

Datasets of egg parameters of long-lived bird species, the white stork *Ciconia ciconia*

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Abstract

Egg traits are central to avian reproductive investment and may reflect environmental conditions experienced during breeding, migration, and wintering. However, standardized long-term datasets of individual egg measurements remain scarce. Here, we compile and describe two datasets for the white stork *Ciconia ciconia*, integrating egg morphology, i.e. clutch size, eggshell thickness, and chemical composition across broad spatial and temporal scales. The first dataset contains 8,785 individual egg measurements from 2,137 clutches collected at 11 study sites in Algeria, Germany, the historical region of Macedonia, Poland, and Spain. It includes egg length, breadth, estimated volume, clutch identity, breeding year, nest identity and site metadata. Clutch size and egg dimensions differed among study sites: Polish populations generally had larger clutches and broader, higher-volume eggs than populations in Spain and Algeria, although egg length showed the opposite pattern. The second dataset comprises eggshell-thickness measurements and concentrations of 17 macro- and trace elements in eggshells and internal egg contents from 190 unhatched or post-hatch eggs collected at four Polish study sites. Eggshell thickness was measured in four longitudinal regions and was greatest at the equator and lowest at the blunt pole. Element concentrations varied among regions of eggshells, and compartments of egg contents (albumen, yolk, mixed contents and embryos). Together, these datasets provide a harmonized resource for investigating spatial and temporal variation in white stork reproductive traits, environmental exposure, and population ecology, and can be combined with climatic, land-use, migration and population-trend data for ecological, evolutionary, and conservation research.

Background & Summary

Egg dimensions are a key component of avian life-history strategies, closely linked to body size, reproductive investment, and environmental conditions during breeding and non-breeding periods [1–3]. Avian eggs are unique in vertebrate reproduction in that they exchange only gases (O_2 , CO_2 , and water vapor) but not solids or liquids with their environment [4]. At the time of egg laying, all the nutrients, water, and ions for the embryo development to hatching are contained in the egg. Because the embryo must be able not only to maintain it self throughout embryonic life but also to complete development to hatching with only the nutrients contained in the egg [4]. Recently, avian reproduction has been recognized as particularly sensitive to environmental changes driven by global climate change [5]. Consequently, long-term datasets on bird reproductive performance are of critical importance. Migratory species, owing to their extensive annual movements across regions and continents, experience reproductive outcomes influenced by multiple environmental factors operating at different stages of their annual cycle [6–8]. As large-bodied, long-distance migratory birds are known as capital breeders, i.e. females accumulate substates for egg production prior to the breeding season, both on the wintering grounds and during migration [9–11], long-term data on egg dimensions and clutch size are crucial for understanding the effects of climate change on their reproduction. While large, harmonized datasets describing avian distributions, environmental variables and body measurements are increasingly available, individual-level datasets on egg dimensions remain relatively rare and fragmented, even for

species with long-term monitoring data. This limits the potential to investigate how variation in egg traits relates to spatial and temporal environmental gradients or to population trends in species with complex annual cycles.

White stork *Ciconia ciconia* is an example of bird strongly related to human presence and activity, whose close connectivity to human settlements is known since at least 4000 years [12]. Thus, it is one of the most intensively monitored bird species worldwide [13]. In some regions it acts as an indicator of changes in agricultural landscapes [14, 15], whereas in other parts of the species range it is strongly associated with urban environments, often relying on anthropogenic food sources and increasingly exploiting municipal waste disposal sites [16, 17].

Besides a vast collection of studies on migration [18], physiology [19], microbiology [20], and breeding biology [21] of this species, multiple researches considering breeding ecology have focused mainly on hatching and fledgling success, phenology, or survival [2, 22–27], whereas egg traits such as length, breadth and volume have only rarely been compiled into unified, multi-year and multi-regional datasets [2, 21, 28]. As a result, despite a long tradition of field studies on this emblematic species in many countries, open, standardized data resources on white stork egg morphology remain scarce and scattered.

Over at least the last three decades, white stork population has been increasing across much of its range [29]. However, while in Western European and North African countries, particularly Spain and Algeria the populations have increased substantially [17], in some Central-Eastern European countries it is stable or even declining. As a result, population trends differ markedly among regions. Although Poland and Spain are among the main strongholds of the white stork [29] the populations differ markedly not only in their demographic trends [17, 30], but also in the extent to which they exploit landfills. The Spanish population relies strongly on landfill-derived food resources [17, 31–33], whereas landfill use in the Polish population appears to more occasional, although some local populations have gradually shifted to nesting sites closer to waste disposal sites [34, 35]. Algerian population of the white stork is also known from exploiting landfills as a source of organic wastes, and the effects of these anthropogenic food sources have been reported as positive for reproduction [36–38].

Hence, these five geographically distant populations of the white stork, differing in ecology and migratory behavior, are exposed to contrasting conditions during both breeding and non-breeding periods [18]. Clutch size and egg dimensions are known to vary geographically and temporally in response to environmental conditions and resource availability, making them key reproductive traits for studying population differences [39–42]. Combining egg measurements collected across multiple locations and years in these distinct populations therefore provides a unique basis for investigating geographic, environmental and temporal variation in reproductive traits [5]. When assessing population change, it is important to consider not only the number of breeding pairs and fledged offspring but also other breeding parameters, such as clutch size and egg volume, as well as how these change over time, as these have been shown to depend on environmental conditions during the non-breeding period [2].

While measurements of clutch size and egg dimensions provide valuable information on reproductive investment, they do not reveal how resources and potential contaminants are partitioned into the egg. The chemical composition of egg contents and shell, such as macro and trace elements, can reflect both maternal condition and exposure to environmental stressors, making eggs useful bioindicators of habitat quality and pollution [43, 44], but also condition of studied population [45]. Therefore, complementing morphological data with chemical analyses of eggs, or at least with robust proxies of their compositions, is crucial for understanding how environmental conditions and anthropogenic pressure shape reproductive investment and offspring quality in these populations.

Here, we present a standardised datasets of individual egg measurements of the white stork collected across several regions in Algeria, Germany, historical region of Macedonia, Poland, and Spain during short- and long-term field studies. The samples cover different periods, i.e. four collections are historical data, 1938–1961 from historical region of Macedonia, 1924–1972 from Germany, two collections from Poland spanning from 1968 to 2002, and two collections from Spain recorded in 1990, with several more recent data from Algeria (2002–2004), Poland (2003–2026), and Spain (2003–2024) (Fig. 8, Table 1). In total, first dataset includes measurements of 8785 egg lengths and breadths, derived volume estimates and associated metadata on nest location, breeding season, and study site. It is formatted to facilitate reuse in comparative analyses, e.g., in combination with global trait databases, population-trend estimates and environmental layers at local and regional scales. Second dataset consists of results of eggshell thickness and chemical analyses of 190 white stork eggs collected on four study locations across Poland. Datasets contains measurements of concentration of 17 chemical elements (Al, As, Ca, Cd, Co, Cr, Cu, Fe, Hg, K, Mg, Mn, Na, Ni, Pb, Se, Sr) in eggshells and egg contents.

We provide summary statistics, and visualisations describing the structure and variability of the datasets, as well as basic quality-control assessments, to support robust reuse of these data in future ecological, evolutionary and conservation studies.

Egg dimensions

As the comparisons of egg dimensions and clutch sizes describe the available samples, which differ in temporal coverage, we are not interpreting them as purely geographical differences. Clutch sizes (number of eggs in a clutch) differed significantly between study sites (K-W $\chi^2 = 39.4$, $df = 10$, $p < 0.0001$, $n = 2137$ clutches). In general, storks from Polish populations laid more eggs in a clutch than in Spain and Algeria (except one population in Southern Cordoba in Spain). Eggs laid by storks from Polish populations were also bigger in volume (K-W $\chi^2 = 101.81$, $df = 10$, $p < 0.0001$, $n = 2123$ clutches) and broader (K-W $\chi^2 = 353.97$, $df = 10$, $p < 0.0001$, $n = 2123$ clutches) but shorter (K-W $\chi^2 = 140.69$, $df = 10$, $p < 0.0001$, $n = 2123$ clutches). Detailed descriptive statistics are included in the Table 1, and distributions of these parameters are visualized in Figs. 1,2,3, and 4.

Table 1. Summary of data on egg measurements collected over 11 study areas. Values for clutch size (number of laid egg in a clutch), length (mm), breadth (mm), and external volume (cm³) are expressed as means ± se (n).

Eggshell thickness

Out of 190 collected eggshells, due to technical constraints we measured thickness of 143 of those, however for summaries and descriptive statistics calculations only egg with measurements of all 4 eggshell regions were used – 138 eggs. The thickness varied from 0.271 to 0.773 mm. On average eggshell was the thickest on equator (0.520 mm) and the thinnest on blunt pole (0.484 mm). Differences were statistically significant (Friedmann test = 100.6, $p < 0.001$). Details are collected in Table 2, and graphically presented in Fig. 5.

