

Archaeological bird remains from Norway as a means to identify long-term patterns in a Northern European avifauna

Samuel James Walker

Thesis for the degree of Philosophiae Doctor (PhD)
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Scientific environment

This PhD has been conducted at the osteological research collections within the Department of Natural History at the University Museum of Bergen. This project was funded by a four year PhD research fellow position from the University of Bergen.

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Abstract

Birds are currently facing a biodiversity crisis. Seabirds, birds in agricultural landscapes, and montane birds are particularly vulnerable to extinction. Whilst their modern distributions are well studied, how past events and processes have shaped modern avian distributions in Norway and Scandinavia remains mostly unknown. Past bird populations can help us to better understand how birds react to environmental change.

The overall aim of this project is to better understand the faunal histories of birds in Norway during the Holocene (the last ~ 10,000 years). This was achieved through studying bone remains, reconstructing past avian communities, and identifying changes over time. A multi-disciplinary approach has been implemented throughout this project. Zooarchaeological methods form the basis of the research, through the use of comparative morphology, metric and statistical analysis. I have also drawn on palaeoecological techniques and careful consideration of ornithological studies regarding the species found within the archaeological record.

The findings of **paper I** show that despite climatic fluctuations and the rise of urban centres during the Medieval period in Norway, re-examination and compilation of bird bone assemblages found little evidence to suggest that the Medieval bird fauna differed from the modern one. Interestingly, species that are now ubiquitous in urban areas, such as pigeons, corvids and gulls are mostly absent from Medieval urban centres.

The first occurrences of domestic chicken in Norway indicate that they were imported by the Vikings. However, in very small numbers, and it is not until the Medieval period that chickens become more common place (**Paper I-II**). The reasons for the introduction of non-native species to Norway are varied. This research has found evidence for the use of *G. gallus* in blood sport (**Paper II**), the presence of more elaborate chicken types/breeds (**Paper II**), and the introduction of other exotic species (**Paper I**). Furthermore, increased use of falconry (**Paper I, IV**) during the Medieval and Post-Medieval periods show a significant and widespread change in attitude toward bird species.

The current biodiversity crisis facing bird species has given rise for the need to better understand past responses to change. This research found that Atlantic Puffin expanded northwards during a period of climatic oscillations in the mid-Holocene (**Paper III**). Furthermore, I have identified body size changes (**Paper I, III-IV**) in response to change. These responses can occur over a relatively short time frame. Whereas morphological changes to the skeleton are more of a long-term response, which has so far not been detected in the Holocene avifauna of Norway. But, more robust skeletal elements have been identified (**Paper III**).

This work has not only significantly expanded the knowledge of avifaunal history within Norway, but has also placed Norwegian data into a regional (Scandinavian) and continental (northern European) perspective. In addition, the resulting data presented here highlight new questions and research directions.

List of Publications

Paper I:

Walker SJ., Hufthammer AK., & Meijer HJM. 2019. Birds in Medieval Norway. *Open Quaternary* 5(5): 1–33. DOI: 10.5334/oq.58

Paper II:

Walker SJ., & Meijer HJM. 2020. More than food; evidence for different breeds and cockfighting in *Gallus gallus* bones from Medieval and Post-Medieval Norway. *Quaternary International* 543: 125–134. DOI: 10.1016/j.quaint.2020.03.008

Paper III:

Walker SJ., & Meijer HJM. 2021. Size variation in mid-Holocene North Atlantic Puffins indicates a dynamic response to climate change. *PLOS ONE*. 16(2): e0246888. DOI: 10.1371/journal.pone.0246888

Paper IV:

Walker SJ., & Meijer HJM. A long-term study of size variation in Northern Goshawks *Accipiter gentilis* across Scandinavia, with a focus on Norway. Manuscript.

Declaration of contributors to the thesis

	Paper I	Paper II	Paper III	Paper IV
Conceptualisation	SJW, HJM	SJW, HJM	SJW, HJM	SJW, HJM
Origin of material	UMB	UMB	UMB, NHMD, NHMUK	UMB, NHMD, LUOMUS
Methodology	SJW, HJM	SJW, HJM	SJW, HJM	SJW, HJM
Data collection	SJW	SJW	SJW	SJW
Analysis	SJW	SJW	SJW	SJW
Investigation	SJW, AKH, HJM	SJW, HJM	SJW, HJM	SJW, HJM
Visualisation	SJW	SJW	SJW	SJW
Writing - original draft	SJW	SJW	SJW	SJW
Writing - review & edit	SJW, AKH, HJM	SJW, HJM	SJW, HJM	SJW, HJM
Supervision	HJM	HJM	HJM	HJM

Abbreviations: SJW = Samuel James Walker, HJM = Hanneke Johanna Maria Meijer, AKH = Anne Karin Hufthammer, UMB = University Museum of Bergen, NHMD = Natural History Museum of Denmark, NHMUK = Natural History Museum at Tring, UK, LUOMUS = Finnish Museum of Natural History.

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1. Introduction

Currently, Norway hosts approximately 255 breeding bird species. Recent ornithological work has shown that 22% of all breeding birds within Norway are declining in numbers, with 3 species likely to disappear within the next decade (Shimmings & Øien, 2015). Some of the most vulnerable species are seabirds, birds in agricultural landscapes, and montane birds (Henriksen et al., 2015). Whilst their modern distributions are well studied, how past events and processes have shaped modern avian distributions in the region remains mostly unknown.

During the last glacial maximum, the Eurasian ice sheet forced many animals and plants southwards. As the climate warmed and the ice sheets started to retreat following the glacial maximum (21-17,000 years ago), flora and fauna underwent northern range expansions from their southern refugial locations (Bennett et al., 1991; Hewitt, 2000). In Europe, the Scandinavian Peninsula was one of the last areas to be recolonised. A number of studies have focused on how various flora and fauna recolonised the Scandinavian Peninsula (for instance, see Riede et al. (2013) on human recolonisation of southern Scandinavia, Knop and Merila (2009) on the Moor Frog (*Rana arvalis*), and Sannikov and Sannikova (2016) on Scots Pine (*Pinus sylvestris*) and Norway Spruce (*Picea abies*)). The postglacial history of birds in this region, however, has received little attention thus far (Holm & Svenning, 2014).

The projected changes in temperature over the next 100 years as a result of increased atmospheric concentrations of CO₂ are likely to cause substantial environmental change, with the most severe effects expected to occur in northern biomes (Pithan & Mauritsen, 2014). How organisms will respond to future global warming is a topic of considerable interest in conservation management. To make reliable predictions of future distributions and ensure effective conservation planning, it is important to identify how species responded to past climatic changes (see for instance Lagerholm et al., 2017 for a study on ptarmigans). Of particular interest here are periods during which the magnitude of climatic change was similar to, or even surpassed, projected climate changes in the future. This project has mainly focused on the Holocene, with particular interest in the mid-Holocene period (7,300–4,800 years

BP) where summer temperatures were around 1.5–2.0°C warmer than present (Bjune et al., 2004; Snowball et al., 2004; Bjune et al., 2005; Seppä et al., 2009; Balascio & Bradley, 2012). This was followed by a period of decreasing summer temperatures and increased precipitation (Snowball et al., 2004; Seppä et al., 2009; Balascio & Bradley, 2012). Another period of distinct climatic change is the Medieval period, with alternating warmer and colder periods (Zawiska et al., 2017). During the 11th, 13th, and 15th century, temperatures were 1.0–2.0°C warmer than present summer temperatures, whereas they were 1.0–2.0°C colder in the 12th and 14th centuries. A prolonged cold period between 1550–1800 CE is known as the Little Ice Age (LIA).

Work on post-glacial Scandinavian birds has been done mostly from an archaeological perspective and on a site-specific basis. Mannermaa's (2003) work in Finland collates avifauna from archaeological sites, focusing on the Mesolithic through to Bronze Age. The most recent work conducted in Denmark is by Gotfredsen (2013; 2014) looking at subsistence and cultural implications of species represented from specific sites. For Sweden, Ericson and Tyrberg (2004) summarised all available sub-fossil and written sources of Swedish avifauna over a time period of 14,000 years (Weichselian-19th Century). Although their work is descriptive only, it is the most comprehensive study of the history of a Scandinavian avifauna thus far, and suggests a number of broad patterns occurred after the last glacial maximum.

Within Sweden, recolonisation began with the cold-adapted species such as the ptarmigan (*Lagopus mutus*) and the Snowy Owl (*Nyctea scandiaca*) leading the way, with less hardy species arriving as the climate became milder. During the late Boreal (9000–8000 years ago) and Atlantic (8000–5000 years ago) periods, the Swedish landscape was dominated by forests which caused a retreat in open landscape species such as Kestrel (*Falco tinnunculus*) and Corncrake (*Crex crex*) whilst forest species such as Tawny Owl (*Strix aluco*) likely immigrated at this time. During the Subboreal (5000–2300 years ago), human impact reduced forest area, a process that still continues. This has caused an increased abundance in open area species but decreased the range of many forest species. The Medieval period and the creation of large urban centres brought an increase in scavenger species like Red Kite (*Milvus milvus*). It should be noted that Ericson and Tyrberg (2004) show fluctuations in range and

abundance of species likely dependent on both climate and human impact, but their study was descriptive in nature and no statistical analyses or data modelling was performed.

For Norway, work on subfossil and archaeological avian assemblages has been mostly site specific (See for example; Olsen, 1967; Undheim, 1985; Marthinussen, 1992). Some work has focused on specific species, such as Montevecchi and Hufthammer's (1990) work on Northern Gannets (*Sula bassana*) and Northern Fulmars (*Fulmarus glacialis*), as well as the Great Auk (*Pinguinus impennis*) (Hufthammer, 1982; Bengtson, 1984). Other than these species there are no macroecological studies on the avifaunal history of Norway, leaving a clear need to collate the research being conducted within Norway and the Scandinavian countries. This would enable us to draw comparisons with modern species distributions to produce overall patterns on avian biogeography in Scandinavia.

1.1 Project objectives

The overall aim of this project was to better understand the faunal histories of avian species in Norway during the Holocene (the last ~ 10,000 years). I aimed to achieve this by reconstructing past avian communities in Norway based on subfossil and archaeological bird remains. In doing so, I was able to identify factors and processes that have shaped current bird distributions. The primary objectives of the project were as follows:

1. To (re)assess past bird remains present in archaeological sites across Norway, forming a general view of species present. **(See; Paper I & Synopsis discussion)**
2. To better understand the timings and reasons for introduced species to Norway. **(See; Paper I, Paper II & Synopsis discussion)**
3. To identify past range shifts and to link these to palaeoecological (e.g. pollen records) and palaeoclimatic data (e.g. summer temperatures) to identify potential environmental drivers of avian range shifts. **(See; Paper I, Paper III & Synopsis discussion)**
4. To identify any morphological and body size changes in bird species through the Holocene **(See; Paper III & Paper IV)**
5. To put the Norwegian data in a broader perspective by collating the data from Norway with those from across Scandinavia and northern Europe to identify regional (Scandinavian Peninsula) and continental (northern Europe) changes in avian assemblages. **(See; Paper I - Paper IV & Synopsis discussion)**

This work not only significantly expands our knowledge of avifaunal history within Norway, but also places Norwegian data in a regional (Scandinavian) and continental (northern European) perspective. In addition, the resulting data presented here highlight new questions and research directions.

