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The number of pores per area of eggshells is not always a reliable indicator of *Rheidae* species

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RESUMEN: Desde finales de Pleistoceno hasta el Holoceno tardío, huesos y abundantes cáscaras de huevos atestiguan la explotación de los *Rheidae* de las regiones Pampeana y Chaqueña (ñandú, *Rhea americana*) y la Patagonia Argentina (choique, *R. pennata*) por parte de las poblaciones indígenas. El conteo de poros en una determinada área de la cáscara, esto es, la densidad, ha sido método tradicionalmente utilizado para identificar la especie. En el presente trabajo, utilizando un nuevo método que facilita el conteo, evaluamos la fiabilidad de dicho procedimiento sobre una amplia muestra. Confirmando lo ya publicado, comprobamos que las cáscaras de ñandú tienen una densidad de poros superior a la del choique. Sin embargo, la variabilidad en la densidad de poros en ambas especies, e incluso dentro de sectores de un mismo huevo, puede dar lugar a identificaciones erróneas. Esto se produce cuando el número de poros por cm^2 se ubica próximo a los valores más bajos de las cáscaras de ñandú o a los más altos de las del choique. En general, parece ser más frecuente el considerar erróneamente un fragmento de cáscara de ñandú como perteneciente al choique que a la inversa. La probabilidad de cometer dicho error depende de la ubicación del fragmento en la cáscara ya que, al parecer, el método no verificó en su momento la totalidad de los rangos de densidad de poros en cada especie. Nuestros resultados muestran que la identificación de fragmentos basada en el método original no sería tan fiable como la que aquí proponemos y que su precisión, en cualquier caso, merecería ser corroborada exhaustivamente, utilizando muestras mayores y procedentes de un espectro más amplio de poblaciones de ambas especies.

PALABRAS CLAVE: ARQUEOZOOLOGÍA, CÁSCARAS DE HUEVO, RHEIDAE, POROS, DETERMINACIÓN DE ESPECIES

ABSTRACT: From the end of the Pleistocene and up until the late Holocene, bones and abundant eggshell fragments testify to the hunting by the indigenous people of *Rheidae* in the Pampas and Chaco regions (greater rhea, *Rhea americana*), and in the Argentinian Patagonia (lesser/Darwin´s rhea, *R.pennata*). The traditional method to set apart eggshell fragments from these two species consisted in counting the number pores on a given area to estimate their density. In this paper we evaluate the validity of this method with a new protocol to facilitate counting and assess its reliability on a large eggshell sample. As has been repeatedly proved, the greater rhea has a larger pore density than the lesser rhea. However, the variability of this density within each species, and even within the same egg, needs to be considered as this may lead to erroneous identification. More so when the number of pores per cm^2 falls in the lowest range of the greater rhea or the highest range of the lesser rhea. In general, it is easier to misidentify a greater rhea

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eggshell fragment for that of the lesser rhea than the other way around. The possibility of misidentification also depends on the area of the shell that is being analyzed, since the original method did not apparently assess the density of pores in different areas of the same egg for each species. Although our results indicate that identification based on the original method is not as reliable as the one we propose here, a reappraisal of it with larger samples deriving from a larger specter of populations from both species would be recommendable.

KEYWORDS: ARCHAEOZOOLOGY, EGGSHELLS, RHEIDAE, PORES, SPECIES DETERMINATION

INTRODUCTION

The use by humans of two of the *Rheidae* species present in the Pampas and the Chaco regions (*Rhea americana*), and in the Patagonia (*Rhea* -formerly *Pterocnemia- pennata*) of Argentina has been recorded in different archaeological sites dated from Late Pleistocene to the end of late Holocene. Human food refuses, such as bones and, especially, abundant fragments of eggshells are frequent in that period (Medina *et al*., 2011 a, b).