Table 2
White stork eggshell thickness with inner membrane attached (mm) of four egg regions. Summary contains only eggs where all four measurements were performed (n = 138).

region	mean ± se	range
Sharp pole	0.497 ± 0.005	0.271–0.723
Equator	0.520 ± 0.004	0.335–0.680
Shoulder	0.507 ± 0.004	0.393–0.770
Blunt pole	0.484 ± 0.005	0.345–0.773

Chemical elements and their concentrations in eggshells

Due to some damages in eggshells, and therefore limited material for chemical analyses out of 190 collected eggs we performed analyses for 141 eggs, however for some elements the sample size is even lower due to processing constraints (e.g. level of detection). Concentration of chemical elements varied substantially over the areas of eggs. These data has been extensively analyzed and published by Orłowski et al., (2019). Here we present only descriptive summaries (Table 3) and graphical presentation (Fig. 6).

Table 3

Concentrations of 17 elements (ppm dry weight, average $\pm$ se; number of samples where the element was measured above the detection limit; [range]) in eggshells without inner membranes of white stork eggs ($n = 141$ eggs) pooled across all specimens and split by eggshell areas.

Element	Sharp pole	Equator	Shoulder	Blunt pole
Al	8.015 $\pm$ 1.734 (90)	9.364 $\pm$ 1.844 (89)	7.883 $\pm$ 1.746 (86)	4.720 $\pm$ 1.270 (87)
	[0.017–119.000]	[0.021–91.600]	[0.016–98.100]	[0.009–98.100]
As	0.028 $\pm$ 0.001 (140)	0.028 $\pm$ 0.001 (141)	0.028 $\pm$ 0.001 (139)	0.026 $\pm$ 0.001 (139)
	[0.010–0.078]	[0.010–0.070]	[0.012–0.072]	[0.010–0.065]
Ca	221775.573 $\pm$ 3006.689 (140)	217575.887 $\pm$ 3126.904 (141)	218159.717 $\pm$ 3152.888 (139)	214722.618 $\pm$ 3594.733 (139)
	[95713.956–313333.333]	[92900.000–315666.667]	[94626.298–313000.000]	[49100.000–312410.611]
Cd	0.018 $\pm$ 0.004 (7)	0.023 $\pm$ 0.002 (81)	0.026 $\pm$ 0.006 (9)	0.020 $\pm$ 0.006 (11)
	[0.008–0.039]	[0.006–0.151]	[0.007–0.052]	[0.006–0.064]
Co	0.040 $\pm$ 0.001 (140)	0.039 $\pm$ 0.001 (141)	0.040 $\pm$ 0.001 (139)	0.057 $\pm$ 0.001 (139)
	[0.012–0.086]	[0.013–0.065]	[0.014–0.066]	[0.013–0.100]
Cr	0.014 $\pm$ 0.001 (105)	0.023 $\pm$ 0.002 (129)	0.013 $\pm$ 0.001 (89)	0.012 $\pm$ 0.001 (80)
	[0.005–0.068]	[0.006–0.106]	[0.005–0.090]	[0.005–0.092]
Cu	0.490 $\pm$ 0.157 (7)	0.392 $\pm$ 0.063 (6)	0.443 $\pm$ 0.120 (5)	0.360 $\pm$ 0.091 (6)
	[0.211–1.407]	[0.214–0.541]	[0.251–0.864]	[0.215–0.795]
Fe	224.442 $\pm$ 17.706 (140)	174.542 $\pm$ 13.690 (141)	280.106 $\pm$ 22.945 (139)	324.295 $\pm$ 27.171 (139)
	[1.015–1510.385]	[0.800–1190.000]	[1.307–1944.277]	[1.553–2310.431]
Hg	0.349 $\pm$ 0.023 (140)	0.437 $\pm$ 0.028 (141)	0.281 $\pm$ 0.018 (139)	0.313 $\pm$ 0.020 (139)
	[0.010–3.388]	[0.013–4.170]	[0.014–2.573]	[0.009–2.922]
K	409.034 $\pm$ 12.220 (140)	389.757 $\pm$ 10.134 (141)	501.791 $\pm$ 13.073 (139)	490.733 $\pm$ 13.419 (139)
	[220.364–1423.333]	[159.000–1060.000]	[264.000–1402.754]	[111.000–1378.423]
Mg	596.823 $\pm$ 26.488 (140)	565.097 $\pm$ 25.811 (141)	560.765 $\pm$ 37.326 (139)	698.039 $\pm$ 29.465 (139)
	[194.190–3230.000]	[112.000–3306.667]	[179.636–5223.333]	[32.700–3250.000]

Element	Sharp pole	Equator	Shoulder	Blunt pole
Mn	3.395 ± 0.212 (140)	3.997 ± 0.259 (141)	3.471 ± 0.226 (139)	6.859 ± 0.469 (139)
	[0.231–15.012]	[0.217–18.500]	[0.235–15.240]	[0.510–33.097]
Na	721.390 ± 24.917 (140)	697.487 ± 17.858 (141)	781.665 ± 32.939 (139)	802.750 ± 20.722 (139)
	[340.097–3330.000]	[342.000–2160.000]	[55.800–4670.000]	[36.500–1920.000]
Ni	0.121 ± 0.087 (4)	0.138 ± 0.023 (19)	0.029 ± 0.013 (4)	0.162 ± 0.060 (9)
	[0.006–0.373]	[0.015–0.420]	[0.005–0.060]	[0.006–0.591]
Pb	0.200 ± 0.064 (25)	0.251 ± 0.075 (24)	0.232 ± 0.071 (24)	0.156 ± 0.052 (22)
	[0.007–1.362]	[0.010–1.490]	[0.009–1.315]	[0.007–1.014]
Se	0.712 ± 0.056 (19)	0.496 ± 0.013 (141)	0.713 ± 0.020 (139)	0.742 ± 0.021 (139)
	[0.324–1.196]	[0.235–1.160]	[0.286–1.715]	[0.172–1.828]
Sr	140.692 ± 4.003 (140)	135.030 ± 3.821 (141)	139.867 ± 4.047 (139)	142.709 ± 4.293 (139)
	[61.541–271.567]	[45.000–263.000]	[54.600–273.280]	[30.500–286.987]

Chemical elements and their concentrations in egg contents

Due to different stages of egg decomposition and accessibility of material for analyses, out of 190 collected egg we analyzed 143, however the sample sizes differed a lot among types of counterparts and embryo stages. Concentrations of chemical elements in egg contents varied across compartments and developmental stages. Because sample sizes were highly uneven across categories, we present descriptive results only. Table 4 reports concentrations of 16 elements by egg-content compartment, pooled across developmental stages; Fig. 7 shows 11 of these elements by compartment and developmental stage.

Table 4

Concentrations of 16 elements (ppm wet weight, average $\pm$ se; number of samples where the element was measured above the detection limit; [range]) in internal egg compartments of white stork eggs ($n = 143$ eggs including 2 eggs with completely desiccated contents from 7.Sieniawka Village as the obtained concentrations did not exceeded the ranges of wet egg contents) pooled across all specimens; mixed = entire egg content disintegrated; BDL = below detection limit. Note: Sr was BDL in all the samples.

Element	Albumen	Yolk	Mixed	Embryo
	($n = 62$)	($n = 63$)	($n = 53$)	($n = 37$)
Al	6.16 $\pm$ 0.79 (62)	6.20 $\pm$ 0.93 (63)	6.23 $\pm$ 0.96 (53)	3.93 $\pm$ 0.53 (37)
	[1.21–32.1]	[0.93–50.7]	[1.17–45.1]	[1.04–14.8]
As	0.028 $\pm$ 0.022 (5)	0.032 $\pm$ 0.026 (5)	0.035 $\pm$ 0.011 (5)	0.013 (1)
	[0.001–0.115]	[0.003–0.137]	[0.0011–0.060]	-
Ca	1508 $\pm$ 193 (62)	1344 $\pm$ 135 (63)	1972 $\pm$ 317 (53)	938 $\pm$ 156 (37)
	[142–8130]	[205–5670]	[502–11500]	[97–3980]
Cd	BDL	BDL	0.017 (1)	BDL
	-	-	-	-
Co	BDL	BDL	0.028 (1)	0.003 (1)
	-	-	-	-
Cr	1.53 $\pm$ 1.53 (2)	0.08 $\pm$ 0.07 (2)	0.015 $\pm$ 0.001 (2)	BDL
	[0.0005–3.06]	[0.007–0.155]	[0.014–0.016]	-
Cu	1.71 $\pm$ 0.25 (62)	3.63 $\pm$ 0.38 (62)	1.91 $\pm$ 0.19 (53)	1.86 $\pm$ 0.55 (35)
	[0.04–12.3]	[0.17–17.10]	[0.63–8.41]	[0.11–14.90]
Fe	10.4 $\pm$ 1.1 (51)	23.9 $\pm$ 3.5 (60)	17.2 $\pm$ 2.3 (52)	32.7 $\pm$ 17.5 (32)
	[0.14–43.5]	[0.58–132.8]	[0.65–84.5]	[0.44–572]
Hg	0.06 (1)	0.004 (1)	2.48 (1)	0.16 (1)
	-	-	-	-
K	1885 $\pm$ 107 (62)	1913 $\pm$ 138 (63)	2151 $\pm$ 201 (53)	1684 $\pm$ 100 (37)
	[520–5150]	[532–8510]	[964–9700]	[626–3420]
Mg	227 $\pm$ 30 (62)	232 $\pm$ 19.7 (63)	193 $\pm$ 15.3 (53)	220 $\pm$ 39 (37)
	[52–1580]	[39–810]	[43–532]	[11.4–927]
Mn	0.27 $\pm$ 0.03 (62)	0.50 $\pm$ 0.08 (63)	0.42 $\pm$ 0.08 (53)	0.34 $\pm$ 0.10 (37)