2. Material

2.1 Area of study

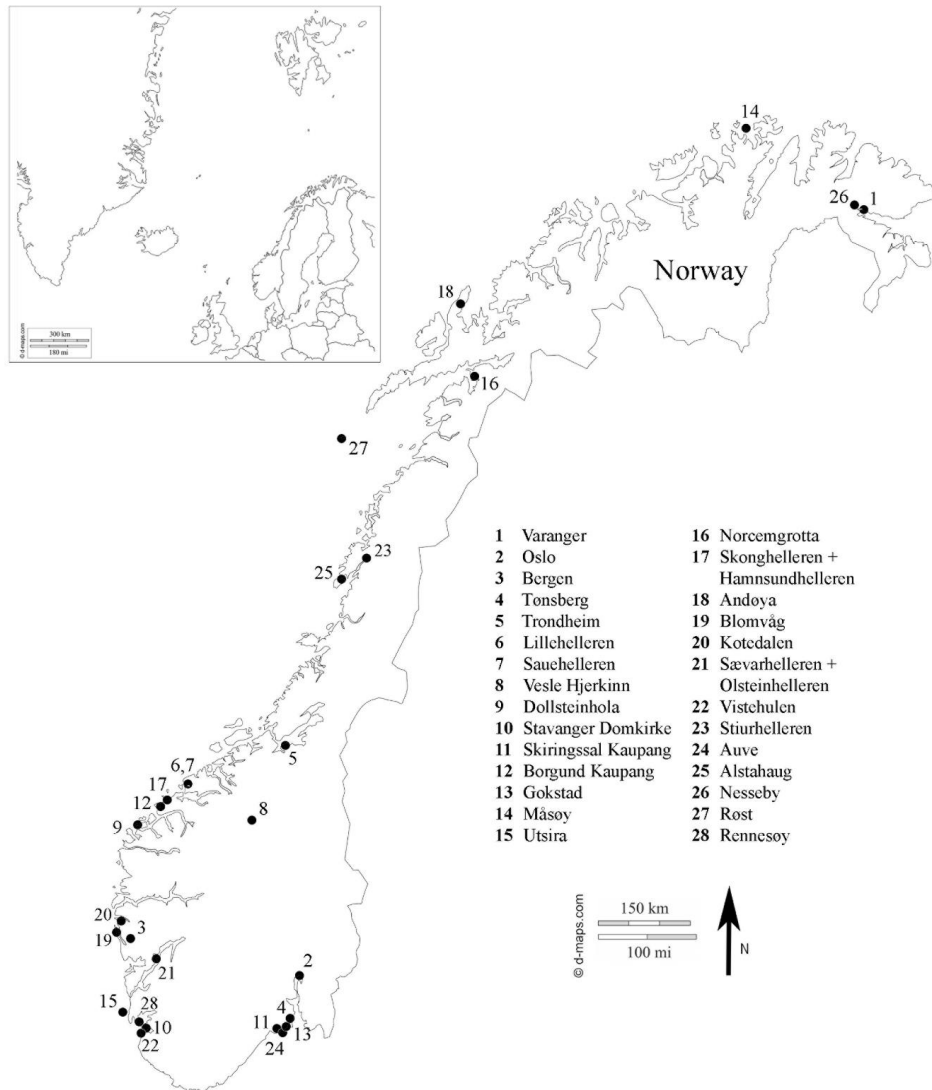


Figure 1. Map of the main sites mentioned within this synopsis. More detailed maps can be found within **Paper I-IV**, this is simply to give an overview of the study area.

The present project primarily concerned itself with patterns in Norwegian bird taxa. This is because all the archaeological material available to me is from Norwegian sites. However, countries are arbitrary and often have little effect on species distribution. As a result, I have always looked to compare the Norwegian material with the countries in the Scandinavian peninsula (Sweden, Denmark and Finland). Furthermore, in **Paper III** I include modern comparative material from Greenland, Scotland and the Faroe Islands. Archaeological sites mentioned within this synopsis are shown in figure 1.

2.2 Archaeological material

The Natural History collections at the University Museum of Bergen hold the largest collection of subfossil and archaeological faunal material from Norway, with material from over 1800 localities. Approximately 400 sites are known to have avifaunal remains (over 107,727 bones from dated localities) ranging in age from Post-glacial to Medieval. This large quantity of avian subfossil material available is unique and has allowed me to explore large-scale patterns in past avian distributions across time and space.

The preservation of archaeological bone material varies across Norway. In general, open air sites do not preserve well, with the exception of the Medieval period where we have large assemblages of well preserved remains (**Paper I**). Prehistoric sites in the north are fairly well preserved, even open-air sites such as the ones around Varanger (Olsen, 1967). Along the west coast of Norway, the majority of preserved prehistoric remains come from cave or rock-shelter sites (Bergsvik & Hufthammer, 2007; Lund & Degerbøl, 1951). Material from prehistoric sites in the east and south-east is generally burned and fragmentary (Hufthammer, 2014), which prevents many bird specimens from being identified.

As well as differences in site preservation, certain elements are more susceptible to processes of bioerosion and weathering. The synsacrum, sternum, skull and mandible generally do not preserve well (Davis, 1997), whilst the long bone elements have a better survivorship. Furthermore, recovery bias must be considered; many of the older sites involved hand recovery which often favours the long bones of larger bird species. To ensure that the smallest bird species are recovered it is necessary to sieve

using 1–2 mm mesh (Lyman, 2012; Baker & Worley, 2019). Systematic sieving of archaeological material was not introduced in Norway until 1973 (Lie, 1988) with the excavations at Mindets Tomt, Oslo. As a result of the preservation and excavation biases, the species which have been identified within the archaeological record are often biased towards larger bird species, with smaller species such as passerines being under-represented.

The chronological framework of this project generally follows that which is laid out in Figure 2. It is important to note that one cultural period does not abruptly end as another begins, and that often the transition from one period to another can take over a century. The dates I outline here are simply measures of time which allow me to link the archaeological remains with historic and climatic time periods. The terms which have been adopted throughout the project have been BCE (Before the Common Era), CE (Common Era) and BP (Before Present), where present is regarded as the year 1950. The dates for each period are the most generally accepted. The Mesolithic is dated from 9500–4000 BCE (Bjerck, 2007; Nærøy, 2018) and the Neolithic from 3950–1700 BCE (Prescott, 2020). The Bronze Age is interpreted as 1700–500 BCE. The Iron Age is dated to 500 BCE–1032 CE. The Viking Age is here considered part of the Iron Age, and dates to late 700–c.1032 CE (Barrett, 2008). The Medieval period is from 1032–1550 CE and the Post-Medieval encompasses from 1550 to the start of the industrial revolution. In addition to these sources, Vandkilde (1989), Olsen (1992), Nærøy (1993), Bergsvik (2002) and Hufthammer (2006) were also consulted on the chronological periods of Norway.

Year (BCE/CE)	Cultural Periods	Epoch
2000	Post-Medieval	Holocene (Post-glacial)
1500	Medieval	
1000	Viking Age	
500		
0	Iron Age	
500		
1000	Bronze Age	
1700		
2000	Late Neolithic (1700 – 2350)	
2500	Middle Neolithic (2350 – 2700)	
3000	Early Neolithic (2700 – 3950)	
3500		
4000		
4500		
5000		
5500		
6000	Late Mesolithic (4000 – 6500)	
6500	Middle Mesolithic (6500 – 8000)	
7000	Early Mesolithic (8000 – 9500)	
7500		
8000		
8500		
9000		
9500		
10,000	Palaeolithic	Pleistocene (Weichselian)

Figure 2. Overview of Norwegian time periods. Adapted from Hufthammer (2006).

2.3 Contemporary comparative material

Natural History Museum's hold large skeletal and skin collections of species, often collected over the last century. These collections provide a unique opportunity to look back at how species vary across time and space. In order to carry out the aims of this project (Section 1.1) a large number of modern comparative skeletal specimens were assessed. The University Museum of Bergen (UMB) houses the largest and most complete comparative bird skeletal collection in Norway, comprising of around 4000 specimens representing 95% of northern European bird species. In addition to the

natural history collections at UMB, two SYNTHESYS grants (DK-TAF-2419 and FI-TAF-2548) were successfully acquired, allowing modern specimens from the Natural History Museum of Denmark, Copenhagen, and the Finnish Museum of Natural History, Helsinki, to be included within the project. Further specimens were also analysed from the Natural History Museum at Tring, UK.

It is important when comparing archaeological specimens with contemporary populations to consider that the archaeological populations may represent a population that no longer exists or has undergone changes which no longer make it comparable to modern populations. However, I worked on the assumption that there are differences and as long as these are kept in mind and reflected within the discussions and conclusions they can be accepted. The main criteria for selection of contemporary specimens were geographic location, sex and date of acquisition. Many bird species are migratory, and around half of the c.500 bird species found in Norway are not permanent residents. This can lead to mixed species assemblages or shifts whereby one species is replaced by another. For example, it is important to look at breeding times and ranges. In the case of **Paper III**, only modern *F. arctica* specimens collected during the breeding season were considered to prevent mixing of subspecies.

A number of bird taxa (e.g. Atlantic Puffin (*Fratercula arctica*)) exhibit clinal body size variations. This intraspecific variation within a species must be considered when selecting comparative specimens for archaeological comparison, as it can greatly affect metric-based studies. In general, it is important to include a large sample of specimens from different geographical locations so as to take into account intraspecific variation (i.e. clinal variation, sexual dimorphism, and geographic variation).

To better understand the patterns observed, avian ecology was considered for all archaeological species. For general species overviews on sexual dimorphism, habitat, breeding times and distributions, the Cornell Lab of Ornithology, Birds of the World (online resource, formerly Handbook of Birds of the World) was used extensively. For more specific details on the distribution and breeding ranges of bird species in Norway, the Norsk Fugleatlas (Gjershaug et al., 1994) was consulted.

3. Methods

3.1 Zooarchaeology

The (re)assessment of archaeological faunal material was achieved through morphological comparisons with modern bird material at the University Museum of Bergen. As mentioned above the University Museum of Bergen has an extensive comparative collection. Species-specific identification criteria can be found within the methods of each of the 4 papers.

Species abundance is quantified here based on the Number of Identified Specimens (NISP). To prevent over-representation of species, ribs, vertebrae and phalanges were not included in this study. The approach throughout this project has been to make every effort to identify the species where possible. However, particular importance has been placed on acknowledging when it is not possible to reliably identify a specimen, to reduce the number of misidentifications. Several species are particularly hard to distinguish based upon morphological characteristics. For these species, outlined in Table 1, identifications were placed at a higher taxonomic level, unless diagnostic characters or metrics were available. For a synopsis of guidance on how to identify certain species I refer the reader to Stewart & Carrasquilla (1997). In addition, the species in Table 1 are further discussed in the methods section of **paper I**.

Table 1. Species which are difficult to distinguish osteologically, and the higher taxonomic level they were placed in.

Species	Identification level
<i>Lagopus lagopus</i> (Willow Grouse)	<i>Lagopus</i> sp.
<i>Lagopus muta</i> (Rock Ptarmigan)	
<i>Anser</i> sp.	Anserini sp.
<i>Branta</i> sp.	
Duck sp. that could not be assigned to tribe	Anatinae sp.
<i>Uria aalge</i> (Common Murre)	
<i>Uria lomvia</i> (Thick-billed Murre)	<i>Uria aalge/lomvia/Alca torda</i>
<i>Alca torda</i> (Razorbill)	
<i>Larus argentatus</i> (Herring Gull)	
<i>Larus fuscus</i> (Lesser Black-backed Gull)	<i>Larus argentatus/fuscus</i>
<i>Columba livia</i> (Rock Pigeon)	
<i>Columba oenas</i> (Stock Dove)	<i>Columba livia/oenas</i>
<i>Turdus iliacus</i> (Redwing)	
<i>Turdus philomelos</i> (Song Thrush)	Small <i>Turdus</i> sp.
<i>Turdus pilaris</i> (Fieldfare)	
<i>Turdus torquatus</i> (Ring Ouzel)	
<i>Turdus merula</i> (Eurasian Blackbird)	Large <i>Turdus</i> sp.
<i>Turdus viscivorus</i> (Mistle Thrush)	

3.2 Metrics and statistical analysis

Measurements were taken wherever possible, for fully mature specimens, with digital callipers to the nearest 0.1 mm. The measurements were based upon Von den Driesch (1976), with additional measurements taken from Kraft (1972), Erbersdobler (1968) and Otto (1981).

Statistical analyses were performed using the analytical programs PAST 4.03 (Hammer et al., 2001) and R (R Core Team, 2017). Explorative analyses such as Principal Components Analysis (PCAs) and box plots were used to initially explore the data. Specific details on the statistics used within each paper can be found within the respective methods sections.

3.3 Taxonomy

The taxonomic framework throughout this project follows the two volumes of the Handbook of Birds of the World (HBW) and BirdLife International illustrated checklist of Birds of the World (Non-passerines: del Hoyo & Collar 2014; Passerines: del Hoyo & Collar 2016), as does the English names for species. Osteological descriptions broadly follow Livezey and Zusi (2006). In the case of domestic fowl (*Gallus gallus* var. *domesticus*) and domestic goose (*Anser anser* var. *domesticus*) we refer to these species throughout the text as simply *Gallus gallus* and *Anser anser*.