Unambiguous taxonomic identification of a sample of archaeological eggshells at the species level rather than at the family level is of archaeozoological and paleobiogeographic interest (Medina *et al*., 2011b), particularly among species that have macroscopically very similar eggs. The geographic location of an archaeological site could be taken as a first indicator of the probable rhea species to which a sample belongs, given that the overlap in the present distribution range of these ratite birds occurs only in NE Patagonia (Handford & Mares, 1982) or does not occur at all (Birdlife International, 2016, 2018) (Figure 1). However, a more precise assignment of rhea eggshells is essential because the large and robust eggs of these birds could have been easily preserved and transported long distances either whole as a fresh or cooked food resource, or broken as like-containers, and could have even constituted objects for supra-domestic social interaction and trade (Medina *et al*., 2011a, b). Also, climatic changes during late Pleistocene and early Holocene could have led to chorological changes in *Rheidae* populations (Tambussi & Acosta Hospitaleche, 2002), so fragments of eggs belonging to both ratite species could be present outside their current range.

The geographic distribution of these two birds is primarily conditioned by climatic factors: the greater rhea is present in a much more humid region than that of the lesser rhea (Tambussi & Acosta

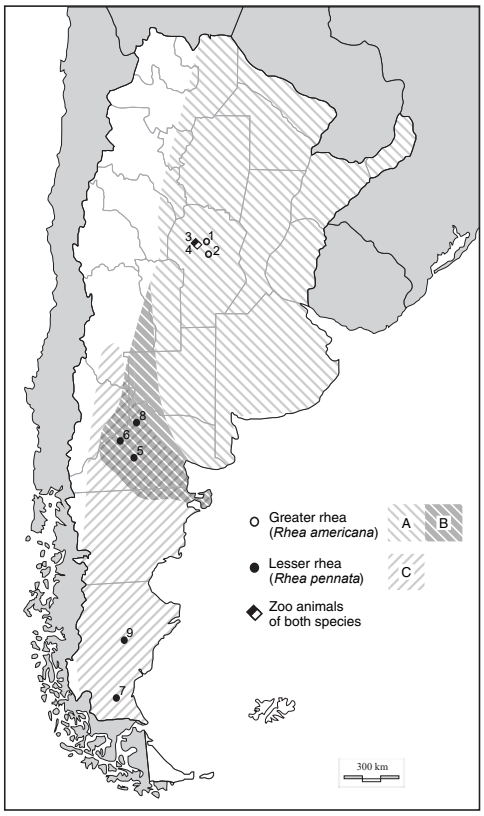

FIGURE 1

Map showing the present distribution of the greater rhea (*Rhea americana*) (A) in Argentina according to Birdlife International (2016), the extended region (B) for this species *sensu* Handford & Mares (1982), and the range of the lesser rhea (*Rhea pennata*) (C) stated by Birdlife International (2018). The geographic locations of the nine sites from where the eggshells of both species proceeded are also indicated.

Hospitaleche, 2002). In all avian species, the eggshell characteristics should have evolved via several different changes to match the surrounding environmental conditions (Tullett & Board, 1977; Tullett, 1978; Grellet-Tinner, 2006). The specific adaptive variation in eggshell structure may thus be useful as a way of discriminating to which species an egg or a shell fragment belongs. The pore density is one of the architectural traits of the eggshell that has probably evolved to adapt *Rheidae* species to climates with such differences in potentials of water evaporation. Following this hypothesis, Apolinaire & Turnes (2010) explored the possibility of using pore counts as a highly reliable method for determining to species level the eggshell fragments found in archaeological sites. These authors found that the eggshell of the lesser rhea presents lower pore density than that of the greater rhea. As a result, they proposed a non-invasive method for assigning eggshell fragments to the correspondent rhea species, based on the assessment of the pore density through a systematic quantification of pores in the surface of the shell. Their method was adopted later in several archaeological works (Bonomo *et al*., 2008; Medina *et al*., 2011 a, b; Caracotche *et al*., 2017; Mange *et al*., 2018).