	[0.001–1.67]	[0.02–3.00]	[0.04–4.23]	[0.01–3.72]
Na	2393 ± 88 (62)	2298 ± 99 (63)	2431 ± 97 (53)	2135 ± 112 (37)
	[1010–3400]	[379–3400]	[1300–3400]	[805–3400]
Ni	0.06 ± 0.02 (38)	0.12 ± 0.03 (46)	0.08 ± 0.02 (33)	0.09 ± 0.04 (24)
	[0.01–0.77]	[0.002–0.78]	[0.001–0.71]	[0.01–0.70]
Pb	0.02 ± 0.01 (2)	0.05 ± 0.02 (8)	0.12 ± 0.05 (5)	0.20 ± 0.03 (3)
	[0.01–0.03]	[0.005–0.14]	[0.05–0.33]	[0.13–0.24]
Se	0.55 ± 0.04 (62)	0.75 ± 0.06 (63)	0.74 ± 0.08 (53)	0.58 ± 0.09 (37)
	[0.05–1.87]	[0.10–2.96]	[0.24–3.25]	[0.11–3.26]

Methods

Study sites

Egg measurements were carried out in 13 study sites, one in Algeria: 1. Ain Azel in Sétif area, north-east Algeria; one in Germany, 2. Mecklenburg region; one in Macedonia, which in present is divided by the State of North Macedonia and Greece, and in this publication is called 3. Historical Macedonia; six in Poland: 4. Village of Kłopot, 5. Leszno District, 6. Ostrów Wielkopolski District, 7. Village of Sieniawka, 8. Upper Silesia Region, and 9. Podlasie Region; four in Spain: 10. A town of Guadalix de la Sierra – Fresneda Guadalix, 11. *Dehesa* Soto del Real, 12. Southern Córdoba, and 13. *Dehesa* de Abajo, South of Sevilla (Fig. 8). For egg measurements we used all study sites except 7 and 9. For chemical analysis we used 187 unhatched white stork eggs and three post-hatch eggshells sampled from 126 nests, only in four sites in Poland: 5, 7, 8, 9.

*The Historical Macedonia dataset comprises egg measurements collected in present-day Greece (regions of West, Central, and East Macedonia) and State of North Macedonia. This region does not entirely cover the former geographical and historical region of Macedonia.

1. Ain Azel, Algeria

In this study site in northern Algeria, the Sétif area (centre 35.82°N, 05.52°E) three concentrations of white storks were investigated. Nests were predominantly located on trees, especially ash *Fraxinus angustifolia* and elm *Ulmus campestris*, where most nest supports are 3–10 m high. Breeding colonies were located at approximately 900 m a.s.l. in a semi-arid landscape characterized by a long drought period extending from mid-May to early October. In this region, natural prey availability is likely constrained during the breeding season, but storks have access to predictable anthropogenic food sources from nearby rubbish dumps and poultry farms, where the main refuse consumed consists

largely of chicken remains [36–38]. Access to this extra food sources has been shown to increase egg volume and mass of hatchlings, particularly enhancing the reproductive value of the last-laid eggs within clutches [36], and to improve breeding success in nests located close to disposal sites, with the strength of this positive effect depending on interannual variation in rainfall and on colony size, as larger colonies may deplete natural prey more rapidly in dry years [37]. Here we include 301 egg measurements from 74 clutches collected over 3 breeding seasons (2002–2003).

2. Mecklenburg, Germany

Here, in total 103 egg measurements were collected, in 1972 in 26 localities in and around the former Bad Doberan district and the neighbouring urban and rural districts of Rostock, Mecklenburg, north-eastern Germany (approximate centre 54.12°N, 11.88°E). These localities form a relatively compact study region in the low-relief agricultural and coastal landscape west, south and south-east of Rostock. The material was obtained from an unpublished manuscript by G. Graumann and H. Zöllick, dated 1 June 1972, originally entitled *Eizählung und –vermessung Ciconia ciconia (L. 1758) im Kreis Bad Doberan und angrenzende Gebiete der Kreise Rostock–Stadt und Rostock–Land*. This dataset was supplemented by two historical clutches from villages in southern Mecklenburg, measured in 1957 and 1924, respectively, and communicated by Wolfgang Makatsch in a letter dated 19 December 1980. These two clutches were retained as part of the broader Mecklenburg dataset. Exact nest coordinates and fully standardised field protocols were unavailable for the historical material.

3. Macedonia

We are using the term *Historical Macedonia* (approximate centre 40.88°N, 21.37°E), which relates to an area occupying present-day Greece (regions of West, Central, and East Macedonia) and state of North Macedonia. The historical Macedonian egg dimensions dataset comprises 98 white stork eggs from 24 clutches collected between 1938 and 1961 (in years 1938, 1939, 1940, 1943, and 1961) by Wolfgang Makatsch and provided to one of the co-authors (PP) in a letter written in late 1980 and originate from two geographically distinct areas within the historical region of Macedonia. Most records (71 eggs from 17 clutches) were collected in Greek Macedonia, chiefly in the lowland area around Thessaloniki. The remaining 27 eggs from seven clutches originated from the Pelagonia region of present-day North Macedonia, around Bitola, situated in the Pelagonia valley in the southern part of North Macedonia, close to the Greek border. Consequently, this dataset is treated as collected within a single, contiguous study area. Exact nest coordinates were not available for the historical records.

4. Kłopot, Poland

The white stork colony in Kłopot village composed of approximately 50 households, located in the Oder River valley in western Poland (52.12°N, 14.72°E), represents one of the most extensively studied breeding aggregations of the species in Europe. The site has been monitored continuously since 1968

until recent years. The village, situated within the Krzesiński Landscape Park, is surrounded by extensively managed agricultural lands including meadows, pastures, and the former Krzesińsko-Bytomiecki dry retention reservoir, which provided important foraging habitats. The colony exhibited considerable temporal variation in size throughout the monitoring period, with the number of breeding pairs fluctuating between 19 and 33 during 1968–2003, and peaking in the early 1980s. A marked decline was observed from the mid-1990s onward, with the number of occupied nests dropping to 19 by 2002–2003, representing the lowest values since the monitoring began. More recent data indicate that the colony has partially recovered, with 22 breeding pairs recorded in some years during the 2010s [48]. Long-term research has revealed that the average number of fledglings per successful pair showed significant declining trends. Breeding success at Kłopot is negatively correlated with high water levels in the Oder River during April, likely due to reduced availability of key prey items, such as earthworms and small mammals following flooding events. The most important factor contributing to the population decline after 1990 was the cessation of traditional agricultural practices, particularly the abandonment of cattle grazing and meadow mowing following the collapse of state farms [48]. Due to its exceptional concentration of white stork nests, Kłopot has been designated as a "stork village" and serves as an ecotourism destination of European significance. In this dataset we included 363 egg measurements from 156 individual clutches spanning between 1968 and 1980 (12 breeding seasons: 1968–1971, 1973–1980).

5. Leszno District, Poland

The white stork population in the Leszno District (former voivodship), located in western Poland (centre 51.84°N, 16.57°E), has been extensively studied over the past decades. The region is characterized by a mosaic landscape of agricultural fields, pastures, and scattered woodlands. Nesting sites are predominantly found in rural areas, with most nests built on artificial structures such as electricity poles equipped with specially installed platforms, as a result of long-term conservation efforts aimed at securing breeding sites [27, 35, 49]. Breeding performance in this population is influenced by habitat quality, weather conditions and anthropogenic factors during breeding [27, 35] and non-breeding period [2, 50]. Storks nest here solitary, occasionally forming small colonies up to 5 breeding pairs with density ranging from 5 to 7 pairs/100 km² [35, 49]. Following a long decline, that started in the late 1980s, and culminated in the lowest recorded numbers in 2009 [51], the populations appears to be recovering, with increasing productivity observed in recent years [27]. In Leszno District we collected 88 eggs from 57 nests for chemical analyses, and measurements of 4342 eggs from 1029 clutches from 246 different nests over 23 breeding seasons (2003–2007, 2009–2026). Eggs were sampled during an extensive study on white stork reproductive biology started in 2003 and being continued until recently [2, 27].

6. Ostrów Wielkopolski District, Poland

Ostrów Wielkopolski District, located approximately 90 km east of Leszno (centre 51.65°N, 17.80°E), has been the subject of a long-term white stork monitoring and research [52]. The region is characterized by

a mosaic agricultural landscape situated within the Barycz River valley, part of the extensive Barycz Valley Landscape Park. This area encompasses one of Europe's largest complexes of fish ponds, extensive wetlands, pastures, and scattered woodland fragments, creating diverse foraging habitats for breeding white storks. Storks, similarly to Leszno District, nest predominantly in rural settlements, with most nests constructed on human-made structures. The best-documented breeding site is located in the village of Przygodzice, where a nest on the chimney of the Municipal Office has been continuously monitored via internet camera since 2006 as part of the "Close to Storks" education and research project [52]. Population trends and densities are very similar to those in the neighbouring Leszno district. In this work we included 105 egg measurements from 25 clutches recorded during short-term study (2024,2025) on effects of stork landfill foraging on reproduction (Triveillot et al., *under review*).