The use of the term breed in relation to archaeological *G. gallus* is a contentious issue (Foster, 2018). In **Paper II** the term breed is used. However, it is not used in the modern sense, where strict uniformity is required by modern poultry exhibitors and the ‘British Poultry Standards’, but rather to indicate that there are multiple morphotypes of archaeological *G. gallus*. This is covered in more detail within the methods section of **Paper II**.

4. Results

4.1 Bird taxa from archaeological sites in Norway

The (re)assessment of 21 Norwegian Medieval sites resulted in 11,023 specimens that were (re)analysed, with 5,938 specimens being identified to species/family/order, leaving 5,085 specimens unidentified. It was possible to identify a minimum of 55 different species representing 15 orders. This was the largest analysis of bird bones to have been conducted for Norway and has resulted in the first overview of species presence and abundance on Medieval sites. The full results can be found in **paper I**. Here I shall outline the main results of the species representation for Medieval Norway.

Wild and domestic Galliformes formed 80% of the identified bird specimens from Medieval Norway (See Fig. 3). The majority of these were domestic fowl (*Gallus gallus*) making up 50% of the total Medieval bird specimens. Domestic fowl were widespread; they were present on 17 of the 21 sites studied. However, its dominance is heavily linked to the larger urban centres (Oslo, Bergen, Tønsberg and Trondheim), and they are less common on rural sites and sites in the north. Wild Galliformes were also well represented (just under 30%); the majority of these were *Lagopus* sp., Western Capercaillie (*Tetrao urogallus*) and Black Grouse (*Lyrurus tetrix*).

Anseriformes (ducks and geese) were also of importance during the Medieval period. The majority of these were Greylag Goose (*Anser anser*) (6%). These were interpreted as being the domestic form (*Anser anser* var. *domesticus*). This was based upon the fact that *A. anser* are rarely found on sites prior to the Medieval period and that they are mostly found in towns, not in their natural habitat. I do not rule out the possibility that some of these may be wild *A. anser* but I believe the majority to be domestic.

Other important orders included Accipitriformes (hawks and eagles), Charadriiformes (Specifically; Laridae and to an extent Alcidae) and Passeriformes (perching birds and songbirds), specifically the family of Corvidae (See Fig. 3).



Figure 3. Birds represented in Medieval Norway by order. Data taken from **Paper I**, which is based upon 21 Medieval sites across Norway.

Post-Medieval sites were briefly looked at as part of **Paper I**. The trend in Post-Medieval sites appears relatively similar to the Medieval period, with increasing reliance upon domestic species (*Gallus gallus* and *Anser anser*). The largest faunal assemblage for Post-Medieval Norway is the Erkebispegården site in Trondheim (Hufthammer, 1999). Erkebispegården is dominated by domestic species, but still has a good representation of wild species. In addition, a number of non-native/exotic species have been recorded at Erkebispegården, these include; Common Pheasant (*Phasianus colchicus*), Grey Partridge (*Perdix perdix*), Indian Peafowl (*Pavo cristatus*) and Turkey (*Meleagris gallopavo*). It is important to note that Erkebispegården was a high-status site and had both a monastic and a military phase. As such the species represented here, and their abundance, are not representative for the whole of Norway. At two other Post-Medieval sites, Revierstredet and Kontraskjæret in Oslo, domestic fowl is the most abundant species (c.40%). However, the abundance of *A. anser* here

is higher (10-15%) than seen in the Medieval period. This reflects the increasing importance of domestic goose from the Medieval period onwards.

4.2 Introduced species

An overview of the non-native bird species that have become established in Norway are outlined in Table 2. Mute Swan (*Cygnus olor*), Bar-headed Goose (*Anser indicus*) and Canada Goose (*Branta canadensis*) were all introduced to Norway around 20th century (Bevanger, 2005). The Mandarin Duck (*Aix galericulata*) is likely to have spread to Norway after it was established in Britain c.1700 CE (Bevanger, 2005). There is, perhaps unsurprisingly, no archaeological evidence of *C. olor*, *A. indicus*, *B. canadensis* or *A. galericulata* in Norway.

There are a number of *Columba livia* (Rock Dove) specimens, a species which is now considered to be feral (Michaelsen & Refvik, 2003), present within the archaeological record for Norway (Table 2). These are mostly from west coast sites, particularly from Lillehelleren where 19 bones have been attributed to *C. livia*, 4 of which are juvenile. Morphologically *C. livia* are very similar to *C. oenas*, which is a breeding visitor to south-eastern Norway (Baptista et al., 2020). This may result in misidentification, and DNA analysis is needed to confirm the early occurrences of *C. livia*. Due to the high status of Erkebispegården, it is possible that specimens of *C. livia* from this site represent kept *C. livia* (**Paper I**).

Phasianus colchicus, has been identified from the Erkebispegården site, in contexts dating to 1708–1783 CE (Hufthammer, 1999). This currently represents the earliest example of *P. colchicus* in Norway. Based upon the literature the first documented introduction of *P. colchicus* is at Bærum, Oslo in 1875–1876 CE (Bevanger, 2005). Another introduced Galliform is *Perdix perdix*. However, specimens from Post-Medieval Kontraskjæret and Medieval Vesle Hjerkin initially identified as *P. perdix* were re-identified as Hazel Grouse (*Bonasa bonasia*), a similar-sized species native to Norway (**Paper I**). Specimens from Dollsteinhola layer 2 (3460 BP) and layer 5 (3820–5630 BP) (Lie, 1989) are also most likely to be *B. bonasia*. The specimen from Post-Medieval Erkebispegården should also be considered with caution but may

represent one of the first introductions of *P. perdix* to Norway, given that other exotic species have been imported here.

Table 2. Non-native bird species in Norway and the first archaeological related evidence for these species. With the exception of *C. olor*, *A. indicus*, *B. canadensis* and *A. galericulata* for which the evidence is document based (see; Bevanger, 2005).

Species	Archaeological evidence	Dates
Wild		
<i>Cygnus olor</i>	None	1869/1870 CE (Bevanger, 2005)
<i>Anser indicus</i>	None	1950 CE (Bevanger, 2005)
<i>Branta canadensis</i>	None	1936 CE (Bevanger, 2005)
<i>Aix galericulata</i>	None	Later than 1700 CE (Bevanger, 2005)
<i>Columba livia</i>	Erkebispegården (JS 845)	1708–1783 CE (Hufthammer, 1999)
	Stavanger domkirke (JS 493)	(Medieval) - possible <i>C. oenas</i> (Paper I)
	Sauehelleren (JS 6)	Iron Age - see section 5.3
	Lillehelleren (JS 7)	Iron Age - see section 5.3
	Flatåsen III (JS 265)	Early Iron Age - see section 5.3
	Dollsteinhola (JS 706)	Bronze Age layer - (Lie, 1989) see section 5.3
<i>Phasianus colchicus</i>	Erkebispegården (JS 845)	1708–1783 CE (Hufthammer, 1999)
<i>Perdix perdix</i>	Erkebispegården (JS 845)	1537–1660 CE (Hufthammer, 1999)
	Kontraskjæret (JS 628)	(Post-Medieval) - reidentified as <i>B. bonasia</i>
	Vesle Hjerkin (JS 712)	(Medieval) - reidentified as <i>B. bonasia</i> (Paper I)
	Dollsteinhola (JS 706)	(Stone Age) - (Lie, 1989) possible <i>B. bonasia</i>
Domestic		
<i>Gallus gallus</i>	Kaupang in Skiringssal	Early 800–900 CE (Barrett et al., 2007)
	Borgund Kaupang	9 th /10 th century (Walker & Hansen, Unpublished)
<i>Anser anser</i>	Multiple Medieval sites	Medieval - (Paper I)
<i>Pavo cristatus</i>	Erkebispegården (JS 845)	1640–1672 CE (Hufthammer, 1999)
	Revierstredet (JS 600)	1624–c.1730 CE
	Mindets Tomt (JS 537)	(Medieval) - reidentified as <i>T. urogallus</i> (Paper I)
	Gokstad (JS 71)	895–905 CE (Hufthammer, In Press)
<i>Melagris gallopavo</i>	Erkebispegården (JS 845)	1708–1783 (Hufthammer, 1999)

In **Paper I** I have shown that *G. gallus* were becoming more frequent in the archaeological record around 1100 CE but were not abundant in Norway until around 1300 CE. The earliest evidence for *Gallus gallus* in Norway is currently dated to the

8th century from the Kaupang at Skiringssal (Barrett et al., 2007). Recently 5 *G. gallus* specimens from the Borgund Kaupang near Ålesund were radiocarbon dated as part of the NFR funded Borgund Kaupang project. Our early results show that *G. gallus* are present in some of the Viking Age contexts of the site (Walker & Hansen, Unpublished).

The introduction of *Anser anser* into Norway appears to occur during the Medieval period. Evidence within **Paper I** highlights the sites of Televerkstomten and Bibliotekstomten, Trondheim as having *A. anser* in contexts dating to around 1100 CE. Several sites show that *A. anser* and *G. gallus* are present within the early layers (Mindets Tomt, Oslo and Dreggsalmenningen, Bergen) but with *G. gallus* being more abundant. *Anser anser* increases in abundance by the mid/late Medieval period (**Paper I**).

There are few instances of *Pavo cristatus* in the archaeological record for Norway. The earliest instance of *P. cristatus* is from the Viking Age ship burial at Gokstad (Hufthammer, In Press). A specimen from Medieval Mindets Tomt, Oslo, was re-assessed and found to be *Tetrao urogallus* (**Paper I**). Post-Medieval *P. cristatus* were identified from the Erkebispegården (Hufthammer, 1999) and Revierstredet (Lie, 1981). In addition, the only archaeological *Meleagris gallopavo* from Norway was also recovered from Erkebispegården in contexts dating between 1798–1783 CE (Hufthammer, 1999).

4.3 Morphological and body size changes

The results of this project have shown body size changes in certain bird taxa over the Holocene. In **Paper III** I examined the skeletal metrics of modern and archaeological Atlantic Puffin (*Fratercula arctica*). The study focused on the limb bones, as these elements are well represented in the archaeological record. The results showed no distinct difference between modern *F. arctica* and archaeological *F. arctica* remains from Måsøy dated to 1620–1770 CE (Fig. 4). In contrast, I found the *F. arctica* assemblage from Dollsteinhola (dated to c.6600–3600 BP) to be somewhat different from modern *F. arctica*. Although the majority of bone elements from this assemblage fell within the size range of modern *F. a. arctica* and *F. a. grabae* subspecies. The

mean dimensions of *F. arctica* ulna, carpometacarpus, femur, tibiotarsus and tarsometatarsus from Dollsteinhola were smaller than the means of modern subspecies. Interestingly, the Dollsteinhola population displayed slightly shorter yet sturdier skeletal elements than their modern counterparts. This was particularly the case for the carpometacarpus (Fig. 4), where around half of the specimens were shorter than modern populations of both the nominate and the subspecies. (**Paper III**).

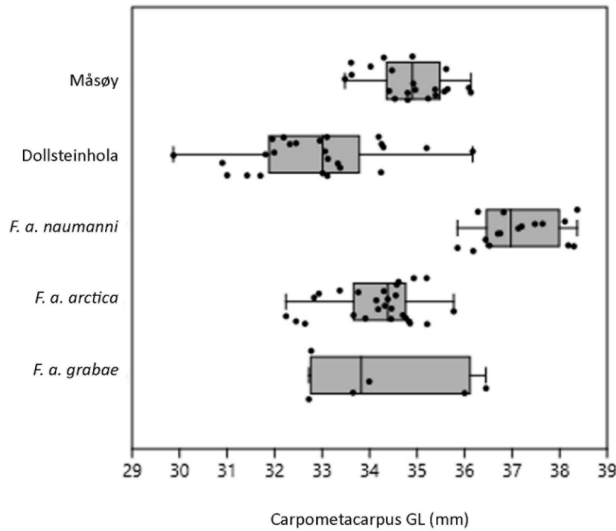


Figure 4. boxplots showing the size variation in the carpometacarpus greatest length (GL) of Atlantic Puffin populations. Måsøy n=21, Dollsteinhola n=25, *F. a. naumanni* n=16, *F. a. arctica* n=27 and *F. a. grabae* n=6. Data taken from **Paper III**.

