Sexual dimorphism among Mesoamerican turkeys: A key for understanding past husbandry

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A R T I C L E   I N   F O

Article history:
Received 26 August 2015
Received in revised form 20 March 2016
Accepted 28 May 2016
Available online xxxx

Keywords:
Gaussian mixtures
Log size index
Log shape ratio
Meleagris gallopavo
Morphometrics
Zooarchaeology

A B S T R A C T

Few animals have been domesticated in Mesoamerica and the organization of husbandry practices in this part of the world remains little known. The turkey (Meleagris gallopavo), one of these few animals, shows an evident sexual dimorphism that allows for the analysis of past demographic structure from the study of archaeological bone remains. Here we document sexual dimorphism in turkey populations from the Classic to the Post classic (200–1521 CE) in northern Mesoamerica. We present a morphometric approach based on both size and shape that allows the distinction of two groups in the archaeological populations, corresponding to males and females. Group delimitation with no prior knowledge of their number and parameters is conducted with Gaussian mixture analyses. The accuracy of the method was first evaluated using bibliographic data from the Southwestern USA and then applied on 120 Mesoamerican bone remains of unknown sex coming from five archaeological sites. We point out an imbalanced sex-ratio in Mesoamerican turkey flocks that account for more females than males. We also show that there were no significant size variations between the different sites tested in this study even if they are situated in both lowlands and highlands.

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1. Introduction

Turkey (Meleagris gallopavo) was one of the few domesticated animals in Mesoamerica at the time of the European contact. The details reported by Sahagun in his description of the bird, the existence of multiple Nahual terms to depict the different body parts, and the expressions related to turkeys in common language (Dibble and Anderson, 1975) all show its importance in Aztecs daily life, as do more sporadic mentions of other 17th century authors (see review in Latsanopoulos, 2011). However, few studies have been conducted on the conditions of its domestication and on husbandry practices.

According to Schorger (1966), the extent of the natural distribution of the wild turkey coincides with the northern part of Mesoamerica (Fig. 1). The earliest evidence of its management is the discovery of six bones of wild turkey outside of its natural range, in the Pre-classic deposits (cal 327 BCE–54 CE) of El Mirador, northern Guatemala (Thornton et al., 2012) enabling archaeologists to consider turkey as a domesticate in pre-Hispanic southern Mesoamerica. Nonetheless, in central Mexico, because the wild turkey is present in the natural environment and, so far, no clear morphological traits have been found to successfully distinguish domestic and wild forms, we suggest in this paper to consider husbandry practices as distinct from the domestication concept. Indeed, as introduced by Jarman et al. (1976), the term of animal husbandry is not necessarily restricted to domestic animals but deals with the behavioral aspects of the relationships between man and animals, without requiring any selective breeding, whether intentional or not.

If we can establish the population structure of an archaeological sample, in particular sex-ratio, we then gain specific information on human strategies regarding animal selection. This topic has been widely used to characterize wild mammals hunting strategies (e.g. Fernández and Monchot, 2007; Jones, 2006; Monchot, 1999; Weinstock, 2000), the first steps of mammal domestication (e.g. Helmer et al., 2005; Vigne et al., 2012; Zeder, 2001) and economic systems of mammal husbandry (cf. the model proposed by Payne, 1973).

Fewer studies dealing with birds have been conducted towards this purpose. Bird sex-ratios seem highly dependent upon the species considered and its natural behavior. For example, as they are polygamous birds, domestic fowls can be raised with a ratio of one male for five females in a mixed “meat and eggs” economy, while monogamous geese would need a balanced sex ratio to reproduce (Albarella, 1997; Serjeantson, 2002). Turkeys show a clear sexual dimorphism enabling an analysis of sex-ratio from archaeological bone sample. It has been...
studied in Southwestern USA (Badenhorst et al., 2012; Munro, 1994; Speller and Yang, this volume), but Mesoamerica lacks similar studies.

Three different characters can be used to determine turkey sex from their bones: the presence or absence of spurs on the tarsometatarsus, the presence of medullary bones, and size dimorphism.