Notwithstanding their thorough analyses, Apolinaire and Turnes did not mention that in rhea eggshells there are dimples and, which is more critical, pore depressions that may contain one or two (rarely three) pore mouths (as stated by Tyler & Simkiss, 1959; Board *et al*., 1977) (Figure 2), and that those pore depressions with more than one pore mouth are elongated. Apolinaire & Turnes (2010) did not detail this issue in their paper, and as they did not discriminate between single and double-mouthed pores in their method, the latter were added as one pore to the total count, to avoid overcounting (L. Turnes, *in lit*.). Additionally, our previous preliminary observations on eggs of both rhea species lead us to speculate that, as found in another ratite bird (Koyama & Tenysson, 2016) a non-negligible variation in the eggshell architecture may exist among and within rhea populations of the same species, and even among different portions of the same egg. Thus, if full variation in pore density of these two closely related species overlaps to some degree, it may lead to incorrect determination of shell fragments, even more so if fragmented shells came from unidentified portions of the egg.

Given that reliable identification of eggshells of each species among *Rheidae* is essential for several disciplines and purposes, the variability in their porosity deserves to be more exhaustively assessed to reach conclusive determinations. In this work, we explore the likelihood of having correctly or incorrectly assigned eggs and eggshell fragments from different sites to the greater rhea and the lesser rhea, based on the number of pores per area. Unlike Apolinaire & Turnes (2010), we here used a destructive method, addressing the two recognised types of pores, in different portions of the eggshells.

MATERIALS AND METHODS

Eggshell samples

We examined eggshells from 53 greater rhea eggs and 21 lesser rhea eggs collected during the 2001/2002 reproductive season. The former ones

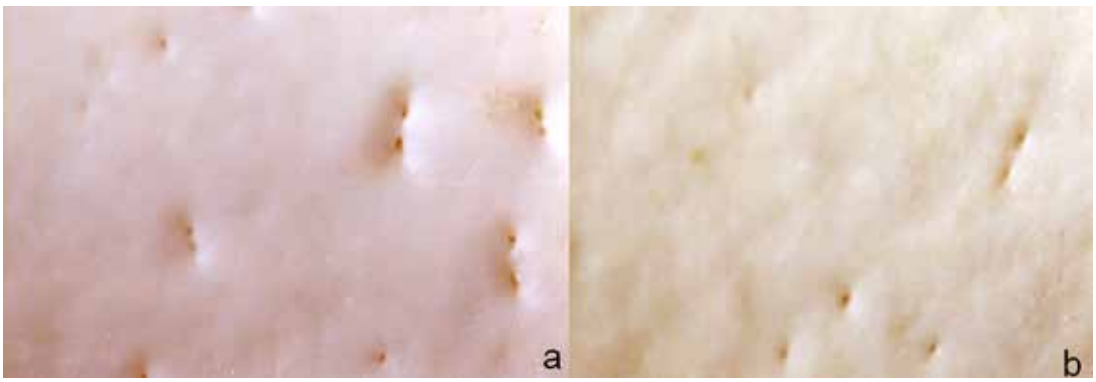

FIGURE 2

Magnified view of the untreated surface of eggshells of (a) greater rhea (*Rhea americana*) at 4x, and (b) lesser rhea (*Rhea pennata*) at 2.5x, in which single and double-mouthed pores, and dimples are easily distinguished.