7. Sieniawka, Poland

The village of Sieniawka (50.78°N, 16.77°E) is located in the Lower Silesia Region (*Dolny Śląsk*, SW Poland), within a study area covered by long-term population monitoring (since 1984) [53]; [54]. In Sieniawka, 19 eggs were collected from a single nest between 2005 and 2014. These eggs had been thrown out of the nest (some were intact after falling) by adult white storks at different stages of the breeding period, i.e. between 11 April and 22 June. We included four eggs that had been incubated for prolonged periods, up to 33 days beyond the normal incubation period [55], and three post-hatch eggshells. The embryonic status of all 19 eggs was assessed immediately after they had been discarded from the nest [55].

8. Upper Silesia Region, Poland

The white stork population in Upper Silesia (*Górny Śląsk*), located in southern Poland (approximate centre 50.33°N, 19.00°E), has been the subject of long-term population monitoring conducted since the beginning of 20th century [56]. This region represents a unique study area characterized by its heavily industrialized and urbanized landscape, being one of the most densely populated metropolitan areas in Central Europe with population density reaching 375–379 people/km²—approximately three times the national Polish average. The landscape is dominated by a polycentric urban agglomeration that developed around coal mining and heavy industry since the 19th century, creating a distinctive mosaic of industrial areas, urban settlements, agricultural land, and scattered forests. Despite intensive urbanization, agricultural lands—including arable fields, meadows, and pastures—persist in the matrix, particularly in river valleys and less industrialized zones, providing foraging habitat for white storks [56].

During the last 20 years, storks have been declining, with a dramatic 35.5% decrease between 2004 and 2024 [15]. This particular population has decreased by from 564 to 367 breeding pairs ([56] suppl. with new data). As a main causes of the decline land use conversion and high juvenile mortality are considered (Profus and Siekiera 2019).

Recently, an average breeding density is 3.4 pairs/100 km² [56]. This decline contrasts sharply with the stable or increasing trends observed in other regions of Poland during the same period. The population decline in Silesia was found to be inversely related to altitude, with lowland areas experiencing declines approximately twice as severe as mountainous regions. Changes in land use—including loss of grasslands, agricultural intensification, afforestation, and continued urban sprawl—were examined as potential drivers [15]. In Upper Silesia Region, particularly Opole District, we collected 34 eggs from 28 nests in 2014–2015 (between 15th June and 15th July) for chemical analyses, and 368 egg measurements from 92 clutches over the period 1974–2002 (17 seasons: 1974, 1977, 1978, 1980, 1987–1989, 1991–1995, 1998–2002).

9. Podlasie, Poland

In Podlasie Region (NE Poland), near the town of Siedlce (52°10' N, 22°16' E), stork breeding density is substantially higher, than in west and south of Poland, and achieve values almost 40 pairs/km² with a long-term stable or moderate increasing trend [57]. A mosaic of traditionally managed agricultural lands (arable field, meadows/pastures interspersed with coniferous forest) provide favorable habitats for breeding storks. In this study site we collected 46 eggs from 43 nests in 2014 and 2015, for chemical analyses only. Eggs were collected between 15 June and 10 July during the ringing of chicks, when they were approximately four weeks old.

The heterogeneity of population trends across Poland suggests that the country may represent a transitional zone between areas of population increase and decrease, with the western border of these contrasting trends coinciding with the division between eastern and western migratory flyways.

10. A town of Guadalix de la Sierra - Fresneda Guadalix, Spain

Guadalix de la Sierra colony is located in central Spain (40.78°N, 3.68°W) in an pasture composed of grassland with ash trees *Fraxinus* sp., devoted to sheep raising. Some of the breeders in this colony were regularly foraging at the closest landfill of Colmenar Viejo, which is 15 km away. The colony expanded from 20 nests recorded in 1989 (Vergara et al., 2007) to an estimated 100 nests during recent years (J.I. Aguirre, personal observation). In this study we collected 92 egg measurements from 19 clutches in two seasons (2007, 2008).

11. Soto del Real, Spain

Near the town of Soto de Real (40.74°N, 3.89°W) two adjacent colonies (on a farm Prado Herrero and on *dehesa* nearby) form the most prominent white stork aggregation, located in central Spain, in the province of Madrid. The core of the colony is situated on trees and poles within a *dehesa* dominated by ash (*Fraxinus* spp.), a traditional agro-silvopastoral landscape where forestry, livestock grazing, and crop cultivation coexist. The colony has expanded from a single nest recorded in 1989 [58] to an estimated

215–250 breeding pairs in recent years, making it the largest white stork colony in the Madrid province [17, 59]. White storks nesting within this colony forage on the nearby pastures and other agricultural lands, and also on the municipal landfill, Colmenar Viejo (40.65°N, 3.72°W, 12 km from the colony). There is documented ingestion of plastics and microplastics by individuals from this colony, underscoring the environmental risks associated with foraging near landfills [60]. Long-term breeding ecology monitoring yielded 2653 egg measurements from 652 clutches over a period of 2003–2024 (11 seasons: 2003, 2007, 2008, 2016–2019, 2021–2024).

12. Southern Córdoba, Spain

The study area is the agricultural lowlands of southern Córdoba in Andalusia (southern Spain, centre 37.79°N, 4.73°W), characterised by an intensively farmed landscape with only small, scattered patches of remaining natural or semi-natural vegetation. Within this matrix, most land is occupied by large, open fields of dryland crops such as wheat and sunflower, together with extensive olive groves and some vineyards, giving a structurally simple habitat with very few hedgerows or uncultivated field margins. These conditions create a highly productive but homogenised environment where traditional wetlands and pastures are scarce, so white storks rely heavily on predictable, human-derived food sources such as municipal refuse tips for foraging. In the period of this study, breeding colonies were located close to these landfills, and storks commuted between nest sites and dumps to feed, meaning that food abundance was largely decoupled from natural prey availability in fields and more directly linked to waste management practices [33]. The southern Córdoba study area can be described as an intensively cultivated Mediterranean farmland mosaic with minor natural remnants, where refuse tips function as key artificial foraging hotspots that shape the timing and output of white stork breeding [33]. Here we include 30 egg measurements from 7 clutches collected only in one season – 1990.

13. de Abajo, South of Sevilla

13. *Dehesa* de Abajo, South of Sevilla

Dehesa de Abajo colony, south of Seville (37.20°N, 6.17°W) in the region of Andalusia, is a mosaic of open pasture and scattered wild olive trees, embedded in a wider lowland landscape dominated by extensive rice cultivation in the Bajo Guadalquivir. The pastures and wild olive woodland (*dehesa* of *acebuche*) form a savanna-like structure used for cattle grazing and support one of Europe's largest colonies of white stork nesting in natural trees, while the surrounding rice fields and nearby wetlands provide rich aquatic foraging areas for waterbirds. White storks nest here on trees and buildings.

In general, white stork population in Spain has been increasing since 1980s, in some regions performing even threefold increase due to extensive exploitation of anthropogenic sources of food from municipal landfills [17, 33]. Here we include 57 egg measurements from 17 clutches collected only in one season – 1990.

Egg dimension measurements

In accessible white stork nests, we performed direct inspections using a ladder (3–16 m in length), a mobile cherry-picker, or climbing equipment, depending on nest accessibility. Egg measurements were taken in fully laid clutches during the second half of incubation to ensure the completion of egg-laying. Broods that experienced partial losses (e.g., due to stork fights) were excluded from the dataset. Each egg's length (L) and breadth (B) were measured using a calliper with an accuracy of at least 0.1 mm [2]. Subsequently, we calculated total egg volumes (with shell) using an equation: $EV_{\text{total}} = 1.1203 + 0.4820(L + 1.1) \times (B + 1.1)^2$ [28, 46]. To test differences between populations we use Kruskal-Wallis test and we performed the test on averaged egg dimensions from a single clutch.

Egg processing and sample preparation for chemical analysis

The distribution of our sampling of eggs was heavily skewed, as only one egg was sampled in each of 94 nests. More than one egg was taken from the other 32 nests (including Sieniawka) – 96 eggs in all: two eggs from 21 nests (42 in all), three eggs from 5 nests (15 in all), four eggs from 5 nest (20 in all), and 19 eggs from one nest but from different years. Even though we took more than one egg from an individual nest, only some of these eggs were at the same stage of embryonic development.

After collection, each egg from plots 5. Leszno District, 8. Upper Silesia, and 9. Podlasie Region in Poland, was placed in a plastic bag and frozen at -20°C. After thawing (in July 2016), eggs were washed under tap water to remove visible external dirt and the grey film coating the shell surface. If possible each egg was weighted (with accuracy of 1 g), and it's length and breadth was measured with calliper to the nearest 0.1 mm. It was then opened along its broadest part and the contents placed in a glass dish to examine them for the presence of a dead embryo (if present, its maximum diameter was measured) and to separate the major internal egg compartments, i.e. yolk, albumen, putrefied entire egg contents (this last presumably consisting of mixture of yolk, albumen and various egg fluids), and embryos at different developmental stages. These separated egg compartments were then transferred to plastic containers and stored at -20°C until further processing. The eggs from 7. Sieniawka village were stored unfrozen, so their content dried out completely; only their shells were used in the chemical analysis.