Spurs occur almost exclusively on the tarsometatarsus of males, although protuberances can occasionally appear on some domestic females (McKusick, 1986, p. 32; Schorger, 1966, p. 122). As spurs grow with age (Schorger, 1966, p. 122), it is not always possible to observe them on young animals. The dimension and thus the visibility of the spurs also seem to vary within sub-species or populations, since differences have been observed between various subspecies (Schorger, 1966, pp. 80–86). Spurs might also be absent on some males individuals (Speller, 2009).

Medullary bone is a granular deposit of calcium that appears inside the cavity of bird bones during the breeding period. It constitutes a supply of minerals used during the production of eggshell (Driver, 1982; Lentacker and Van Neer, 1996; Rick, 1975). Unlike what was previously thought (Rick, 1975), medullary bone is present in almost all anatomical elements and can be abundant even in the most pneumatized ones, such as humeri (Laroulandie and Lefèvre, 2014; Lentacker and Van Neer, 1996).

Finally, turkeys show a high sexual size dimorphism, males being larger than females, as indicated by the two most complete osteometric studies conducted on wild turkeys (Bochenski and Campbell, 2006; Steadman, 1980). Other observations conducted on indigenous breeds currently raised in Mexico (López Zavala et al., 2006), on archaeological domestic birds (Badenhorst et al., 2012; Munro, 1994; Speller, 2009) and mentioned in historical descriptions (Sahagún, 1880, p. 710) also indicate a size dimorphism. However, it has been shown that some measurements of males and females might overlap (Bochenski and Campbell, 2006; McKusick, 1986).

The first two characters (spur on tarsometatarsus and medullary bone) give an absolute sex determination, but, in the first case, they are limited to a single element, the tarsometatarsus, and, in the second case, to sexually mature females killed during the breeding period. Therefore sexual size dimorphism is the most reliable way to apprehend demographic structure of turkey by gaining advantage of the entire bone sample. But as some measurements of both sexes overlap, univariate and bivariate methods are not the strongest ones to discriminate between the sexes and that is why this study aims to propose a more accurate metrical approach.

We evaluate hence the relevance of sexual dimorphism to characterize the population structure by using two morphometric tools allowing form description through a multivariate approach: the log size index and the log shape ratio. We focused this investigation on mature specimens to limit ontogenetic bias.

2. Material and methods

2.1. Turkey bone sample

2.1.1. Reference collection

We used a reference sample from the Collections d’Anatomie Comparée of the Muséum national d’Histoire naturelle (MNHN) of Paris containing eight complete skeletons. Four males and four females were identified on the criteria of presence or absence of the spur on the tarsometatarsus and the catalogue information (Table S1). They were all raised in captivity even if some birds were argued to be from wild populations. Most of the specimens come from the 19th/early 20th centuries and we can expect their morphology to be more similar to domestic turkeys from historical times than modern breeds.

2.1.2. Bibliographic data

We used as a reference a series of published measurements of archaeological turkey bones collected in the southwestern USA and adjacent northwestern Mexico sites for a genetic study (Speller, 2009; Speller and Yang, this volume). We selected the mature measured specimens that yielded a positive genetic identification for sex using the method presented in Speller and Yang (this volume). The bones represent 119 different individuals from 29 archaeological sites (Table S2).

2.1.3. Mesoamerican archaeological material

The 120 archaeological turkey bones analyzed in this paper, all from mature individuals, come from five archaeological sites dating from the Classic and Post-classic periods (200 CE–1521 CE), all located in northern Mesoamerica (Fig. 1, Table 1). Four of these sites are in the Mexican central highlands. The fifth one, Vista Hermosa, is situated in the eastern lowlands. In the latter case, turkey skeletons were found in association with human burials; in other contexts, turkey remains were found in middens and platform fillings.

The site of Malpaís Prieto (Mich31) is an urban settlement in the Basin of Zacaup, northern Michoacán, occupied for a short period during the middle Postclassic (Pereira and Forest, 2011; Pereira et al., 2012,
The excavation of a trash deposit associated with a large domestic unit yielded a high number of animal remains (NISP = 1030), dominated by medium vertebrates (in particular pocket gopher, cf. *Cratogeomys fumosus*, NISP = 255, cottontail, *Sylvilagus* sp., NISP = 122) and turkey (*Meleagris gallopavo*, NISP = 248) (Manin *et al.*, 2015). Thirty-six measurable specimens account for a minimum of six individuals.