were obtained from three captive populations: Repsol-YPF, close to Montecristo (site 1, n = 31), Cargill, close to Pilar (site 2, n = 11), and the Córdoba city Zoo (site 3, n = 11), all located less than 50 km from the city of Córdoba, Argentina (Figure 1). The birds that compose these captive stocks came from wild populations of central Argentina, and may have some degree of genetic relatedness, as a few individuals were exchanged between the Zoo and the other two captive populations in the past. The lesser rhea eggs were infertile eggs from five captive populations and an abandoned incomplete clutch in the wild. The former samples were from the Córdoba city Zoo (site 4, n = 6), three farms in Río Negro province (Choique Malal, close to Los Menucos, site 5, n = 1; Choique Hué, close to Lonco Vaca, site 6, n = 3; Choique Ruca, in General Roca, site 8, n = 2), and one farm in the south of Santa Cruz province (La Carolina, site 7, n= 2), whereas the wild clutch (site 9, n = 7) was also collected in central Santa Cruz (Figure 1). The reproductive stocks in Río Negro and the Zoo share some degree of genetic relatedness because part of the former birds come from complete wild clutches collected in neighbouring ranches and incubated at the Estación Experimental Agropecuaria Bariloche of Instituto Nacional de Tecnología Agropecuaria (Río Negro), and the birds at the Córdoba Zoo came from one of the farms in Río Negro (Choique Malal). On the other hand, the stock of the farm in Santa Cruz came from eggs legally collected from the wild in the vicinities of the farm, and no genetic relatedness with the stocks in Río Negro and the sampled wild clutch can be suspected, given that these sites are separated by a vast distance (Figure 1). All these populations constituted the first generation of rheas bred under captive conditions and given their high genetic similarity with wild animals (Alonso Roldán *et al*., 2010), there is no basis for assuming that porosity of their eggs has been influenced in any way by farming.

Each egg was individually identified with a code written in pencil in the shell and measured with a Vernier caliper. Three portions of equal length, corresponding to the acute pole, equator, and blunt pole, were marked in the shell of each egg.

The greater rhea eggs were artificially incubated and when near hatching, each one was transferred to a separate compartment in a hatcher. Upon hatching or after maximum incubation period had elapsed, each complete eggshell or its large remaining pieces were obtained and classified based on the corresponding portion of the egg.

The eggshells of both species received the same treatment, as follows: large pieces from the three identified portions of each eggshell were separated and carefully broken, to obtain smaller fragments with a diameter > 6.5 mm (approximate size of the visual field of the microscope used for counting the pores). Twelve of those fragments were taken at random from each of the three portions of each egg (i.e. 36 fragments per egg), and were washed, dried and then dropped into a boiling solution of sodium hydroxide 5%, where they were kept for 5 min to remove membranes and the plugs of protein that fill up the pores (Tyler & Geake, 1953). Later the fragments were washed in tap water, dried, immersed in concentrated nitric acid for 10 sec for removing the pore clogs composed of amorphous waxy material (Board *et al*., 1977) and for enlarging the pore diameters to facilitate the counting process and then were washed with water again (Tyler, 1953).

We placed each fragment in a Bausch & Lomb binocular StereoZoom microscope at 3x and counted the pores within one fixed visual field (0.336 cm^2). In total, the twelve fragments represented an area of 4.03 cm^2, which represents four times the minimum area recommended by Tyler (1953) to obtain a reliable determination of pore density.

Two types of pores were separately counted: single and double-mouthed (as defined by Tyler & Simkiss, 1959) (Figure 2). The number of pores of each type (where each double-mouthed pore accounted as one pore) and their sum were converted in density (number per cm^2) for the twelve fragments from each portion, and then we obtained the respective average density of each pore type for each of the three portions of an eggshell.

Statistical Analysis

We used linear mixed-effects (LME) models to determine differences in mean porosity between the two species. We built separate models for each pore type (single-mouthed, double-mouthed and total). Each model included the species as the fixed effect. Because we had three samples per egg (corresponding to different portions), we considered egg as a random effect in each model. Data were analysed using the lmer procedure (Bates *et al*., 2015) in the statistical platform R ver. 3.4.1 (R Core Team, 2017).