After opening eggs and removing the visible remnants of the contents from the inner shell surfaces (these were also rinsed in tap water), one person (Jerzy Karg) measured the shell thickness of the thawed eggs (from plots 5, 8, and 9) together with the attached inner shell membrane with micrometer (YATO YT-72305) to the nearest 0.001 mm; this measurement was performed immediately (within ~ 0.5 h) after opening eggs, so the (wet) membrane adhered tightly to the shell. The shell thickness was measured over longitudinal sections in four regions of an egg: sharp pole (one measurement), equator (the broadest region of an egg; three measurements; thereafter averaged), shoulder (i.e. halfway between equator and blunt pole; one measurement) and blunt pole (one measurement) (egg region terminology after [61]). Around 2–3 cm² shell samples were taken from each of these four regions; they

were then desiccated and stored at room temperature for several months until further processing. The shell thicknesses of a few eggs found broken (partly dried) in nests, as well as post-hatched shells and dried eggs (plot 7) were also measured; however, some of these measurements (and sampled shell fragments) were from unknown egg regions. All the measurements were taken 3 times and mean was calculated as a final result. To compare thickness between eggshell regions we performed Friedmann test with egg ID as a blocking factor.

Chemical analysis

Macroscopic examination of the content of our sample of white stork eggs showed quite a consistent distribution of embryonic developmental stages. So for our major analyses we pooled the eggs into three groups representing consecutive classes of advancement (classes) of embryonic growth: no embryos visible (e0), small embryos – up to 10 mm of diameter (e1), and large embryos – ranged from bigger than 10 mm of diameter to almost hatchlings (e2). Such a classification of eggs with respect to their developmental stage is biologically justified in the context of embryo-induced functional changes in the morphological and chemical properties of avian eggs [62]. Owing to time and technical constraints, as well as the stench of the contents of rotten eggs, the internal egg compartment samples were analysed on a wet weight basis. Only small portions of the embryos were used, and these were taken in the frozen state to limit the stench. It should be stressed, however, that measurement of trace elements in the major internal egg compartments on a wet weight basis may be more appropriate for evaluating metal-induced teratogenic effects and embryonic mortality or contaminant concentrations [63–65].

Inductively coupled plasma mass spectrometry (ICP-MS) was used to measure the concentrations of 17 chemical elements (Al, As, Ca, Cd, Co, Cr, Cu, Fe, Hg, K, Mg, Mn, Na, Ni, Pb, Se, Sr) in the samples, including eggshells without shell membranes, yolk, albumen, mixed egg contents and embryo tissues. Embryo samples consisted of approximately half of the embryo in early developmental stages (up to c. 2 cm in diameter), or a small part of a more advanced embryo, e.g. skin with breast muscle. The chemical analyses were performed at Chespa© chemical laboratory (Chespa Sp. z o.o., Krapkowice, Poland), specializing in food security analysis for global food producers.

Accurately weighed 0.1 g (the precision of measurement was ± 0.0001 g) samples of shells and internal egg compartments were digested in 10 ml of concentrated high-purity nitric acid in closed Teflon containers in an Ethos Up Milestone Microwave Digestion System (MLS, Sorisole, Bergamo, Italy). High-purity reagents designed for ICP-MS analysis were used during sample preparation and dilution to ensure minimal contamination: ultrapure water (microbiologically pure) along with trace metal grade nitric acid. The 10 ml of digested material was poured from the digestion vessels into clean centrifuge tubes. The digestion vessels were then rinsed with high purity distilled water to ensure complete recovery of material from them, and this rinse water was added to the samples in the centrifuge tubes. The 10 ml samples were made up to a final volume of 25 ml by diluting with ultrapure water.

The sample solutions were analysed in a Shimadzu ICPMS-2030 in conjunction with a Shimadzu AS-10 Autosampler, equipped with a mini-torch and helium (He) gas collision system, as well as a process of developing analytical methods, the Diagnosis Assistant (DA) and Development Assistant Function, which automatically diagnoses spectral interference and assures the quality of analytical methods [66]. Creating analytical methods for the Shimadzu ICPMS-2030, the analysis involves selecting the measured and target elements. Then, based on the qualitative analysis data (for all mass numbers) from a representative sample, the DA automatically selects the optimal mass numbers and internal standard elements for the target elements and automatically specifies the concentration range for calibration curve samples [66]. Prior to quantitation, various parameters such as torch position and focusing lens voltages were automatically optimized as part of the routine tuning procedure of the instrument, and the following other conditions of the measurement were used: Radio Frequency (RF) power, 1.2 kW; sampling depth, 6 mm; plasma gas flow rate, 8.0 l min⁻¹; auxiliary gas flow rate, 1.10 l min⁻¹; nebulizer gas flow rate, 0.60 l min⁻¹; spray chamber, cyclone (electronic cooling). Internal standards of concentrations of three rare earth elements (Ho; Sc; Y) were added automatically using the internal standard addition kit along with the peristaltic pump included with the instrument. The internal standards were added at a constant rate and concentration to all calibration standards and unknown samples. The final concentration of the internal standards was 10 ppb. Calibration curves were generated immediately prior to analysis to ensure the most accurate quantitation, and the condition of analysis was automatically monitored during the entire measurement process [66]. The measurement was also conducted for a blank sample (nitric acid), and this was subtracted from the results obtained for all the samples of eggshells/egg contents. The detection limit of each element was: Al, 0.0003 ppm; Ca, 1.02 ppm; Fe, 0.00013 ppm; K, 0.0204 ppm; Mg, 0.00013 ppm; Na, 0.0013 ppm; Cu, 0.0043, ppm; Ni, 0.00029 ppm; for the remaining 9 elements (As, Cd, Co, Cr, Hg, Mn, Pb, Se and Sr) it ranged between 0.000024×10⁻³ (Sr) ppm to 0.056×10⁻³ ppm (Cr). The concentrations of elements were expressed in milligrams per kilogram (mg kg⁻¹ or parts per million; ppm) of dry mass (d.w.) for eggshells and wet mass (w.w.; ppm) for internal egg compartments.

The measurement process was validated using DORM-3 (fish protein) certified reference material (CRF) provided by the Institute for National Measurement Standards of the National Research Council Canada (Ottawa, Ontario, Canada). The mean recoveries in six replicates of CRF sample (100 mg) expressed the method's precision, or the difference between the mean value obtained by analysing CRF. The validated values were as follows: As (-2.9%; i.e. the measured value was 2.9% less than the values reported in CRF), Cd (+ 5.2%; i.e. the measured values was 5.2% more than the values reported in CRF), Cr (+ 4.6%), Cu (+ 4.2%), Hg (-1.2%), Fe (-0.2%), Ni (+ 3.2%) and Pb (+ 3.3%); they were obtained from the same sample and were within 5% of the concentrations stated for the reference material.

Concentrations of elements in eggshells have already been published and extensively described by Orłowski et al., (2019). Chemical element concentrations of egg contents are presented descriptively because sample sizes were highly unbalanced among embryo-development classes within egg compartments (range: 1–57 samples per compartment × developmental-stage combination).

Declarations

Ethical statement

All the measurements were carried out according to country-level legislation and with permissions from local nature protection authorities: WPN-II.6401.167.2015.AS.2, WPN-II.6401.345.2019.KL, WPN-II.6401.77.2021.MT, WST.6401.2362023.MK.2, WST.6401.165.2024.MK, WGZ.6401.201.2025.MK

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Author contributions

MT wrote the first draft of the manuscript, gathered data from different data sources, collected data in Poland and Spain, performed statistical summaries, prepared figures and tables, JIA, JTB, SD, ŁD, ZJ, ALG, ER-E, PP, FST, NT contributed in egg measurements, RC-D, ED performed chemical analyses of collected eggs, MT, JTB, ŁD, IK, AS, JS, AW collected eggs for chemical analyses, GO performed egg preparation and analyses, wrote part of the first draft. All the authors contributed in revising and writing the manuscript.

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Table 1

Table 1 is available in the Supplementary Files section.