The site of El Cuizillo del Mezquital (JR74) is a Preclassic settlement located in the valley of Acámbaro, southern Guanajuato (Faugère, 2013). The faunal remains (NISP = 273) were recovered in the filling of a pit structure (*patio hundido*) and are probably dated from an early Classic occupation of the area, as indicated by associated Mazatlan ceramic sherds. Only four remains of turkey were identified, from which two were measured. They represent a minimum of one individual. Pauceity of turkey remains is characteristic of Preclassic sites in this region (Valadez Azúa and Rodríguez Galicia, 2004).

Calixtlahuaca (Cal) is a Postclassic city located in the Toluca valley, considered from various evidence to be the regional capital of Matlazinco, the most powerful city of the valley until the Aztec Conquest in 1478 (Smith *et al.*, 2013; Tomaszewski and Smith, 2015). The site was occupied during the Middle and Late Postclassic (Huster and Smith, 2015). Excavations were conducted in various household compounds; the faunal remains (NISP = 247) were found in both middens and platform fillings. Twenty-six remains of turkey were identified, and only four were complete enough to be measured. They represent a minimum of three individuals.

Tizayuca (Tiz) is located in the northeast of the Basin of Mexico. Excavations conducted by the Proyecto de Salvamento Arqueológico de Tizayuca since 2002 have identified a series of occupations from the Classic to Late Postclassic (Huster and Smith, 2015). The faunal remains (NISP = 1030), dominated by medium vertebrates (in particular pocket gopher, cf. *Cratogeomys fumosus*, NISP = 255, cottontail, *Sylvilagus* sp., NISP = 122) and turkey (*Meleagris gallopavo*, NISP = 248) (Manin *et al.*, 2015). Thirty-six measurable specimens account for a minimum of six individuals.

Vista Hermosa (VH) is a Huastecan site located in the lowlands of southern Tamaulipas and occupied during the Late Postclassic (Stresser-Péan, 1975). A large amount of animal bones (NISP = 1019) were recovered in both domestic and funerary contexts (Manin and Lefèvre, in press). Turkey is the predominant animal (NISP = 651, MNI = 27); specimens were mostly recovered as complete skeletons in funerary deposits (MNI = 22). Measurements were taken on 39 remains of animals from funerary contexts and account for a minimum of seven individuals.

We took a total of 300 measures spread on 120 mature Mesoamerican turkey bones from the Classic and Postclassic period, representing a minimum of 23 individuals (Table 2). The MNI has been calculated on each site on the frequency of the most abundant skeletal part.

### 2.2. Methodological approach

Log size index (LSI) and log-shape ratio (LSR) are two methods of morphometrics based on linear measurements (Marcus, 1990; Reyment, 1985). They both allow partitioning the bone form in size and shape parameters, following the relationship exemplified by Needham (1950): Form = Size + Shape.

Reference and archaeological bones were all measured with the same digital caliper (IHM 150 mm, accurate to 0.01 mm) and by the same person [AM]. Measurements were taken following von den Driesch (1976), with some additions (Table S3). Left elements were preferentially measured in the comparative collection, but in case of missing or damaged elements, the right side was chosen. This occurred in eight elements, as indicated in Table S4. In order to estimate measurement error, we measured three reference skeletons of close dimensions, 10 times. A principal component analysis (PCA) was conducted on these log-transform measurements; in the end, inter-individual variation visually overcomes intra-individual variation (Fig. S1).

#### 2.2.1. Log size index (LSI)

The LSI is a scaling technique that normalizes each measure with a standard measure to create an independent index; it allows obtaining larger sets of data that are comparable, no matter the element from which they come from (Ducos, 1991). It is particularly interesting on fragmented bones, as the normalization allows to compare multiple measurements taken on different skeletal parts or bones presenting various breaking patterns. This index is defined as the natural logarithm of the ratio of the measurement on an archaeological specimen (\(x_i\)) to the same measurement on a comparative specimen (\(M_i\)) (Simpson, 1941 in Meadow, 1999):

\[
\text{LSI} = \log \left( \frac{x_i}{M_i} \right)
\]

In order to obtain an estimation of size for each bone, we averaged all measurements for a same element

\[
\text{LSI}_x = \frac{1}{n} \sum_{i=1}^{n} \log(x_i) - \frac{1}{n} \sum_{i=1}^{n} \log(M_i)
\]

with \(n\) the number of measurements taken on one bone.