Even if there are significant differences in the mean porosity between species, it does not mean that a given eggshell fragment will be correctly classified as belonging to one of the two species. In that sense, it is better to apply a classifier on data and then assess the accuracy of the classification. We used the method proposed by Apolinaire & Turnes (2010) with the two critical cutoff thresholds they suggested, so eggshells with a pore density ≤ 65 or ≤ 70 pores per cm^2 were classified as belonging to lesser rhea, while the rest, with higher pore densities, were considered greater rhea. Afterwards, we calculated the threshold that provides the "best" classification of our fragments, taking into account that one can know, or not, to which portion of the egg a given fragment belongs.

The classification was evaluated based on sensitivity and specificity metrics for determining the correct species without considering the site from where the eggs came. In this case, sensitivity represents the proportion of lesser rhea eggshells that are correctly identified as such, whereas specificity represents the fraction of greater rhea eggs correctly recognised.

RESULTS AND DISCUSSION

Fragments of greater and lesser rhea eggshells appeared indistinguishable if only the density of single-mouthed pores was taken into account. However, the densities of double- mouthed and total pores seem to show greater differences between species (Figure 3).

LME models show significant differences between species in the average density of double-mouthed ($F_{1, 5.32}$ = 11.64; p=0.02) and total pores ($F_{1, 5.3}$ = 12.2; p=0.02). Eggshells of greater rheas show a higher and more variable pore density than those of lesser rheas. On the other hand, the average density of single-mouthed pores does not differ between both species ($F_{1, 5.16}$ = 4.81; p=0.08).

Although the eggshells of greater rhea eggs, as expected and previously published, have on average a higher total pore density than those of lesser rheas, the comparatively high variability of this measure in both species, as we show below, can jeopardise a precise classification of some fragments. In this sense, substantial overlap in total pore density occurs in the interval from 20 to 54 pores per cm^2 (Table 1).

	Lesser rhea *(Rhea pennata)*	Greater rhea *(Rhea americana)*
n (eggs)	21	53
Minimum	1.49	4.46
5%	5.46	20.34
1st Quartile	17.86	31.75
Mean	28.78	51.24
Median	28.52	45.14
3rd Quartile	40.67	65.97
95%	51.98	100.89
Maximum	69.94	170.63
SD	15.20	26.61

TABLE 1

Descriptive statistics of total pore density per cm^2 for each rhea species.

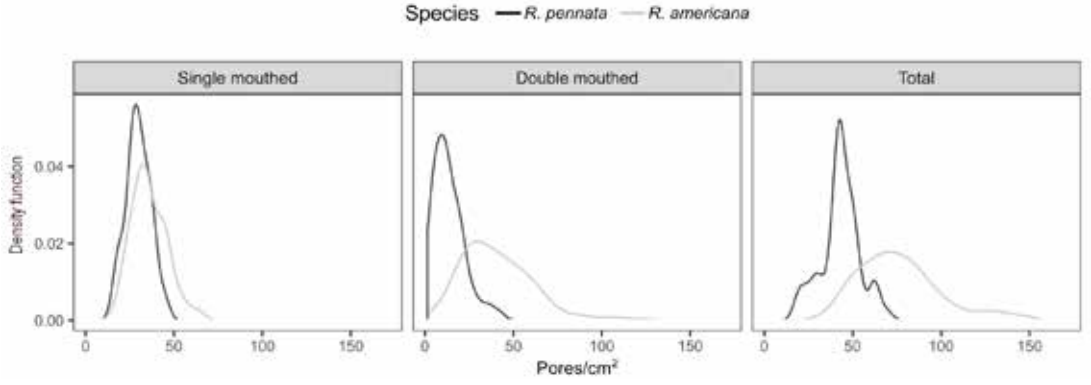

FIGURE 3

Density plot comparing the kernel smoothed distribution of the number of pores per cm^2 for greater rhea (*Rhea americana*) (light grey) and lesser rhea (*Rhea pennata*) (dark grey).