Figures

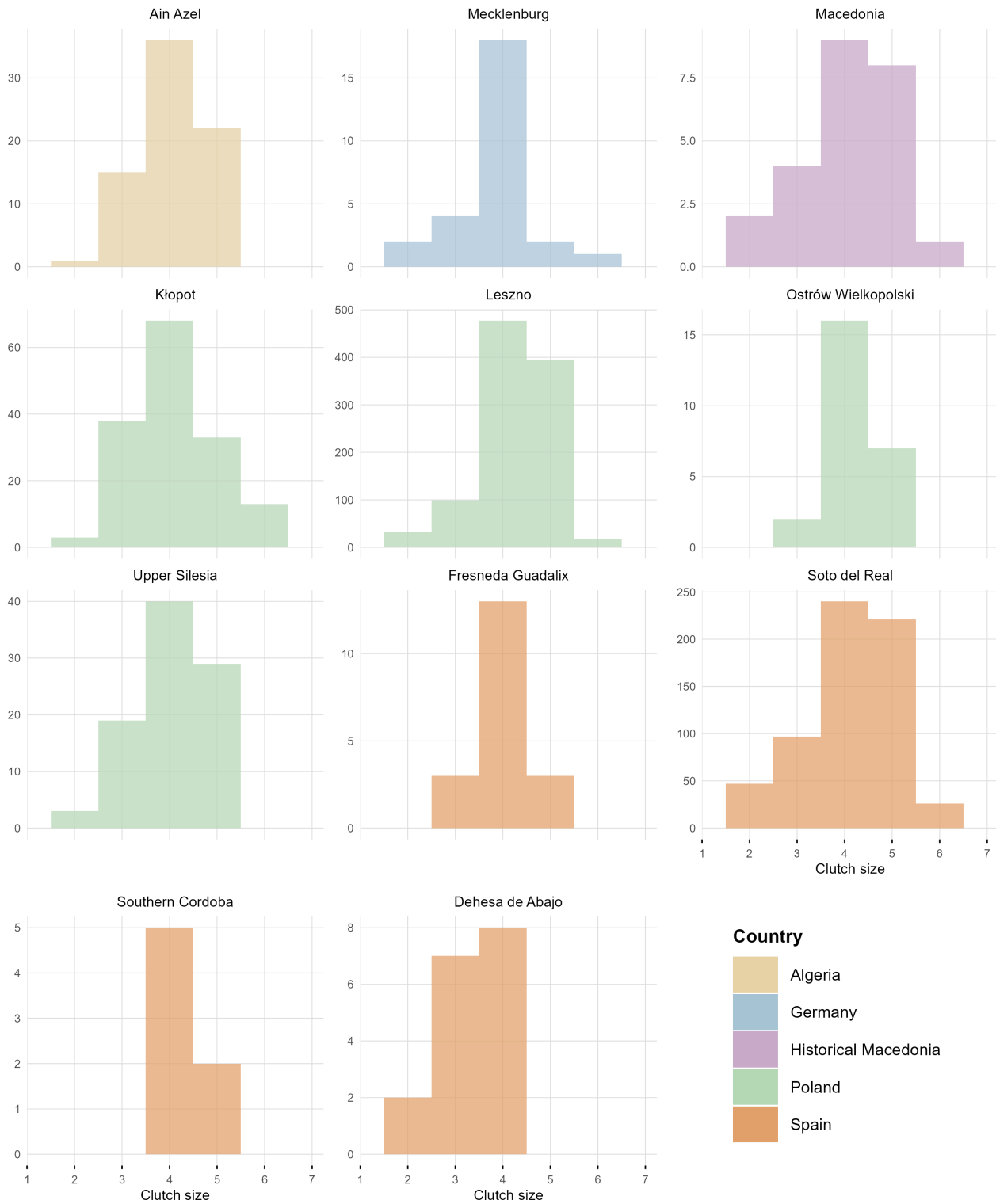


Figure 1

Distribution of clutch sizes (number of laid eggs in the clutch) among different populations of the white stork



Figure 2

Distribution of egg lengths (mm) among studied populations of the white stork.

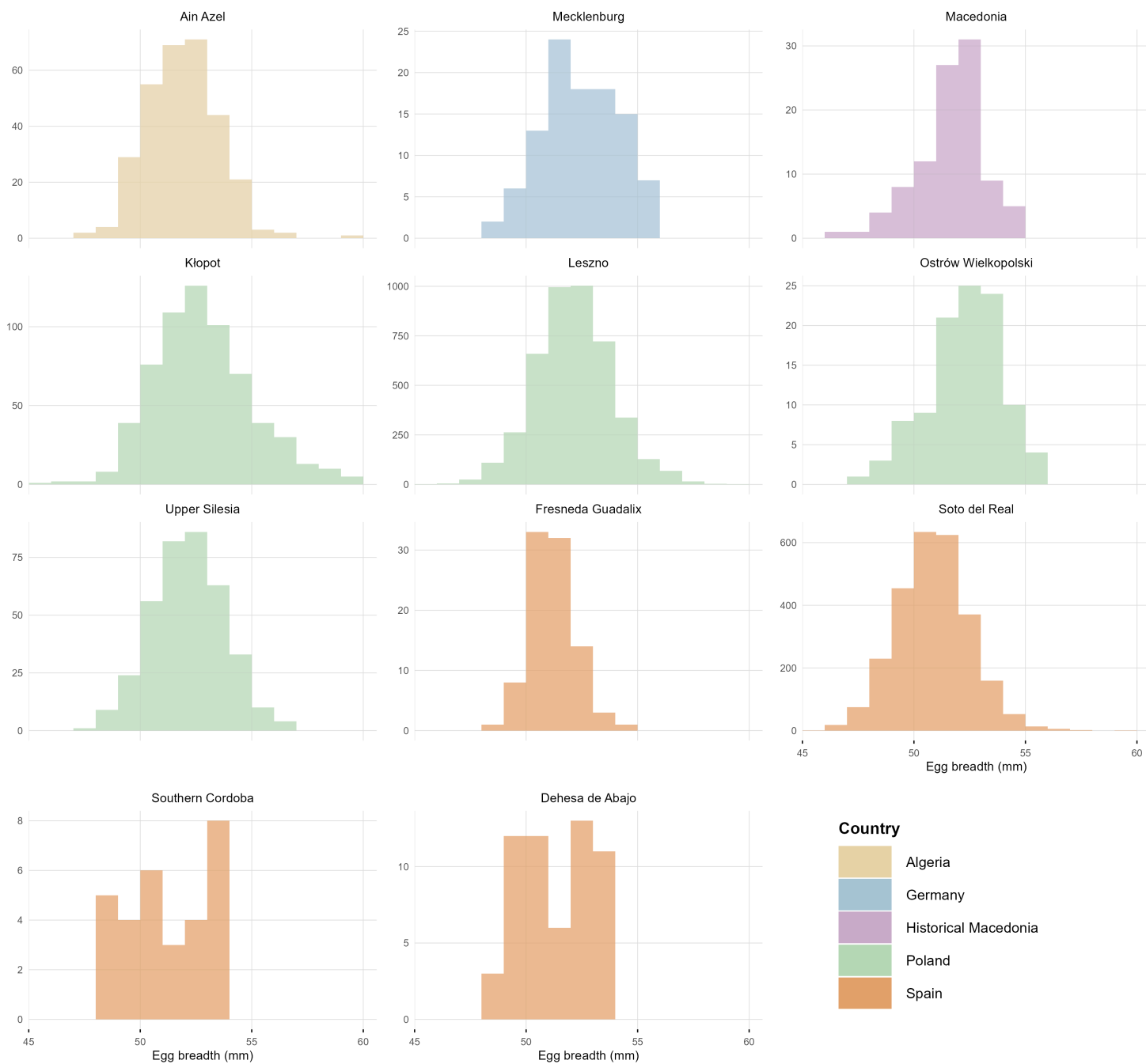


Figure 3

Distribution of egg breadths (mm) among studied populations of the white stork.

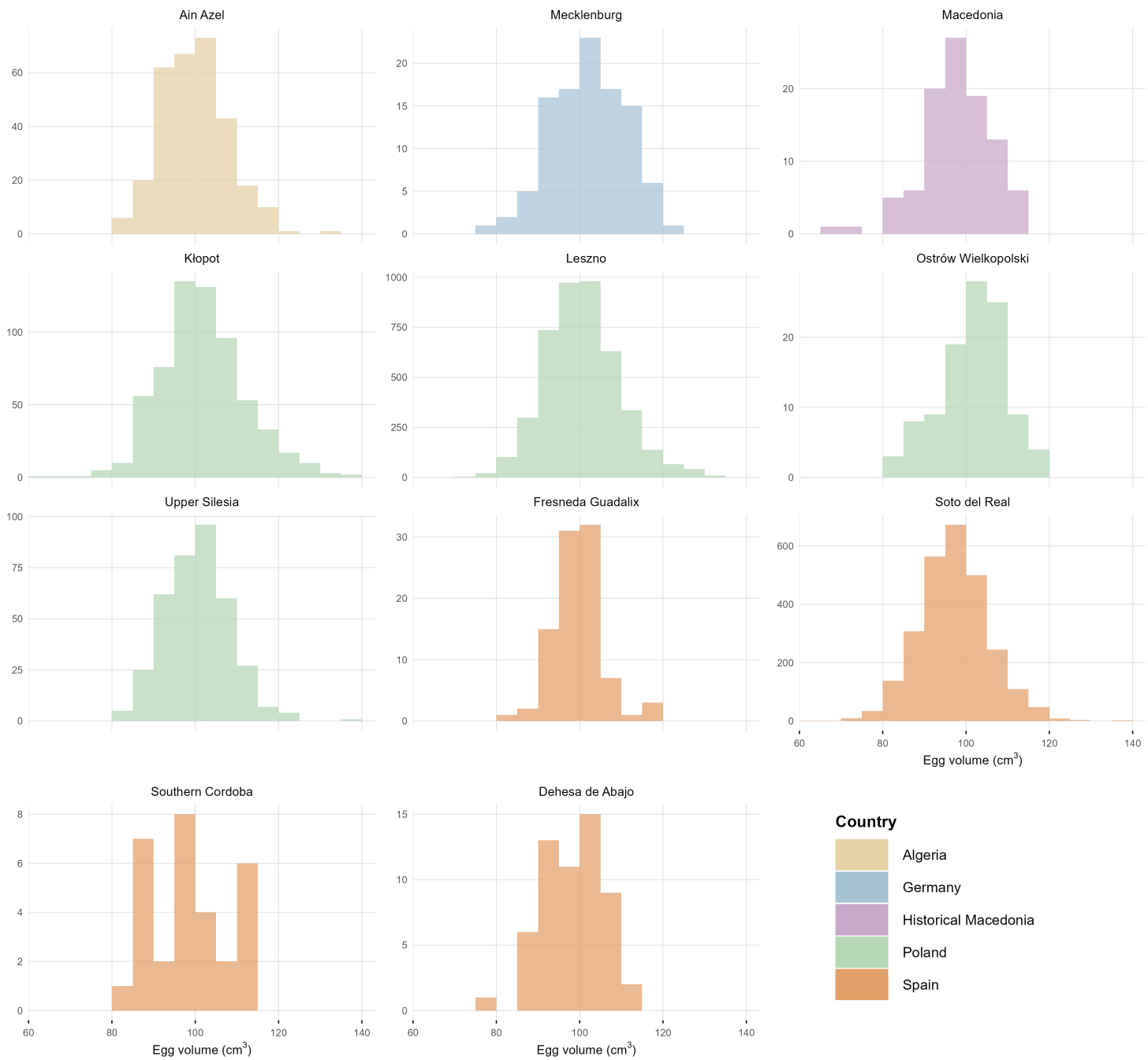


Figure 4

Distribution of egg external volumes (cm³) among studied populations of the white stork. Egg volume was calculated based on length and breadth of egg using equation proposed by [46] (internal volume) and updated by [28](external volume).

