Zeder MA (1996) The role of pigs in Near Eastern subsistence: A view from the Southern Levant in *Retrieving the Past: Essays on Archaeological Research and Methodology in Honor of Gus W. Van Beek*, ed Seger JD (Eisenbrauns, Winona Lake, IN), pp 297-312.
64. Trut L (1999) Early canid domestication: The farm-fox experiment. *Am Sci* 87(2): 160-169.
65. Thesing R (1977) *Die Größenentwicklung des Haushuhns in vor-und frühgeschichtlicher Zeit*. Dissertation (Ludwig Maximilian University of Munich, Munich).
66. MacDonald KC (1992) The domestic chicken (*Gallus Gallus*) in sub-Saharan Africa: A background to its introduction and its osteological differentiation from indigenous fowls (Numidinae and *Francolinus* Sp.). *J Archaeol Sci* 19(3):303-318.
67. Clutton-Brock J (1999) *A Natural History of Domesticated Mammals* (Cambridge Univ Press, Cambridge, UK).
68. Rosenstein NS, Morstein-Marx R (2011) *A Companion to the Roman Republic* (Blackwell Publications, Oxford, UK), Vol 135.
69. Viitanen EM (2010) *Locus Bonus: The Relationship of the Roman Villa to its Environment in the Vicinity of Rome* (Helsinki University, Helsinki).
70. Morley N (2002) *Metropolis and Hinterland: The City of Rome and the Italian Economy, 200 BC-200 AD* (Cambridge Univ Press, Cambridge, UK).
71. Marzano A (2007) *Roman Villas in Central Italy: A Social and Economic History* (Brill, Leiden), Vol 30.
72. Hughes JD (2003) Europe as consumer of exotic biodiversity: Greek and Roman times. *Lands Res* 28(1):21-31.
73. De Cupere B, et al. (2005) Ancient breeds of domestic fowl (*Gallus gallus* f. domestica) distinguished on the basis of traditional observations combined with mixture analysis. *J Archaeol Sci* 32(11):1587-1597.
74. Von Den Driesch A (1976) *A Guide to the Measurement of Animal Bones from Archaeological Sites* (Harvard Univ Press, Cambridge, MA).
75. Levy TE (1995) *The Archaeology of Society in the Holy Land* (Facts on file, New York).
76. Kloner A, Zissu B (2013) The subterranean complexes of Maresha: An urban center from the Hellenistic period in the Judean foothills, Israel. *Opera Ipogea. Journal of Speleology in Artificial Caves* 2:45-62.
77. Allen M *Fishbourne Roman Palace 1961-68 Excavations*. Available at chickenco-op.net. Accessed May 10, 2015.
78. Bourdillon J (1998) Of butchers and breeds: Report on vertebrate remains from various sites in the city of Lincoln. By KM Dobney, SD Jaques and BG Irving. *Archaeol J* 155(1):417-418.
79. Maltby M (2009) *Bones: Mammals, birds and fish in Excavation of an Enigmatic Multi-Period Settlement on the Isle of Portland, Dorset* (British Series 499) ed Palmer S (British Archaeological Reports, Oxford, UK), pp 27-43.
80. O'Connor TP (1988) Bones from the general accident site, Tanner Row in *Archaeology of York* (Council for British Archaeology, London) Vol 15/2.