Further investigations into seabirds in Norway have shown that size changes might also have occurred in the Little Auk (*Alle alle*). However, whilst the mid-Holocene *F. arctica* from Dollsteinhola were showing a reduced size (**Paper III**), *A. alle* appear to show the opposite. *Alle alle* occurs frequently within the archaeological record, and is especially common on the older sites (Larsen et al., 1987; Valen et al., 1996; Hufthammer, 2001). A specimen recovered by geologists in 2018, from a core sample taken from Utsira, southern Norway (Fig. 5B), dates to 20,000–21,000 years BP (John Inge Svendsen pers. comm.). The Utsira specimen was compared to 95 modern *A. a. alle* carpometacarpi from Norway (including Spitsbergen), Denmark, Greenland and Iceland. The results clearly show that the Utsira specimen is larger than contemporary *A. a. alle* populations (Fig. 5A). However, to properly interpret the observed changes seen in the Utsira specimen, measurements of the larger subspecies

A. a. polaris and a larger sample of archaeological specimens from Pleistocene and Holocene contexts from across Norway and Scandinavia needs to be included.

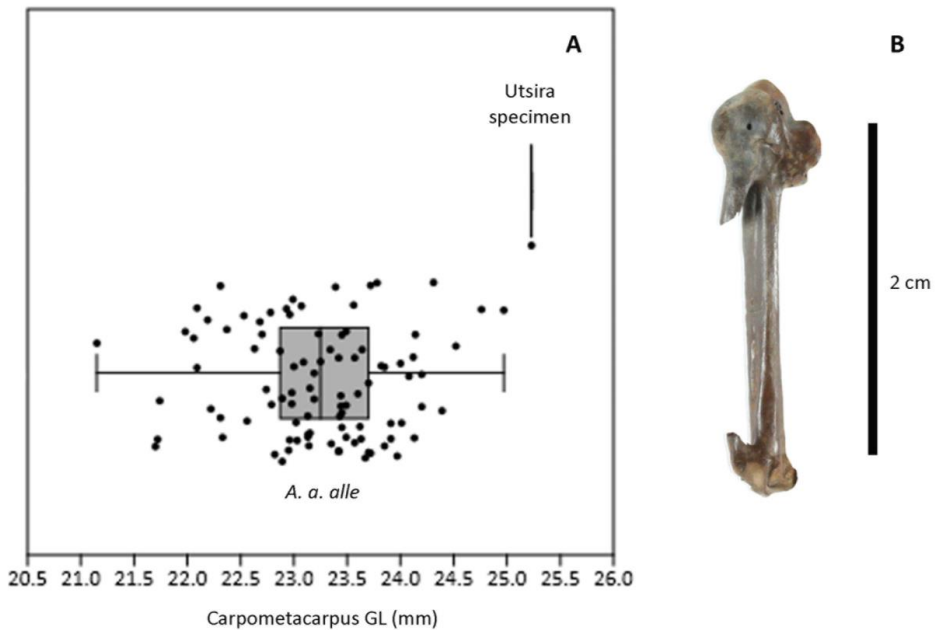


Figure 5. **A**, box, and jitter plot of the carpalometacarpus greatest length (GL), showing modern *A. a. alle* specimens and the Utsira specimen. **B**, photograph of the Utsira *A. a. alle* specimen in ventral view.

A difference in the greatest length of wing and limb bones of Northern Goshawks (*Accipiter gentilis*) in comparison to modern populations was initially identified in **Paper I**. Medieval specimens from Bergen, Oslo and Trondheim were found to be larger than modern specimens. This has been analysed in more detail in **Paper IV** for the humerus, ulna, carpalometacarpus, femur, tibiotarsus and tarsometatarsus. Measurements were taken from 240 specimens of modern *A. g. gentilis*, from Norway, Denmark, Sweden and Finland. This is the largest assessment of modern skeletal measurements gathered for Scandinavian Goshawk populations. The data show that Medieval female Goshawks were larger than modern females. The Viking Age specimens from Gokstad, however, are similar in size to modern Goshawks (Fig. 6). Furthermore, my data show that Northern Goshawks in Scandinavia have been declining in size over the past century.

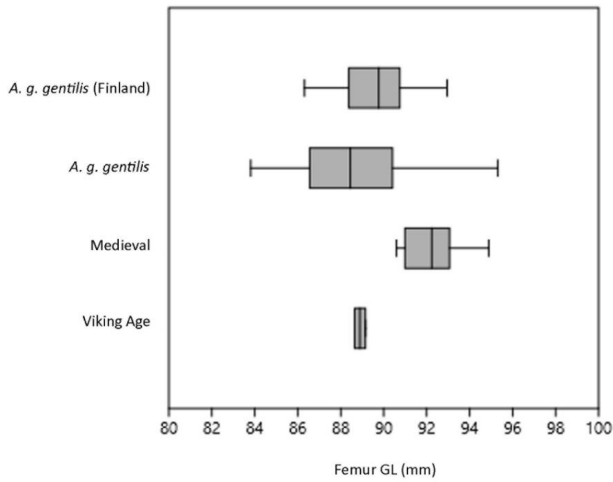


Figure 6. boxplots showing the size variation in the greatest length (GL) of the femur of female Northern Goshawk populations. *A. g. gentilis* (Finland) n=30, *A. g. gentilis* n=69, Medieval n=8 and Viking Age n=3. Data taken from **Paper IV**.

5. Discussion

5.1 Past bird populations in Norway

Records of bird taxa from northern Europe during the last glaciation, known as the Weichselian (115,000–10,000 BP), are relatively few. Some of the best evidence comes from Poland (Tomek & Bocheński, 2005; Lorenc, 2006), Germany (Kahlke, 2000) and Denmark (Aaris-Sbrensen, 1995), an area known as the North European Plain. The avian species identified here give an indication of the species which would eventually inhabit Scandinavia after the Last Glacial Maximum (LGM) around 14,000 years BP. The species identified from the North European Plain have included Anseriformes (e.g. *Cygnus* sp., *Anas platyrhynchos*), Gallinaceous species (e.g. *Lagopus* sp., *T. tetrix*, *T. urogallus*), birds of prey and owls (e.g. *Aquila chrysaetos*, *Buteo buteo*, *Asio* sp., *Strix* sp.), wader species (e.g. *Limosa limosa*, *Gallinago media*) and passerines (e.g. *Turdus* sp., *Hirundo rustica*, Corvid sp.) (Ericson & Tyrberg, 2004).

Most evidence of birds in Norway during the Weichselian come from a number of cave deposits along the west coast of Norway (Larsen et al., 1987; Lauritzen et al., 1996; Valen et al., 1996; Hufthammer, 2001). These sites would have been ice free during inter-stadial periods of the Weichselian (See; Hughes et al., 2016). The earliest bird remains recovered in Norway come from Norcemgrotta, Kjølsvik, in northern Norway. The birds represented here were *Somateria* sp., *P. carbo* and *L. muta* and come from a layer likely to be older than 70,000 years BP (Lauritzen et al., 1996). They are likely to represent an interstadial period of the Weichselian, but it is possible that they date as far back as the late Eemian.

Skjonghelleren is a cave site on Valderøy in Møre & Romsdal, dating to 28,000–33,000 BP (Larsen et al., 1987), and part of the Ålesund interstadial. The vertebrate fauna was studied by Rolf Lie, who found that the bird assemblage was characterised by marine species such as *Alle alle* and *Uria lomvia*. The fauna from nearby Hamnsundhelleren also dates to the Ålesund interstadial, between 28,000–38,000 BP. Anne Karin Hufthammer studied this material and also found a dominance of seabirds, largely *A. alle* (Valen et al., 1996). Evidence from pollen, microfossils, geochemistry and stable isotopes indicates that certain coastal areas, for example Andøya (Alsos et

al., 2020) were ice free during the Last Glacial Maximum (at ~20,000 BP). The presence of *A. alle* at Andøya and Utsira (See section 5.3) highlight the presence of seabirds during ice-free periods of the Weichselian. At the site of Blomvåg (ca. 12,000–12,500 BP), just north of Bergen, marine species once again dominate the bird fauna. Eider ducks are the most abundant (*Somateria mollissima* and *S. spectabilis*) but Alcidae species are still well represented with *Alca torda*, *Uria aalge*, *U. lomvia*, *Cephus grylle* and *Pinguinus impennis* (Lie, 1990).

By around 10,000 years BP, large areas of Norway were ice-free (Hughes et al., 2016). However, areas along the Norwegian coast were already free of ice by around 14,000–13,000 years BP (Hufthammer, 2001; Hughes et al., 2016). During this time pioneer bird species which occurred during the interstadial periods throughout the Weichselian would have returned. On land typical pioneer species would have been *Nyctea scandiaca* and *Lagopus* sp., whilst along the coast, Alcidae species and other hardy seabirds such as the Eider ducks would have been present (Hufthammer, 2006). In addition, species suggested by Ericson and Tyrberg (2004), such as galliforms, waders and passerines, would have expanded from the Northern European Plain up into Norway.

During the Mesolithic (9500–4000 BCE), there is a shift in abundance of bird species represented within sites. The late Mesolithic phases of Kotedalen (6560–5650 cal BCE), located on the west coast just north of Bergen, had relatively few birds. Fish and mammal species were more dominant. The bird species which were identified were all seabirds; *Phalacrocorax carbo* was dominant but Alcidae species were also present (*A. torda* and *U. aalge*) (Hufthammer, 1992). Two late Mesolithic rock-shelters, Sævarhelleren and Olsteinhelleren (7000–4500 cal BCE) located inland from Kotedalen in the Hardangerfjord (Figure 1), show a similar pattern; both rock-shelters have an almost complete absence of birds. The assemblages are mostly fish with some mammals (Bergsvik & Hufthammer, 2007). These sites show that at least for the area around Bergen, away from seabird breeding colonies, birds held little importance during the Mesolithic period.

The Early Neolithic phases at Kotedalen (4040–2790 cal BCE) indicate an increased importance of birds relative to the Mesolithic. Seabirds are dominant,

especially Alcidae. Given the absence of a nesting colony in the vicinity, these are believed to have been caught at sea (Hufthammer, 1992). Despite the increased importance of birds, fish and mammals remain dominant. Other Neolithic sites such as Vistehulen (Lund & Degerbøl, 1951), Sturhelleren (Hultgreen et al., 1985) and the Varanger sites (Olsen, 1967) (Figure 1) show a similar pattern: seabirds are most abundant, particularly Alcidae, and Eider ducks to a lesser degree. In addition, *Lagopus* sp. are also exploited in reasonable numbers on some sites (Olsen, 1967). The middle Neolithic site of Auve in Sandefjord is one of the few prehistoric south-eastern sites in Norway. Birds form 5.8% of the faunal assemblage (Østmo, 1984). It appears that duck species (*S. mollissima*, *Melanitta fusca*, *Mergus serrator*, amongst others) have an increased importance here, rather than the Alcidae as seen on the west coast sites. Alcidae species are represented by *U. aalge*, *A. torda* and *C. grylle* but they are not dominant (Østmo, 1984).

There is a distinct lack of inland sites dating to the Mesolithic and Neolithic, possibly because coastal sites were being favoured to take advantage of marine resources. In Finland evidence from Mesolithic and Neolithic sites indicate that Galliformes are important to inland sites whilst Anatidae species have an importance on the coast (Mannermaa, 2003). Galliformes would likely have been the primary bird species on inland sites in Norway given their presumed abundance and the fact that they are a ground-nesting species. The differences seen between coastal sites in Norway and Finland, i.e. seabirds being more abundant in Norwegian coastal sites than in Finnish ones, is indicative of the absence of large seabird colonies along the Finnish coast. Sites close to seabird colonies often take advantage of this resource, as is also seen in the Scottish Isles (Best & Mulville, 2013; 2014; 2016).

The transition from the Mesolithic period to the Neolithic traditionally represents a shift from hunter-gatherer to agriculture. However, the actual timing of this process in Norway has been difficult to pinpoint. For example, there is a discrepancy between the earliest occurrences of Ribwort Plantain (*Plantago lanceolata*) pollen, a plant indicative of increased grazing activity, and the earliest bones of domesticated animals in western Norway (Hjelle et al., 2006). From the little evidence there is of bird species from Mesolithic and Neolithic sites, there appears to

be a slight increase in their relative abundance within Neolithic faunal assemblages. Whether this is to do with a more sedentary lifestyle remains difficult to say. In general, during both the Mesolithic and Neolithic, people appear to have made the most out of local natural resources (Olsen, 1967), generally favouring mammals and fish over bird species.