The choice of the standard is a rather empirical part of LSI analyses. Indeed, it can be either the measurement of one individual or the mean of a population (Meadow, 1999) and its choice is given to the operator. As nothing preexists for the study of turkeys, three comparative indices were constructed from comparative specimens: (1) the average of the measurements on the four males (st-M); (2) the average of the measurements on the four females (st-F); and (3) the mean of the measurements on the four males and females (st-MF).

### Table 1

<table>
<thead>
<tr>
<th>Site ID</th>
<th>Site name, city, state</th>
<th>Dates of occupation</th>
<th>Number of measured specimens</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mich31</td>
<td>El Malpaís Prieto, Zacapu, Michoacán</td>
<td>Late Postclassic</td>
<td>36</td>
<td>Manin et al. (2015)</td>
</tr>
<tr>
<td>JR74</td>
<td>El Cuizillo del Mezquital, Jerécuaro, Guanajuato</td>
<td>Classic</td>
<td>2</td>
<td>Faugère (2013)</td>
</tr>
<tr>
<td>Cal</td>
<td>Calixtlahuaca, Estado de México</td>
<td>Postclassic</td>
<td>4</td>
<td>Smith (2010)</td>
</tr>
<tr>
<td>VH</td>
<td>Vista Hermosa, Nuevo Morelos, Tamaulipas</td>
<td>Late Postclassic</td>
<td>39</td>
<td>Manin and Lefèvre (in press)</td>
</tr>
</tbody>
</table>

#### Table 2

<table>
<thead>
<tr>
<th>Element</th>
<th>Number of measured specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coracoid</td>
<td>7</td>
</tr>
<tr>
<td>Scapula</td>
<td>13</td>
</tr>
<tr>
<td>Humerus</td>
<td>21</td>
</tr>
<tr>
<td>Radius</td>
<td>5</td>
</tr>
<tr>
<td>Ulna</td>
<td>8</td>
</tr>
<tr>
<td>Carpometacarpus</td>
<td>14</td>
</tr>
<tr>
<td>Femora</td>
<td>26</td>
</tr>
<tr>
<td>Tibiotarsus</td>
<td>20</td>
</tr>
<tr>
<td>Tarsometatarsus</td>
<td>6</td>
</tr>
</tbody>
</table>
measurements of the four females (st-F); and (3) the average of the measurements of all eight individuals (st-T). We calculated the LSI with the three standards so as to choose the one that permits the best discrimination between males and females.

### 2.2.2. Log-shape ratios (LSR)

In order to reduce the importance of size in the analysis of Mesoamerican turkeys, we calculated LSR (Mosimann, 1970). In this way, we expect to detect a sexual dimorphism in shape that ought to be related to metabolic differences between sexes (Badyaev, 2002). LSR have scarcely been used in osteological studies (e.g. Ben Faleh et al., 2013; Calou, 2003; Fabre et al., 2014; Kaufmann and L’Heureux, 2009; but see also Lawrence and Bossert, 1967 for an earlier application) and this study is the first application to zooarchaeological bird bones.

According to Mosimann (1970) and Mosimann and James (1979), from the definition of a size constant (named isometric size, IS), it is then possible to calculate an independent shape matrix. We take as a constant the geometric mean of the measurements \( x_i \) as:

\[
\text{Isometric size (IS)}_n = \frac{1}{n} \sum_{i=1}^{n} \log(x_i)
\]

As a consequence of the IS, Mosimann (1970) defines an independent shape matrix that can be calculated for each measurement \( x_i \) of an element as:

\[
\text{LSR}_i = \log\left(\frac{X_1}{IS} \frac{X_2}{IS} \cdots \frac{X_i}{IS}\right)
\]

To compare the shape residuals (i.e. the elements of the shape matrix), the IS of each individual on a set of identical measurements need to be computed. We evaluated the potential of sex discrimination by LSR for each anatomic part with our set of eight comparative skeletons. A PCA was conducted on the LSR of each element and scores of the two first axes of the PCA were plotted to check for visual differentiation of sexes (Fig. S2). Three elements allow males and females distinction: coracoid, femur and tarsometatarsus. Among them, femur was the most numerous in the archaeological assemblage and therefore it has been chosen to apply LSR for sex identification. We performed LSR on eight reference specimens and 14 archaeological complete femurs from four sites (Cal, Mich31, Tiz and VH), representing at least 13 individuals (MNI calculated on the frequency of left femurs).