Eggshell fragments of lesser rhea were correctly identified by Apolinaire & Turnes (2010) method with the critical threshold fixed at ≤ 65 pores per cm^2 in 98.4% of the cases (high sensitivity), whereas those of greater rhea were correctly identified in only 66.4% of the samples (medium specificity). Here the classification of greater rhea eggshells was more accurate when fragments came from the blunt pole (75.0% correct) than from the acute pole (61.7%), or the equator (62.5%). When the threshold density was raised to 70 pores per cm^2, all lesser rhea fragments, independently of the portion of the eggs where they came from, were correctly classified (sensitivity becomes perfect), but specificity decreased to almost 57% on average, in this case with the best value in fragments from the equator (60%).

The "best" critical threshold of total pore density we calculated for our data, i.e. the one that maximises sensibility and specificity, was 54.31. This value is a lower cutoff than both ones presented by Apolinaire & Turnes (2010), and although it has a lower average sensitivity (88.9%), its specificity is higher (83.2%) than that obtained with the thresholds proposed by these authors. Sensitivity was higher for fragments from the equator portion of the eggshell (95.2%) than for those from the acute or the blunt pole (both 85.7%), whereas specificity was higher when fragments were from the blunt pole (87.5%) than from the equator portion or the acute pole (81.3% and 80.9%, respectively). It is relevant to mention that our critical threshold would have had more reduced accuracy if used for the classification of data of Apolinaire and Turnes, compared to the values they suggested.

CONCLUSIONS

Our results show differences with those of Apolinaire & Turnes (2010) that may have important implications for the correct taxonomic determination of the *Rheidae* species to which eggshell fragments sampled in an archaeological site belong. We found that the greater rhea could produce eggshells with comparatively low pore densities, which are very close and even overlap with the highest values of pore densities observed in lesser rhea eggshells. Therefore, the use of density of total pores (calculated without distinguishing single and double-mouthed pores) or of double-mouthed pores on such eggshell fragments or eggs for taxonomic determination of *Rheidae* species should be applied with caution and must not be taken as conclusive, as it can lead to misleading classifications. When one deals with intermediate total pore densities within this avian group, the most frequent error will happen by mistakenly identifying a fragment of eggshell as belonging to a lesser rhea egg, when it is actually of greater rhea, but the converse error can also occur. The probability of an erroneous classification may be very high in some cases, depending on the fragment's original position at the eggshell. For most portions of the eggs in several of our samples, the error could only be slightly lower than if the species was assigned by tossing a coin.

It should be stressed that a direct comparison of our results with those of Apolinaire & Turnes (2010) should be made cautiously as the methods applied for distinguishing the pores were very different, the pores were not equally classified, the sample sizes differed, and because those authors did not detail precisely the populations from which their eggs came. However, our present work points out some possible flaws in the method most commonly used for the determination of the *Rheidae* species to which whole eggs, fragments or their remains found in archaeological sites belong.

The strength of our work is based on several aspects: these authors did not address the double-mouthed pores as we did, and they averaged just under 4 fields per egg for 17 greater rhea eggs, and 5 fields per egg for 13 lesser rhea eggs. In our case, the sample size was larger, as we counted 12 fragments (fields) from each of three portions of each egg, this is 36 fragments per egg, with 53 eggs of greater rhea and 21 of lesser rhea. Another aspect to take into account is the fact that although these authors mention the geographical sites where their eggs came from, unlike us, they did not give a clear idea of how many different populations were involved in the samples of most sites or the degree of relationship that may exist among them. As found by Koyama & Tenysson (2016) in the ostrich, intra and inter-population variability may account for some eggshell architecture similarities among different populations. Apolinaire & Turnes (2010) may not have fully detected all the spectrum of possible pore densities in the two *Rhea* species.

In summary, we think that at least our work shows that the classification of eggshell fragments of *Rheidae* eggs is not as straightforward as pro-

posed by Apolinaire and Turnes, and the reliability of their non-destructive method deserves to be corroborated using a larger sample size belonging to a broader spectrum of populations of both *Rhea* species. In this way, those branches of science or even other activities such as law enforcement, which require taxonomic accuracy in these type of determinations will benefit.

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