There are relatively few Bronze Age, Iron Age and Viking Age sites with faunal remains for Norway. However, the few Viking Age faunal assemblages that are available show that in contrast to earlier periods, birds were considered precious commodities, and some might have been imported from abroad. The Kaupang in Skiringssal, near Larvik in south-east Norway, documents the first occurrence *G. gallus* in Norway (Barrett et al., 2007). Furthermore, the Gokstad ship burial in Sandefjord contained a pair of *A. gentilis* females (likely kept as falconry birds) and the remains of *P. cristatus* (Hufthammer, In Press).

In contrast to the previous periods, there is a wealth of faunal material available for the Medieval period in Norway (1032–1550 CE). The Medieval period in Norway is a period of change, characterised by the rise of large urban centres and climatic fluctuations (the Medieval Warm Period (MWP) and the Little Ice Age (LIA)). My research shows distinct changes in the exploitation of bird species during the Medieval period compared to previous periods. The biggest of these is the introduction and establishment of domestic bird species (see section 5.2), and a decreasing reliance on wild species. Despite this, there is a large presence of wild Galliform species, while seabirds (in particular Alcidae) become less important. Although birds started to obtain significant importance during the Viking Age, it is clear that by the Medieval period birds are more than just a food source. The use of *G. gallus* in blood sport (**Paper II**), the presence of more elaborate chicken types/breeds (**Paper II**), the introduction of exotic species (**Paper I**) and the increased use of falconry (**Paper I; Paper IV**) during the Medieval and Post-Medieval periods show a significant and widespread change in attitude toward bird species.

5.2 Non-native species

Introduced species are defined as taxa which are not native to the area in which they have advertently or inadvertently been brought into. For Norway there are a number of species which fall into this category (Table 2). With the exception of *C. olor*, *A. indicus*, *B. canadensis* (all three believed to have been introduced during the 20th century) and *A. galericulata* (thought to be introduced after 1700 CE (Bevanger, 2005)), the date and means by which these species arrived are poorly understood. Here I have, for the first time, collated the archaeological evidence for these species (Table 2) in order to better understand their spread and faunal histories. The majority of this work is based upon the research in **Paper I**.

The feral populations of the Rock Dove *C. livia* are an example of a non-native species which are seen as a pest. They are now found across Norway (Gjershaug et al., 1994). However, prior to the Post-Medieval period, there is very little evidence of *C. livia* in Norway. I believe that the specimens of *C. livia* recovered from the Erkebispegården are likely to have been the origin of the feral populations which have become so prevalent in towns across Norway today. The *C. livia* from Erkebispegården are likely to represent kept pigeons, as this was a common practice on monastic sites across Medieval and Post-Medieval Europe (Canova, 2005). *Columba livia* may have escaped from the site or have been released when Erkebispegården ceased to be a monastic centre during the Reformation (1537 CE), which marked the end of the Medieval period in Norway. An earlier Medieval site, the Stavanger domkirke, also has a specimen of *C. livia/oenas*. I have interpreted this specimen as likely to be *C. oenas*, as the breeding range of *C. oenas* extends to the southeast of Norway (Baptista et al., 2020). However, I cannot exclude that it may also represent a monastic kept pigeon. DNA analysis is needed to separate *C. livia* and *C. oenas* accurately. Interestingly, there are earlier reports of *C. livia* within the archaeological record for Norway (See Table 2). It is unclear if these specimens represent natural populations or kept/feral birds (also see section 5.3).

The best archaeological evidence for the introduction of the phasianids *P. colchicus* and *P. perdix* also comes from the Post-Medieval context of the Erkebispegården (Hufthammer, 1999). However, distinguishing between the two

species is difficult. *Phasianus colchicus* is morphologically very similar to *G. gallus*, and *P. perdix* is similar to the native *B. bonasia*. *Perdix perdix* specimens from Kontraskjæret and Vesle Hjerkin were re-identified as the native *B. bonasia* (**Paper I**). Both *P. colchicus* and *P. perdix* from Erkebispegården need to be confirmed with the use of DNA. If confirmed, these two species were likely introduced for hunting purposes. There are no natural populations of *P. perdix* breeding in Norway, which is likely due to the unfavourable climate and poor survivorship of this species through especially cold winters (Gjershaug et al., 1994).

One of the most intriguing introductions to Norway is the domestic fowl. The domestication of *G. gallus* took place in several centres of domestication in East Asia in the Early Holocene (Liu et al., 2006; Miao et al., 2013). Due to their size and ease of transportation, they have become established as a major food source across the globe. It is thought that domestic fowl were introduced to Europe through Phoenician trade routes (West & Zhou, 1988; Serjeantson, 2009; Becker, 2013; Perry-Gal et al., 2015). In northern Europe (i.e. the Netherlands and Germany) evidence suggests an arrival of *G. gallus* around the 7th–8th century BCE (West & Zhou, 1988; Becker, 2013). Evidence for Scandinavia suggests a later introduction, the earliest examples come from Sweden and Denmark around the 1st century BCE and 1st century CE respectively (Lepiksaar, 1977; Tyrberg, 2002; Ericson & Tyrberg, 2004; Gotfredsen, 2013; 2014). The earliest evidence for Finland currently dates to the 8th century CE (Ukkonen & Mannermaa, 2017; Wessman et al., 2018).

The earliest *G. gallus* remains for Norway date to the 9th century CE (Barrett et al., 2007; **Paper I**; Walker & Hansen, Unpublished). However, it is not until 1100 CE that *G. gallus* start to be more common on Norwegian sites, and not until 1300 CE that chickens become abundant within the bird remains. There is no strong evidence for *G. gallus* in Norway pre-Viking Age. This delayed arrival of chickens into Scandinavia, especially Norway and Finland, is in contrast to other elements of the agricultural package, such as cattle, sheep/goats, pigs and dogs, that were already well established in Scandinavia since the Neolithic period (Rowley-Conwy, 2011; Price, 2015).

As the presence of *G. gallus* in northern Europe by the 7th–8th century BCE did not lead to a natural diffusion of chickens into Scandinavia, it is difficult to pinpoint

where they may have been introduced from. It may be that the initial introduction was up through Denmark and Sweden via longer-distance trade routes. Chickens are abundant on Roman sites (Lauwerier, 1993; Maltby, 1997; 2010), and although the Romans never reached Scandinavia, their expansive trading networks extended well into the region (Imer, 2010; Grane, 2013). It is possible that trading networks between the Romans and northern Germanic tribes led to the introduction of the chicken to Scandinavia.

For Norway, Barrett et al., (2007) have suggested that the few specimens from the Viking Age Kaupang in Skiringssal may have been introduced through trade with Denmark or eastern Sweden. Initial evidence from the Viking Age-Medieval Borgund Kaupang suggest trade links with Britain, Germany and France, amongst others (Walker & Hansen, Unpublished). Borgund Kaupang at the time was one of the main trading sites on the west coast of Norway, and the chicken remains from this site may have originated from any of the sites within the trade networks. If the remains from the Skiringssal and Borgund Kaupang's indeed represent the earliest chickens in Norway, it seems Viking trade networks were responsible for the introduction of chickens to Norway.

Medieval occurrences of *G. gallus* are almost exclusively in urban settlements, which would have been the key trading sites in Norway. Once *G. gallus* was established in the towns it spread out to the rural sites. The spread and establishment of *G. gallus* to rural communities did not occur until the late Medieval to Post-Medieval. From the few Medieval rural sites available, i.e. Alstahaug, Nesseby, Velse Hjerkin and Røst, it appears *G. gallus* had little to no importance to these communities, as wild species were still favoured (**Paper I**). Whilst becoming more prominent on urban sites, chickens still remained a fraction of the overall faunal assemblages on sites in Medieval Norway. Birds generally formed less than 5% of the faunal assemblages, and *G. gallus* accounted for on average 50% of the bird bones identified (approx. 2.5% of the overall faunal assemblages). As a result, *G. gallus* represents a relatively small contribution to the diet. In combination with other evidence, this suggests that Medieval and Post-Medieval *G. gallus* were kept for other purposes than just food (**Paper II**).

A total of 93% (n=2642) of the Medieval *G. gallus* specimens were fully mature adults (**Paper I**). This indicates that rather than being slaughtered early for meat, chickens were being kept for secondary products, such as egg production. The small number of juveniles (n=66) suggests that at least some chickens in urban sites were bred locally. In modern keeping of chickens it is often recommended to have no more than 1 male to every 5–10 females, dependant on breed. This is because males are fiercely territorial, and more cockerels will inevitably lead to in-fighting. In the Medieval *G. gallus* material, the ratio of males to females is roughly even (**Papers I-II**). Out of 258 tarsometatarsi, 128 were identified as males and 130 as females. (caveats in sexual identification using the tarsometatarsus of *G. gallus* are covered in more depth within **Papers I-II**). This unusually high ratio of males to females found on Medieval and Post-Medieval sites in Norway indicates that *G. gallus* was kept for other purposes.

In addition to the high percentage of adult males, I identified that many of the bony spurs on the male tarsometatarsi had often been either partially or completely removed (**Paper II Fig 4**). These specimens came from Bergen, Oslo and Trondheim, areas associated with trade and typically male dominated. The removal of the bony spurs seen in the male *G. gallus* specimens is interpreted as evidence for the blood sport of cockfighting in Norway (**Paper II**). Similar specimens have been identified across northern Europe and were also interpreted as evidence for cockfighting (Ehrlich et al., In Press; Moreno-Garcia & Pimenta, 2010; Thys & Van Neer, 2010; Johnstone, 2007; West, 1982). The 16 tarsometatarsi with their spur removed reported here appears to be unprecedented in terms of numbers, and represent the first evidence for cockfighting in Scandinavia.

Finally, my research into *G. gallus* within Norway has identified variation in size that exceeds sexual dimorphism (10–20%) (**Paper II**). The variation in bone length in the Medieval period suggests that there were multiple types/breeds of domestic fowl. In addition, the presence of several skulls with holes or “cranial hernia” indicates the presence of chickens with a feather crest, typical of crested breeds. This supports our theory that domestic fowl were introduced to Norway by multiple trade routes, as I consider it unlikely that a single population formed the basis for the variation in size

and shape seen in the Medieval fowl in Norway. For Post-Medieval Norway, the data suggests that particularly large types/breeds were being introduced, especially in the southeast around Oslo (**Paper II**). This is also seen in the UK, where the largest increase in size of domestic fowl in London is seen between 1220–1600 CE, and also later in the Post-Medieval period (Thomas et al., 2013).

Based on current evidence (**Paper I**) I suggest that domestic geese, *A. anser*, were introduced during the Medieval period. Around 1100 CE, slightly later than *G. gallus*, *A. anser* starts to be seen on urban sites. Domestic geese were almost solely present within urban contexts and became more prolific as the Medieval period went on, and into the Post-Medieval. However, it never dominated assemblages in the same way as *G. gallus*. In the UK goose husbandry was at its peak during the 13th–14th century (Albarella, 2005). This appears to coincide with *A. anser* becoming more abundant in Norwegian towns. Whether this is a coincidence, a rise in importance of domestic geese from the UK, or a shift in preference needs further investigation. Similarly to domestic fowl, there is little evidence of juveniles and the vast majority of *A. anser* remains represent adults. This suggests *A. anser*, much like *G. gallus*, were prized for their secondary products such as feathers and eggs.

The apparent increase in the abundance of *G. gallus* and *A. anser* around 1300 CE is of particular interest. The Black Death reached Norway in 1349 CE, and by all accounts was devastating, with around 60–65% of the population succumbing to the plague (Benedictow & Benedictow, 2004). It has been estimated that around half of all farms in Norway were lost as a consequence of the plague (Hasund, 1919; Lunden, 2002; Moseng, 2006). Prior to the Black Death (early 14th century) documentary evidence suggests that increased precipitation was leading to crop failures and famine, which in turn led to the abandonment of farms (Dybdahl, 2010; Dybdahl, 2012; Thun & Svarva, 2018). The multitude of difficulties faced by people in 14th century Norway may explain as to why poultry and geese increased. The decline in farms would have inevitably had an effect upon the supply of food to towns. This may well have led to an increased reliance upon keeping a small number of domestic species within towns, in particular, poultry which would have been of low cost and needing relatively little space.