### 2.2.3. Gaussian mixtures and other statistical analyses

We explore the structure of both LSI and LSR data without prior knowledge of the number of groups of which they are composed through Gaussian mixtures. The selection of the most probable number of groups and their distributional properties is conducted using maximum likelihood estimations (Fraley and Raftery, 1998). We limit the group estimation to Gaussian distributions as it is the law that fit most with biologic data (Baylac et al., 2003). Gaussian mixtures have perform well in other morphometric studies in identifying size groups (e.g. De Cupere et al., 2005; Dong, 1997; Fernández and Monchot, 2007; Monchot and Léchelle, 2002; Monchot, 1999) as well as groups based on shape (Baylac et al., 2003; Cordeiro-Estrela et al., 2006, 2008).

Gaussian mixtures were performed using the mclust classification algorithm (Fraley and Raftery, 2002; Fraley et al., 2012). Number of groups and group partitions were determined using an expectation-maximization (EM) algorithm for maximum likelihood; the Bayesian information criterion (BIC) is used to determine the model that best fits with the data (see details of the calculation in Fraley and Raftery, 1998). With the EM algorithm, a conditional probability \( z^t \) that each element pertains to each group, given the parameter estimates, was calculated (following Fraley and Raftery, 2003). The element was considered to pertain to the group for which \( z \) is maximal and the uncertainty is calculated as \( 1 - z \). From this value, we estimated the confidence of group attribution with an error threshold of \( \alpha = 5\% \).

To explore the variation of LSI between sites, non-parametric analysis of variance between groups was performed using the Kruskal-Wallis rank sum test, with an error threshold of \( \alpha = 5\% \).

All analyses were conducted with R v3.1.2 (R Core Team, 2014). Log shape ratios were calculated using the “Rmorph” package (Baylac, 2010). The Gaussian model was performed using the “mclust” package (Fraley and Raftery, 2002; Fraley et al., 2012).

In order to test the ability of morphometrics and statistics to distinguish between males and females, each method was first applied on the reference corpus mentioned in Sections 2.1.1 and 2.1.2. In addition, when present in archaeological material, the medullary bone was used as an independent sex indicator.

### 3. Results

#### 3.1. Size analysis

##### 3.1.1. Sex discrimination on bibliographic data

LSI were calculated on published turkey bone measurements (Speller, 2009) using the three standards presented in Section 2.2.2. When applied on this corpus, the Gaussian model permits to distinguish two groups of normal distribution and equal variance (Fig. 2). These two groups correspond to actual males and females with a misclassification of three to nine individuals on the 119, which represents an error rate of 2.5% to 7.6%. It means that the three standards are able to distinguish males and females with an acceptable error. The results of LSI for each standard and misclassification are presented in Table S5.

![Fig. 2. Gaussian mixture models performed on LSI based on bibliographical data (Speller, 2009) for the three different standards. Plain red line = mixture analysis group 1; dashed blue line = mixture analysis group 2; black dots = uncertainty. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)](http://dx.doi.org/10.1016/j.jasrep.2016.05.066)
3.1.2. Sex discrimination on archaeological material

The calculation of LSI on Mesoamerican archaeological material (Table 1) using the three standards was equally plotted with histograms and show a similar distribution. However, even if the Gaussian mixture analyses detect two groups in all cases, st-F and st-T lead to a complete overlap between group 1 and group 2 (Fig. 3). We thus decided to work with St-M, in order to enhance the significance of the results, but it shows that the choice of the standard is not tripping when working with LSI. Of the 120 bones analyzed, 107 fall in the smallest category, group 1, and 13 in the largest category, group 2. As indicated by the bibliographic data (Section 3.1.1), the smallest size group corresponds to females and the largest size group corresponds to males. We can thus consider here that group 1 corresponds to female Mesoamerican turkey and group 2 corresponds to male Mesoamerican turkey. We estimated the general sex repartition of our total assemblage using the most abundant unique skeletal part (left femur) and obtain a sex-ratio of 7.5 females per one male. The results of LSI and Gaussian mixture analyses for each element are given in Table S6.