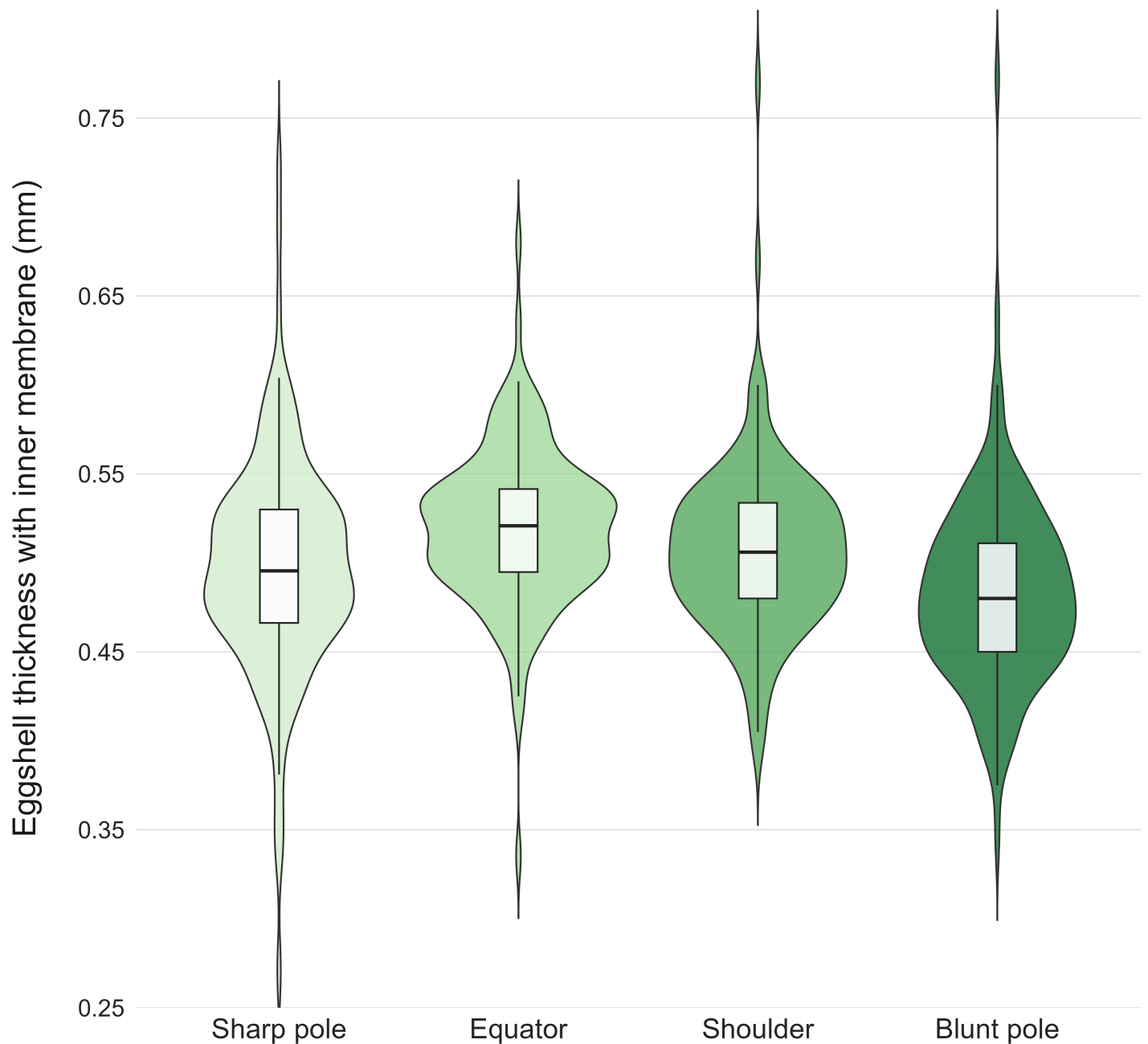


Figure 5

White stork eggshell thickness, including inner shell membrane, measured at four regions: sharp pole, equator, shoulder, and blunt pole. Violin plots show the estimated distributions of thickness. Embedded boxplots show the median and interquartile range; whiskers extend to $1.5 \times \text{IQR}$. Points represent individual eggs. Only eggs with thickness recorded for all four regions were included ($n = 138$).

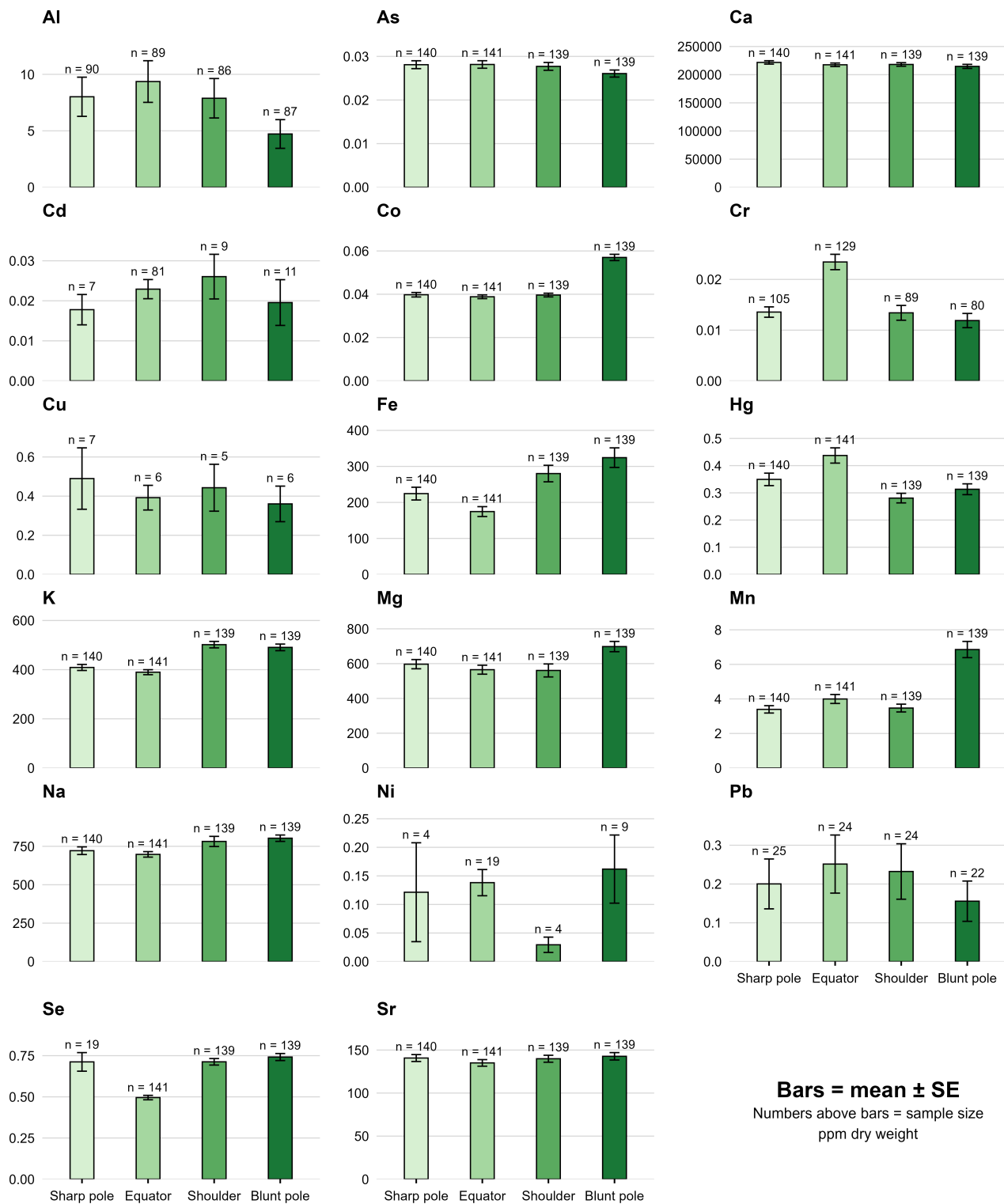


Figure 6

Average ($\pm$ se) concentrations (ppm dry weight; y-axis) of 17 chemical elements measured in eggshells of 141 white stork eggs in four areas of the egg: Sharp pole, Equator, Shoulder, and Blunt pole.