Other non-native species found in the archaeological record for Norway are *Pavo cristatus* and *Meleagris gallopavo*. Peacocks are first found in the Viking Age ship burial at Gokstad dated to 895–905 CE (Hufthammer, In Press) and is not seen again until the Post-Medieval period. The only record of *M. gallopavo* is a single sternum from the Erkebispegården (Hufthammer, 1999). Neither *P. cristatus* or *M. gallopavo* went on to become widespread in Norway and they have very little importance to the general trends seen in Norway. But what they do represent is power and status, as these species are not common and would likely have been traded for a significant price.

5.3 Avian responses to past environmental change

The 2018 BirdLife International report ‘State of the World’s Birds’ clearly outlines the current biodiversity crisis facing bird species. The 5 main threats to bird species are expanding and intensified agriculture, logging, introduced/invasive species, hunting and climate change (BirdLife International, 2018). Global temperatures are expected to rise by between 1.5–2 °C by 2100 (Collins et al., 2013) and this is expected to be amplified in the Arctic regions (Collins et al., 2013; Pithan & Mauritsen, 2014). The direct and indirect effects of climate change will likely contribute to further decline in bird populations. Past bird populations can help us to better understand how birds reacted to climate and environmental change. Two of the most common responses of bird species to past climatic change appear to be range shifts and body size changes (Lagerholm et al., 2017; Stewart & Jacobi, 2015). This pattern is reflected in the results of this thesis (**Papers I-IV**).

During the last Ice Age, temperatures were on average 6–8°C lower than today and an ice sheet covered most of Norway and parts of the Norwegian sea (Eldevik et al., 2014; Kindler et al., 2014; Hughes et al., 2016). However, small areas on the coast were ice-free (Vasskog et al., 2019; Alsos et al., 2020). The presence of bones of Little Auks (*Alle alle*) from Andøya (Alsos et al., 2020) and Utsira (this thesis) indicate that Little Auks were one of the pioneering species, leading the post-glacial colonisation. This is further supported by *A. alle* and other Alcids (i.e. *Uria lomvia*) dominating

interstadial assemblages at Skjonghelleren and Hamnsundhelleren (Larsen et al., 1987; Valen et al., 1996; Hufthammer, 2001) (Section 5.1).

The Utsira specimen is larger in size than modern *A. alle*. This could represent a plastic (i.e. a rapid phenotypic change) response to colder air temperatures. Wojczulanis-Jakubas et al. (2011) suggested that *A. alle* body size increased significantly with air temperature. Secondly, the Utsira specimen and other larger specimens of *A. alle* recovered from Andøya (Alsos et al., 2020; Elverland & Alm, 2012) may represent the larger subspecies *A. a. polaris*. Little Auks display a clinal size increase in body size. The smallest birds breed in the west (Greenland and Jan Mayen), intermediate sized individuals breed on Spitsbergen and the largest are found on Franz Josef Land (Wojczulanis-Jakubas et al., 2011). This would mean that *A. a. polaris* underwent a significant range contraction since the end of the Pleistocene, and that they are currently in a refugial state. Finally, the specimen from Utsira may represent a now extinct species of Little Auk.

In contrast to the larger size observed in late glacial *A. alle*, a body size decrease was seen in mid-Holocene Atlantic Puffin (*F. arctica*) (**Paper III**). Specimens of *F. arctica* from Dollsteinhola (c. 6600–3600 BP) show a large size range that encompasses the modern size range of both *F. a. arctica* and the smaller subspecies *F. a. grabae*. Some Dollsteinhola specimens also fall outside of this range, on the lower end of the scale. This increased size variation is here interpreted as a range shift of *F. a. grabae* (**Paper III**). Its current northern limits lie 145 km south of Dollsteinhola at Utvær, and the climatic oscillations of the mid-Holocene likely led to a northwards expansion of *F. a. grabae*. Stable isotope analysis of the Dollsteinhola Atlantic Puffins would yield insights into whether this range expansion was accompanied by a shift in diet. Although questions remain over whether *F. a. grabae* are a valid subspecies (see **Paper III**, and recent DNA work by Kersten et al., 2020), our data indicate that a population of smaller *F. arctica* is present at Dollsteinhola during a time of climatic oscillations. This suggests that Atlantic Puffins, and potentially other seabirds as well, expanded northwards in response to warming temperatures. For species that already breed at the limit of their geographic range in the high arctic such as the Little Auk this could be problematic.

Interestingly, some of the *Dollsteinhola* specimens exhibit slightly different proportions than modern populations, appearing slightly shorter and stockier. These differences are most pronounced in the carpometacarpus (**Paper III**). Shorter wing bones (and flight feathers) may have reduced drag in the water and could have increased diving efficiency, (Pennycuick, 1987; Livezey, 1988; Livezey, 1989; Louw, 1992). A shorter wing length may also have negatively affected flight ability (Nudds, 2007; Simons, 2010; Wang et al., 2011). Whether these differences in proportions indicate a functional difference in mid-Holocene Atlantic Puffins or signal an influx of a smaller and sturdier morphotype remains unclear.

Changes in body size over time were also identified in the Northern Goshawk (*Accipiter gentilis*) (**Paper I; Paper IV**). Scandinavian Northern Goshawks show a decline in body size during the 20th century (**Paper IV**). In particular, our results show a 2–3% decline in female Norwegian and Swedish Goshawks. Male individuals in Norway and Sweden show little change during this time period. In Denmark females decreased in size by 6–7% and males by 3–4% over the past century (**Paper IV**). When the modern populations were compared with the archaeological specimens from Norway, Medieval Goshawks were larger than contemporary populations, particularly the females. Two Viking Age specimens are similar in size to modern populations but appeared smaller than specimens from the Medieval period. The reasons behind this body size decrease are not clear. A similar decline in modern Finnish *A. gentilis* body size (Tornberg, 1999; Tornberg et al., 2014) has been interpreted as a change in diet to smaller prey. Northern Goshawks in Norway are facing many threats (Heggøy & Shimmings, 2020). Warming temperatures and a subsequent decline in forest habitats since the Medieval period might have driven the birds to forage on different, smaller prey and resulted in a smaller body size in Northern Goshawks (**Paper IV**). Our study shows that significant body size changes in birds can occur over relatively short time spans, and that these effects can vary for males and females.

Despite the significant climatic and environmental change since the end of the glacial period, there is little evidence that indicates that species in Scandinavia became extinct. The exception to this is the Great Auk (*Pinguinus impennis*), as there are a number of archaeological sites along Norway's coastline that have yielded bones of *P.*

impennis. The last occurrence of *P. impennis* in Norway dates to 1500 BP (not calibrated) (Hufthammer, unpublished data). The absence of *P. impennis* from Medieval sites in Norway (**Paper I**) suggests that by this time the species was in heavy decline, and all Norwegian breeding sites had been abandoned prior to the Medieval period (Hufthammer, 1982). A similar pattern has been seen in archaeological assemblages of the Scottish Isles, with Great Auks being absent from the archaeological record by the Viking/Norse period (Best & Mulville, 2014). Recent DNA studies have shown that *P. impennis* were a widely distributed and genetically diverse species prior to human exploitation (Thomas et al., 2019). It is unclear whether *P. impennis* would have survived climatic changes up to this point should they not have become extinct.

The loss of wild *C. livia* from Norway might represent a second possible extinction. The current distribution suggests that the furthest north wild *C. livia* are found is the west coasts of Ireland and Scotland and the Faroe Islands, but these are thought to now be feral (Lowther & Johnston, 2020). Wild *C. livia* is thought to have inhabited Rennesøy, south Norway up until the late 19th century (Collett et al., 1921; Haftorn, 1971; Gjershaug et al., 1994; Michaelsen & Refvik, 2003). Specimens from Norwegian archaeological sites prior to the Medieval period were unexpected. Although the Medieval and Post-Medieval specimens are from monastic sites and likely to represent kept pigeons, the pre-Medieval specimens are all from coastal sites on the west coast (Sauehelleren, Lillehelleren, Flatåsen III (near Trondheim) and Dollsteinhola). The location of these archaeological finds fits with the habitat preferences of wild *C. livia* (steep cliffs with few trees along the coast) (Cramp, 1985). Although *C. livia* and *C. oenas* are difficult to separate osteologically, the location of the specimens does agree with known habitat preferences of *C. livia*. Given the location of the specimens and the presence of juveniles and the fact that wild populations were present in southern Norway (Michaelsen & Refvik, 2003) there may well have been wild Rock Pigeons breeding along the west coast of Norway during the Bronze Age to Iron Age.

The Medieval period saw the rise of large urban centres and significant climatic oscillations (Medieval Warm Period (MWP) and the Little Ice Age (LIA)) (Ahmed et

al., 2013; Zawiska et al., 2017). I therefore expected to see range shifts within the avifauna of Norway. However, the results of our investigation into Medieval bird species show that for the majority of species their distribution has not changed (**Paper I**). Occurrences of most Medieval specimens overlapped with their current distributions. For example, in Western Capercaillie (*Tetrao urogallus*), their distribution covers the majority of Norway, however, their densities are higher east of the Norwegian watershed (Haftorn, 1971; Gjershaug et al., 1994). The Medieval abundances of *T. urogallus* were clearly higher to the east in Oslo than the western Bergen (**Paper I**). Unexpectedly, species which are very common in urban centres today, such as gulls and crows, are relatively poorly represented within the archaeological record within Medieval towns (**Paper I**), whilst in Sweden they have been linked to settlements early on (Ericson & Tyrberg, 2004). Laridae and Corvidae species were expected to increase with the establishment of towns. However, it appears that the dominance of these species in urban centres today is not reflected in the Medieval period. Swedish data suggests that Herring Gull (*Larus argentatus*), were almost exclusively marine species prior to c.1900 (Ericson & Tyrberg, 2004). For Norway it would seem that the dominance of these species increased after the Medieval period and possibly even later than the Post-Medieval period.

6. Conclusion

Overall, my research has not found significant changes in bird species in Norway during the Holocene. However, I observed subtle changes and signs that could be exacerbated in response to future global change. This body of work currently provides the most up-to-date and in depth research into the history of birds in Norway for a wide range of species. My findings include the first evidence for cockfighting in Scandinavia, and a clearer understanding of when and why species were introduced to Norway. There is evidence that species have shifted their ranges in the past and will likely continue to do so in the future in order to adapt to environmental changes. Some species underwent body size changes, sometimes over a short period of time. The research here highlights the importance of natural history collections, and the need for the continued collection and conservation of these important resources. This work has not only significantly expanded our knowledge of avifaunal history within Norway, but has also placed Norwegian data into a regional (Scandinavian) and continental (northern European) perspective. In addition, the resulting data presented here highlight new questions and research directions on the history of birds in Norway.

7. References

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Paper I

RESEARCH PAPER**Birds in Medieval Norway**Samuel J. Walker¹, Anne Karin Hufthammer¹ and Hanneke J. M. Meijer^{1,2}¹ University Museum of Bergen, Department of Natural History, University of Bergen, NO² Human Origins Program, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington DC, USA

Abstract

Whilst modern avian distributions in Scandinavia are well studied, how past events and processes have shaped modern bird communities in the region remains poorly known. This is mainly due to the fact that work on post-glacial avian assemblages has been done mostly from an archaeological perspective, and on a site-specific basis. Therefore, in order to understand the history of bird species in Scandinavia, there is a clear need to collate data on the past occurrences and abundance of birds within the region. Here we present data on the presence of bird species within 21 Norwegian Medieval (1030–1537 CE) assemblages. Despite climatic fluctuations and the rise of urban centres, our re-examination and compilation of bird bone assemblages from Medieval Norway found no evidence to suggest that the Medieval bird fauna differed from the modern one. The most common birds in Medieval assemblages are Galliformes. In urban sites these are mostly domestic fowl, whereas on rural sites wild species are dominant. Our data indicates an introduction of domestic fowl in the early Medieval period and a slightly delayed introduction of domestic geese, with both species becoming more abundant during the mid to late Medieval period. This appears to be later than other Scandinavian countries. Interestingly, species that are now ubiquitous in urban areas, such as pigeons, corvids and gulls are mostly absent from Medieval urban centres. In addition, we found a bias towards the use of female *Accipiter gentilis* in falconry, while *Falco* species may have been exported. This is the first time that data on past avian occurrences for any period are reviewed and collated for Norway. In addition, our work highlights the importance of birds and bird exploitation in Medieval Norway.