However, the size of the remains does not differ significantly in the three sites that yielded the most abundant material, Mich31, Tiz and VH (Fig. 4; Kruskal-Wallis rank sum test, $\chi^2 = 4.444$, df = 2, p-value = 0.1084) and it can suggest that sex-ratio is not substantially different between these sites. Nonetheless the number of individuals in each site is small (one to six) and the calculation of sex-ratio per site would not be relevant on such small samples.

3.2. Femur shape variability

LSR analysis has been performed on eight reference femurs and 14 archaeological femurs from Mesoamerican sites (see the sites in Section 2.1.3). LSR variation was observed using a PCA (Fig. 5): the first two axes represent 92.8% of the variation. Gaussian mixture applied on the first two axes of the PCA shows the presence of two groups. The first one assembles all the reference males and an archaeological femur from Cal. The second one puts together all the reference females and the other archaeological femurs. All group attributions are with great confidence (uncertainty $<$ 0.001). Consequently, we argue that the archaeological specimens grouped with male references are males, and that the archaeological specimens grouped with females are females. Using left femur, we obtain a sex-ratio of 12 females per one male. However, the number of archaeological bones used in this analysis is too small to allow a comparison between sites.

3.3. Correspondence between size, shape and medullary bone

The only femur attributed to male by shape (uncertainty = 0.014) was also attributed to male on the basis of size (uncertainty = 0.047). Another one did not lead to a significant sex attribution based on size (uncertainty = 0.326) and was grouped with females on the basis of shape (uncertainty $<$ 0.001). We were able to observe medullary bone in one femur (ID = FemGPr06; Table S6), that was significantly...
attributed to female on the basis of size (uncertainty < 0.001) and shape (uncertainty < 0.001).

4. Discussion

Our analyses on LSI show that Gaussian mixture allows to discriminate two groups: one of smaller-sized individuals corresponding to females, and one of larger-sized individuals corresponding to males (Fig. 2). Using published data, we argue that this method is accurate to determine the sex of individuals, with a minor error range (2.5% to 7.6%). When we apply this model on archaeological unsexed material, we obtain a sex ratio of 7.5 females (using size data) to 12 females per one male using femur size, 12 females per one male using femur shape). Besides, presence of medullary bone in one of the femurs examined in our study indicates that nesting hens might have been slaughtered too. Moreover, if males were slain before they got their first adult plumage (before 15 weeks according to Latham, 1956, p. 19; Leopold, 1943; Schorger, 1966, pp. 290–291), their most brilliant and colorful feathers could not have been exploited. Indeed, the joint analysis of adult and young turkey bones is essential to further the interpretation of demographic structure and improve the understanding of past Mesoamerican turkey husbandry. We also show that there is no significant size difference between turkey populations from western, central and eastern Mexico, even if one site (VH) is located in the lowlands while the two other (Mich31 and Tiz) are located in the central highlands.

In the case of our study, the absence of significant variation between populations of such different environments as central and coastal Mexico shows that morphological variation might not be as dependent to environmental conditions as proposed by Senior and Pierce (1989), and size variation could have been emphasized by herding practices as mentioned by Speller (2009, p. 132). It could also indicate population mixing between these two areas of Mesoamerica, leading to size homogeneity.

5. Conclusion

This study gives a first insight of the potential of morphometrics-based studies in the investigation of sex-ratio and demographic structure of turkeys in pre-Columbian Mesoamerica. LSI data are supported by a large sample but shape ratios suffer from a reference collection too small to strongly support the results. The results obtained through this study are yet encouraging. A further step will be to increase the reference sample in order to strengthen this preliminary approach. Geometric morphometrics could also be applied on femurs, in order to better understand the morpho-functional meaning of the variations observed between males and females and perhaps recognize other morphological traits susceptible to improve the understanding of past turkey husbandry.

Acknowledgement

We wish to thank J.C. Equihua, B. Faugère, G. Pereira, M.E. Smith and C. Stresser-Pêan who enabled us to study the faunal remains from the archaeological projects they supervise and who supply us all the needed information about contexts. We also thank F. Lanoë for his valuable comments and his help in English proof-reading. Finally, we acknowledge the two anonymous reviewers who contributed to improve this paper with their comments.
Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jasrep.2016.05.066.

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