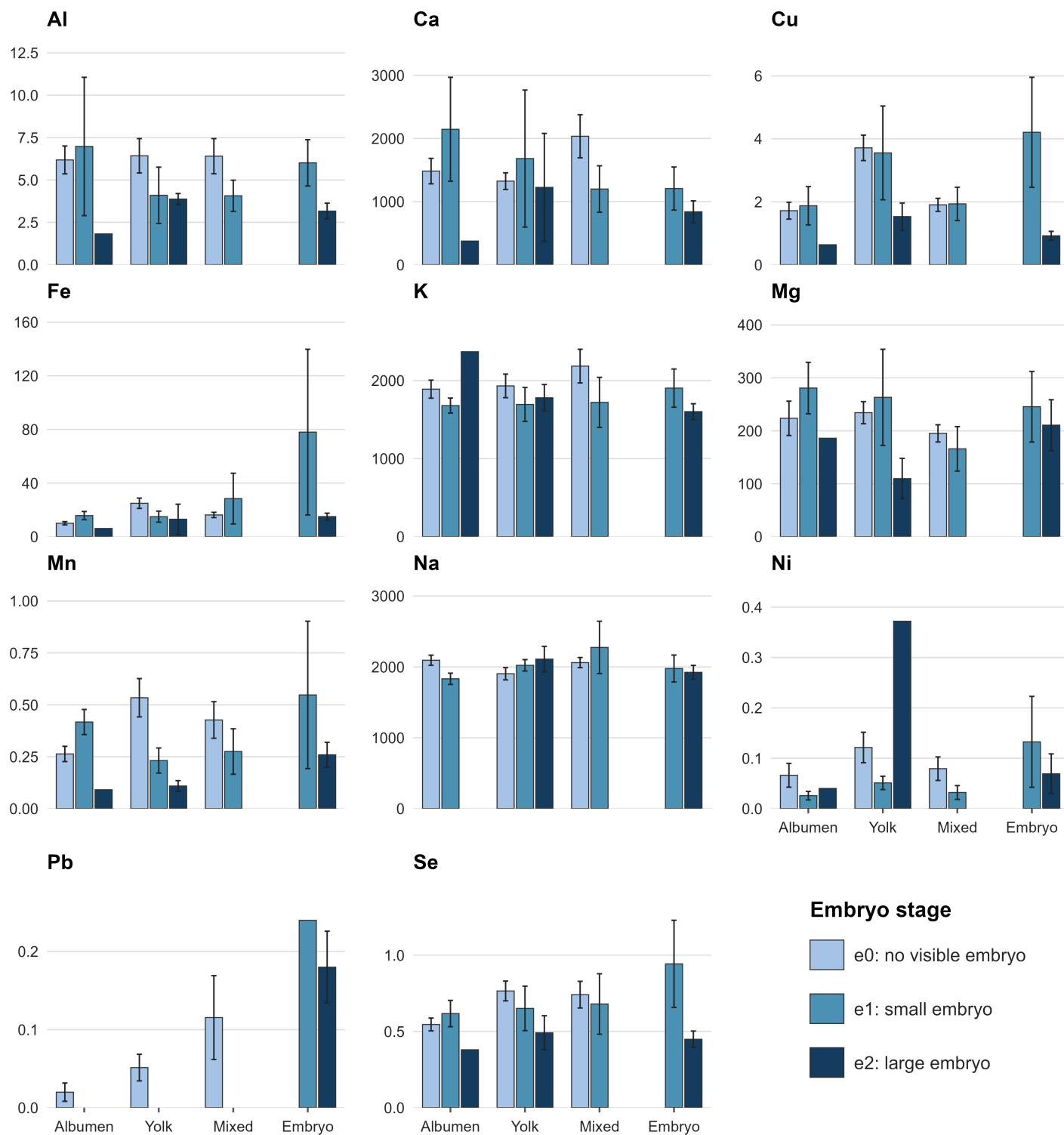


Figure 7

Average ($\pm$ se) concentrations (ppm wet weight; y-axis) of 11 chemical elements measured in internal compartments of 141 white stork eggs (albumen; yolk; mixed = entire egg content disintegrated; embryo) representing three stages of embryonic development: no embryos visible (e0), small embryos (e1) and large embryos (e2). The data relating to the other elements detected in a small number of samples are presented in Table 4.

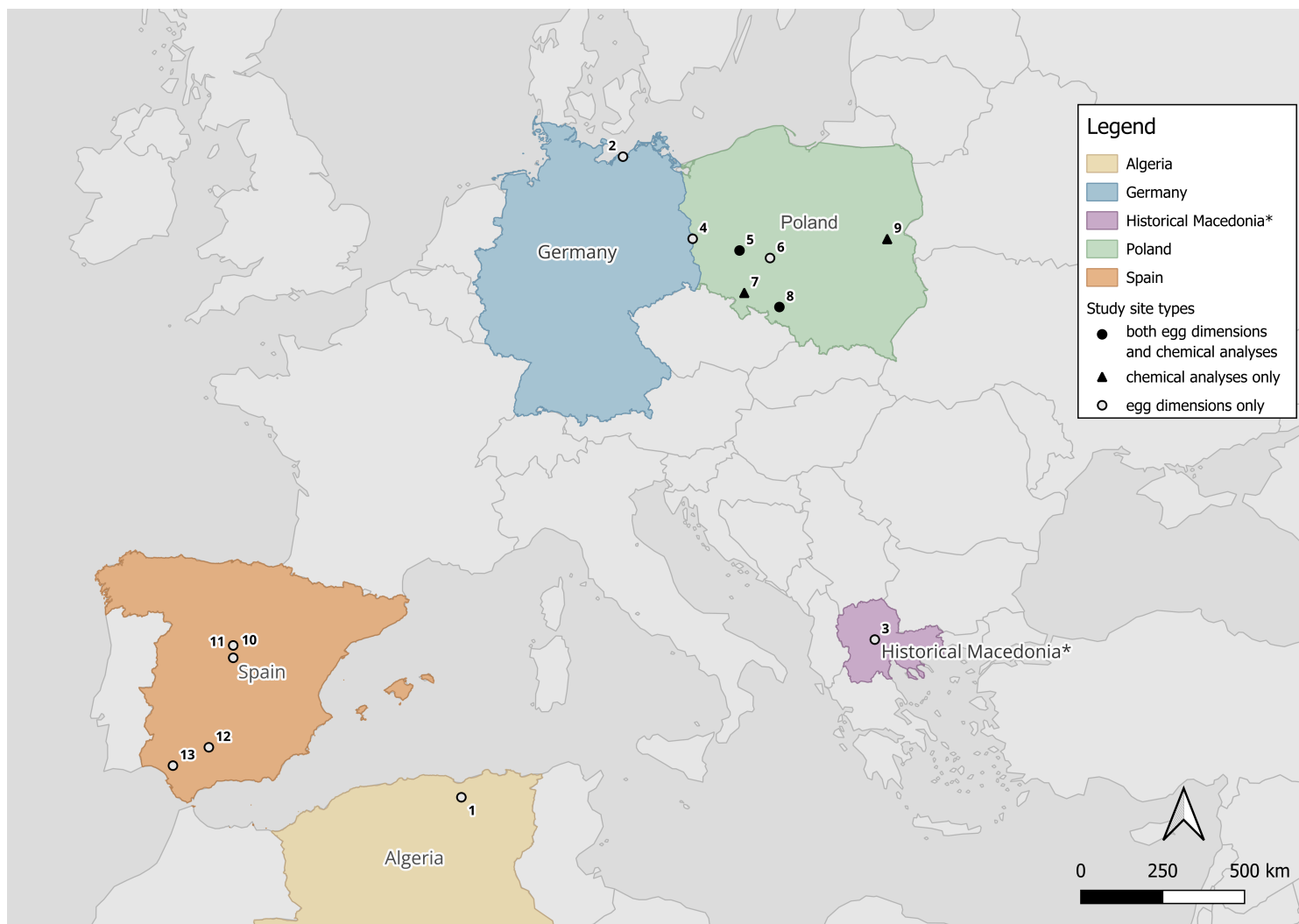


Figure 8

Distribution of white stork study sites included in the datasets. Sites provided only egg-dimension measurements (open circles), egg samples for chemical analyses (filled triangles), and both (filled circles). Study sites were located in Algeria (1. Ain Azel), Germany (2. Mecklenburg), historical Macedonia (3. Macedonia), Poland (4. Kłopot village, 5. Leszno District, 6. Ostrów Wielkopolski District, 7. Sieniawka village, 8. Upper Silesia Region, 9. Podlasie Region), and Spain (10. Fresneda Guadalix, 11. Soto del Real, 12. Southern Córdoba, 13. *Dehesa de Abajo*).

*The Historical Macedonia dataset comprises egg measurements collected in present-day Greece (regions of West, Central, and East Macedonia) and State of North Macedonia. This region does not entirely cover the former geographical and historical region of Macedonia.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Table1.docx](#)