Keywords: Birds; Zooarchaeology; Scandinavia; Middle Ages; Falconry; Domestic fowl

1. Introduction

Norway hosts at least 259 breeding bird species (Gjershaug et al., 1994). Recent ornithological work has shown that 22% of all breeding birds within Norway are declining in numbers, with three species likely to disappear within the next decade (Shimmings & Øien, 2015). Some of the most vulnerable species are seabirds, birds in agricultural landscapes and montane birds (Henriksen et al., 2015). Whilst modern avian distributions in Scandinavia are well studied, how past events and processes have shaped modern bird communities in the region remains poorly known.

Work on post-glacial Scandinavian birds has been done mostly from an archaeological perspective and on a site-specific basis. Mannermaa's (2003) work in Finland collates data on avifauna's from archaeological sites, focusing on the Mesolithic through to the Bronze Age. The most recent work conducted in Denmark is by Gotfredsen (2013; 2014) looking at subsistence and cultural implications of species represented from specific sites. For Sweden, Ericson and Tyrberg (2004) summarised all available data from subfossil and written sources on the Swedish avifauna covering the last 14,000 years (Weichselian-19th century). Although their work is descriptive only, it is the most comprehensive study of the history of a Scandinavian avifauna thus far. In addition, we have consulted work conducted on bird remains from the Scottish Isles, of which there is a wealth of information (Serjeantson, 1988; Best & Mulville, 2010; Best & Mulville, 2013; Best & Mulville, 2014; Serjeantson, 2014).

For Norway, work on subfossil and archaeological avian assemblages has been site-specific only (for example; Olsen, 1967; Undheim, 1985, Unpublished report, see Supplementary Material File 1 (SMF1); Marthinussen, 1992, Unpublished thesis, see SMF1). Some work has focused on specific species such as Montevecchi and Hufthammer's (1990) work on Northern Gannets (*Morus bassanus*) and Northern Fulmars (*Fulmarus glacialis*), as well as the Great Auk (*Pinguinus impennis*) (Hufthammer, 1982; Bengtson, 1984). Other than these works there are no studies on long-term patterns and processes that have shaped current distributions of birds in

Norway. This leaves a clear need to collate research on the past occurrence and abundance of birds within Norway and the Scandinavian countries. This would provide a temporal perspective, enabling us to draw comparisons with modern species distribution, to gather insights on avian biogeography in Scandinavia.

Here, we present data on species representation within Norwegian Medieval bird bone assemblages stored within the University Museum of Bergen. This time period experienced fluctuations in temperature (Zawiska et al., 2017) and saw the rise of large urban centres in southern and central Norway. It is therefore expected that this period documents changes in avian species distributions and abundance related to human impact and climatic change. Furthermore, our work represents the first collation of bird bone material from Norway.

2. Methods

2.1 Sites

Avian bone material from 21 Medieval sites in Norway (Table 1; Figure 1; Supplementary Table 2) has been analysed. The majority of these sites have previously been analysed (see Table 1), however, we re-examined all sites. We selected sites with an avian assemblage of 50 or more bone specimens, in order to prevent assemblages skewed towards one or two species. However, in cases where large assemblages were not available, such as Bergen, where all assemblages with reliable dating, were also included. All 21 sites were from archaeological contexts dating to the Medieval period. The Medieval period, or Middle Ages, in Norway and Scandinavia (Norway, Denmark and Sweden) is the period after the Viking Age, from the Christianisation of Norway to the reformation in 1537 CE, and is generally accepted as 1030–1537 CE.

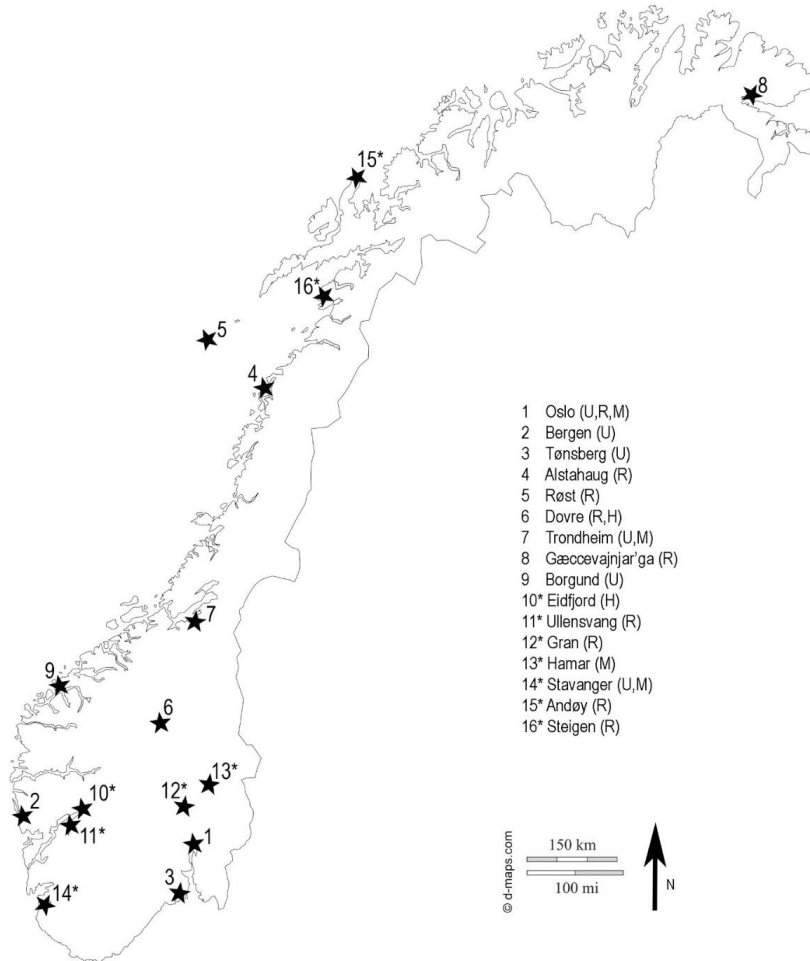


Figure 1. Location of sites with Medieval bird bone assemblages in Norway. Sites marked with * are supplementary assemblages which have not been re-examined. The types of site found are indicated next to the locations (U = Urban, R = Rural, M =Monastic, H = Hunting).

The sites included in this project have been excavated between 1918 and 2016 (Table 1). Excavation methods have improved drastically over this time frame. One of the most important improvements is the introduction of systematically sieving contexts (Lyman, 2012). In Norway, Mindets Tomt excavations in 1973 (Lie, 1988) were the first Medieval contexts to be sieved systematically. As a result, material from earlier excavations is likely to be biased towards larger species and thus less representative of the original species abundance.

The Erkebispegården assemblages have largely been unstudied, with the faunal material from only areas A and B being previously examined (Hufthammer, 1999), we re-examined all the Medieval contexts from areas A and B. In addition to the 21 main sites examined in this study, data from a number of smaller sites are presented here separately for comparisons. These supplementary sites (n = 33) were generally of a smaller assemblage size, some with less secure dating and occasionally lacking archaeological reports. Despite this, these sites are considered here in order to provide a more comprehensive account of the Norwegian Medieval avifauna. The material from these sites has not been re-examined and faunal lists for these sites were considered as is.

Table 1. Norwegian Medieval Sites which contain bird bones. The table includes all the Medieval sites which have been re-examined and all the supplementary sites we have considered. The table gives the sites name, the JS number assigned to the site (this is a catalogue number given by the University Museum of Bergen), information on whether the site has been re-examined or not, the avian NISP for the site, the location of the site, the date of excavation/range if it is over a number of seasons, the specific dates for a site, where known (contexts which are outside of the Medieval period have been excluded), the site type (urban, rural, monastic or hunting), information on sieving and any references to previous zooarchaeological reports and contextual dating sources. In many cases, the reports have not been published, these are listed in the unpublished sources reference list in the supplementary material (Supplementary Material File 1 (SMF1)).

Site name	JS Number	Re-examine	Avian NISP	Location	Date excavated	Date range of site	Site type	Sieved	Site references
Mindets Tomt	537	YES	1052	Oslo	1973	1025-1350 CE	Urban	Yes	Archive Natural History, University Museum of Bergen. (Lie, 1988)
Oslogate 7, Gamlebyen	599	YES	175	Oslo	1977	1150-1600 CE	Urban	No	Archive Natural History, University Museum of Bergen. (Lie, 1979)
Nordre Felt II, Gamlebyen	702	YES	1640	Oslo	1982-1984	Medieval	Urban	Yes	Archive Natural History, University Museum of Bergen.
Bryggen	397,401, 406, 492, 529, 540	YES	911	Bergen	1959-1962, 1967,1970, 1972	Medieval	Urban	No	Archive Natural History, University Museum of Bergen.
Dreggssalmnningen	630	YES	61	Bergen	1980	1170-1527 CE	Urban	No	Archive Natural History, University Museum of Bergen. (Undheim, 1985, unpublished report, see SMF1)
Vågsalmenning	1152	YES	3	Bergen	2000	Medieval	Urban	No	Archive Natural History, University Museum of Bergen.
Kroken 3	1168	YES	3	Bergen	1984-1985	Medieval	Urban	Yes	Archive Natural History, University Museum of Bergen. (Dunlop, unpublished report, see SMF1)
Finnegården 3A	1237	YES	78	Bergen	1982	Medieval	Urban	Unknown	Archive Natural History, University Museum of Bergen. (Golembnik, 1993, unpublished report, see SMF1)
Bryggen Gullskoen	1280	YES	18	Bergen	1955-1979	Medieval	Urban	No	Archive Natural History, University Museum of Bergen.
Bryggesporden	1750	YES	23	Bergen	2016	Medieval	Urban	Yes	Archive Natural History, University Museum of Bergen. (Bejersbergen et al., 2018, unpublished report, see SMF1)
Storgaten 35	563	YES	81	Tonsberg	1974	Before 1200-1400 CE	Urban	Unknown	Archive Natural History, University Museum of Bergen. (Eriksen, 1975, unpublished report, see SMF1)
Storgaten 24-26	637	YES	13	Tonsberg	1979	Mid/late 1200-1350 CE	Urban	Yes	Archive Natural History, University Museum of Bergen. (Lindh, 1984, unpublished report, see SMF1)
Tunsberghus	660	YES	25	Tonsberg	1981	1200-1500 CE	Urban	Unknown	Archive Natural History, University Museum of Bergen.
Baglergaten 2-4	664	YES	17	Tonsberg	1982	C.1200-C.1400 CE	Urban	Yes	Archive Natural History, University Museum of Bergen. (Brendalsmo, 1986, unpublished report, see SMF1)
Blomsøy	151	YES	12	Alstahaug	1918, 1920	Medieval	Rural	No	Archive Natural History, University Museum of Bergen.
Husen	308	YES	26	Røst	1951	Medieval	Rural	Unknown	Archive Natural History, University Museum of Bergen. (Paul Simonsen, pers. comm.)
Toftom	710	YES	41	Dovre	1984-1985	900-1300 CE	Hunting	Unknown	Archive Natural History, University Museum of Bergen. (Lie, 1994)
Vesle Hjerkinm	712	YES	1352	Dovre	1984-1985	Medieval	Rural	No	Archive Natural History, University Museum of Bergen. (Lie & Fredriksen 2007)

Site name	JS Number	Re-examine	Avian NISP	Location	Date excavated	Date range of site	Site type	Sieved	Site references
Erkebispegården	845	YES	236	Trondheim	1992	Ca. 1250-1537 CE (Phases 4-7)	High status (Monastic)	Yes	Archive Natural History, University Museum of Bergen. (Hufthammer, 1999)
Gæceveinjær-ga	715	YES	43	Nesseby	1984	Medieval	Rural	Unknown	Archive Natural History, University Museum of Bergen. (Lie, 1992)
Borgund	344, 357, 374, 410, 411, 430, 431, 432, 1699	YES	108	Ålesund	1955-1961, 2014	Medieval	Urban	No	Archive Natural History, University Museum of Bergen.
Kirke og Klosterruin	162	NO	9	Oslo	1919	Medieval	Monastic	No	Archive Natural History, University Museum of Bergen. (Ole Egil Eide & Alf Tore Hommedal pers. comm.)
Søndre Felt, Gamlebyen	577	NO	37	Oslo	1977	1025-1624 CE	Urban	Yes	Archive Natural History, University Museum of Bergen. (Lie, 1988)
Kanslergate. 10 Grøftgravninger	768	NO	13	Oslo	1987	1100-1700 CE	Urban	No	Archive Natural History, University Museum of Bergen. (Lie, 1991)
Oslogate. 6	784	NO	236	Oslo	1987-1988	Ca. 1100-1624 CE	Urban	No	Archive Natural History, University Museum of Bergen. (Molnag, pers. comm.)
Oslogate. 4 Grøftgravninger	798	NO	19	Oslo	1988	1225-1350 CE	Urban	No	Archive Natural History, University Museum of Bergen. (Lie, 1991)
Nordre Felt I, Gamlebyen	809	NO	169	Oslo	1970s	Medieval and Post-Medieval	Rural	Yes	Archive Natural History, University Museum of Bergen.
Bispeborgen	1273	NO	10	Oslo	1983-1985	Medieval	Monastic	Unknown	Archive Natural History, University Museum of Bergen.
Arupsgate, Gamlebyen	1550	NO	14	Oslo	2007	Ca. 1050-1200 CE	Urban	Yes	Archive Natural History, University Museum of Bergen.
Follobanen, Gamlebyen	1675	NO	41	Oslo	2013	Medieval and Post-Medieval	Urban	Yes	Archive Natural History, University Museum of Bergen. (Sharpe, 2014, unpublished report, see SMF1)
Bryggen 1958	380, 387	NO	7	Bergen	1958	Medieval	Urban	No	Archive Natural History, University Museum of Bergen.
Rosenkrantz gate 4	613	NO	12	Bergen	1978	Medieval	Urban	No	Archive Natural History, University Museum of Bergen. (Lindh, 1980, unpublished report, see SMF1)
Nedre Langgate 25-27	631	NO	5	Tønsberg	1978	Medieval	Urban	Unknown	Archive Natural History, University Museum of Bergen.
Baglergaten 3	644	NO	52	Tønsberg	1979-1980	Late 1100-Early 1300 CE	Urban	No	Archive Natural History, University Museum of Bergen. (Brendalsmo, 1983, unpublished report, see SMF1)
Kammegaten 10	696	NO	1	Tønsberg	1981	1100-1300 CE	Urban	Yes	Archive Natural History, University Museum of Bergen. (Wienberg, 1983, unpublished report, see SMF1)
Storgaten 33/Tjomegaten 1	763	NO	40	Tønsberg	1986	Mid 1200-1300 CE	Urban	Yes	Archive Natural History, University Museum of Bergen. (Nordman et al., 1986, unpublished report, see SMF1)
Essotomten Storgaten. 16-18	796	NO	19	Tønsberg	1988	Medieval	Urban	Unknown	Archive Natural History, University Museum of Bergen.

Site name	JS Number	Re-examine	Avian NISP	Location	Date excavated	Date range of site	Site type	Sieved	Site references
Sumtangen sites	1326,1429,1430	NO	9	Eidfjord	2004-2005	Medieval	Hunting	Yes	Archive Natural History, University Museum of Bergen. (Indrelid et al., 2007; Indrelid & Hufhammer, 2011)
Gildestova	350	NO	2	Ullensvang	1955	Medieval	Rural	No	Archive Natural History, University Museum of Bergen.
Ulsrud Tuft 1	274	NO	1	Gran	1948-1949	Medieval	Rural	No	Archive Natural History, University Museum of Bergen.
Hamar Domkirkeruin	866	NO	36	Hamar	1992	Medieval	Monastic	No	Archive Natural History, University Museum of Bergen.
Stavanger Domkirke	493	NO	12	Stavanger	1967	Medieval	Monastic	No	Archive Natural History, University Museum of Bergen.
Stavanger Torg	1398	NO	26	Stavanger	2004	Medieval	Urban	Yes	Archive Natural History, University Museum of Bergen.
Haakon VII gate	1518	NO	7	Stavanger	2005	Medieval	Urban	Yes	Archive Natural History, University Museum of Bergen.
Gårdshaug, Blomsøy	818	NO	5	Alstahaug	1985	Medieval	Rural	Yes	Museum of Bergen. (Berglund, 1995; Hufhammer, 1993; unpublished report, see SMF1)
Gårdshaug, Tjøtta	819	NO	20	Alstahaug	1985	Medieval	Rural	Yes	Archive Natural History, University Museum of Bergen. (Berglund, 1995; Hufhammer, 1993; unpublished report, see SMF1)
Gårdshaug, Alstahaug	824	NO	2	Alstahaug	1985	Medieval	Rural	Unknown	Archive Natural History, University Museum of Bergen. (Berglund, 1995; Hufhammer 1993; unpublished report, see SMF1)
Alstahaug 1992	865	NO	141	Alstahaug	1992	Medieval	Rural	Yes	Archive Natural History, University Museum of Bergen.
Televerkstomten	632	NO	114	Trondheim	1979	C. 1000-1590 CE (Phase 2-7)	Urban	No	Archive Natural History, University unpublished thesis, see SMF1)
Bibliotekstomten	765	NO	115	Trondheim	1986	900-ca.1475 CE	Urban	Unknown	Archive Natural History, University Museum of Bergen. (Lie, 1989; unpublished report, see SMF1)
Andenes (Ts 4767)	328	NO	6	Andøy	1953	1300-1700 CE	Rural	No	Archive Natural History, University Museum of Bergen. (Paul Simonsen, pers. comm.)
Steigen gårdshaug	360	NO	16	Steigen	1956	Medieval	Rural	No	Archive Natural History, University Museum of Bergen. (Paul Simonsen, pers. comm.)

2.2 Faunal analyses

The faunal remains from the 21 sites were recovered by hand during field excavations and subsequently stored at the University Museum of Bergen. The current analyses of the avian material from the 21 sites was based on morphological comparisons of the subfossil material to skeletons of modern specimens in the University Museum of Bergen's comparative skeletal collection, which houses 4000 bird skeletons representing 95% of the current Norwegian avifauna. In addition, the large comparative skeletal collection at the Natural History Museum at Tring, England, was also consulted. The taxonomic framework throughout this paper follows the two volumes of the Handbook of Birds of the World (HBW) and BirdLife International illustrated checklist of Birds of the World (Non-passerines: del Hoyo & Collar, 2014; Passerines: del Hoyo & Collar, 2016), as does the English names for species. Osteological descriptions broadly follow Livezey and Zusi (2006).

A number of criteria were recorded for each bone specimen, including species, element, side, zones present (Cohen & Serjeantson, 1996: 110–111) and percentage of completeness. Taphonomic markers which were recorded include presence/absence of evidence of erosion (possibly weathering), modern breaks, concretions, surface staining, gnawing, digestion, puncture marks, evidence of burning, cut marks, and any pathologies. Sexing data was recorded where possible based on the presence of medullary bone in females, and for *Gallus gallus*, the presence of spurs on the tarsometatarsus of males (although spurs have also been observed in a number of cases for female *G. gallus* (Serjeantson, 2009)). Medullary bone was recorded for specimens which had an exposed cross section of the shaft. Medullary bone is a useful indicator of sex, and informs us about the presence of breeding females within a locality (Serjeantson, 2009). The absence of medullary bone, however, does not necessarily indicate a male specimen, as females not in lay will not produce medullary bone. Therefore, bone specimens without medullary bone were not sexed. The Western Capercaillie (*Tetrao urogallus*), the Peregrine Falcon (*Falco peregrinus*), the Northern Goshawk (*Accipiter gentilis*) and Eurasian Sparrowhawk (*Accipiter nisus*) are sexually dimorphic species for which it was possible to record sex, with little to no osteological

overlap between males and females. The presence of juveniles was recorded based on ossification stages.

Measurements were based upon Von den Driesch (1976). Additional measurements were taken from Kraft (1972) and Erbersdobler (1968). Species abundance is quantified here based on the Number of Identified Specimens (NISP). In order to prevent over-representation of species, ribs, vertebrae and phalanges were not included in this study. It is worth noting that very few Associated Bone Groups (ABGs) were identified, and these were included within the NISP counts in Table 4. For a breakdown of ABGs by species, they are mentioned within the species accounts in the results and within the supplementary material table (ST2). Every effort has been made to identify the species where possible. However, particular importance was placed on knowing when it is not possible to reliably identify a specimen, reducing the number of misidentifications. A number of species are particularly hard to separate based upon morphological characteristics. This is particularly true for *Lagopus lagopus* (Willow Grouse) and *Lagopus muta* (Rock Ptarmigan). Both species are year round residents in Norway, but do have different habitat preferences. Morphologically, the only elements that can accurately be separated are the cranium and mandible. Kraft (1972) highlights a number of morphological differences, however, we found those to not be overly reliable in the Norwegian modern specimens. Stewart (2007) also notes the unreliability of these morphological differences, preferring to split *L. lagopus* and *L. muta* based on measurements. The most significantly different skeletal elements based on size belonged to the lower limb, in particular the tarsometatarsus (Stewart, 2007). For the Norwegian material we have used linear measurements to compare postcranial elements, specimens which fell into the overlap between *L. lagopus* and *L. muta*, have been grouped at a higher taxonomic level of *Lagopus* in this study.

Due to the assemblages being Medieval in age, along with the urban location of specimens, we have assumed that *Anser anser* identifications are likely to represent domesticated individuals. However, it is possible that some of these specimens are wild *A. anser*. Further work is needed on the separation of the domesticated and wild forms of *A. anser*. Other *Anser* and *Branta* species are morphologically very similar, and have been placed into the broader category of Anserini sp. The same has been done for

ducks; when they could not be identified to tribe, they were placed into the broader Anatinae species group. Within the Alcidae, it was often not possible to separate *Uria aalge*, *Uria lomvia* and *Alca torda*, and these were grouped as *Uria aalge/lomvia/Alca torda*. Similarly, *Larus argentatus* and *L. fuscus* are difficult to separate and were grouped as *Larus argentatus/fuscus*. Passerines are particularly hard to identify due to the small number of diagnostic elements (humerus, cranium and mandible). In order to prevent misidentifications within this order we have taken a cautious approach by placing species into size groups when diagnostic elements are not available. The Turdidae family has been placed into two size groups; small *Turdus* sp. (*Turdus iliacus* and *T. philomelos*) and large *Turdus* sp. (*Turdus pilaris*, *T. torquatus*, *T. merula* and *T. viscivorus*).

Where specimens were not identifiable to taxa, they were placed into broad size categories, based on those used by Ayres et al. (2003). Three size categories were used: ‘unidentified small bird’ (almost exclusively passerine fragments), ‘unidentified medium bird’ (specimens larger than a passerine but not as large as *A. anser*), ‘unidentified large bird’ (specimens in the size range of *A. anser* and beyond). If specimens could not be placed into a size category, they were recorded as ‘unidentified bird’.

To obtain an indication of how reliable previous identifications were, we assigned all our identifications to five distinct categories, namely ‘maintained identification’ (original identification is unchanged), ‘newly identified’ (where the specimen has not previously been identified), ‘more accurately identified’ (this is where it has been possible to further attribute either family, genus or species, e.g. a Galliformes specimen newly identified to *L. tetrix*), ‘more cautiously identified’ (when a specimen has been placed over-confidently into a family, genus or species, e.g. previously identified *L. muta* re-identified to *Lagopus* species) and ‘different taxon’ (where the identification is changed completely, e.g. Falconidae species changed to Accipitridae species).

3. Results

3.1 Taphonomy

Birds generally make up less than 5% of the faunal bone assemblages on Medieval sites in Norway (Table 2). Mammals make up the bulk of the faunal assemblages, with fish also being well represented. The only exceptions in this study are the sites of Husen on the island of Røst, where birds make up 65%, and the Borgund site, where fish are dominant and birds are poorly represented (0.03%). However, the assemblages from these sites are small, and do not represent the general patterns we have observed across Norway during the Medieval period.

Overall, the Medieval bird bone assemblages show very good preservation, with relatively few taphonomic markers identified (Table 3). Many of the bones are complete or have at least one epiphysis present. This high level of preservation is reflected by the fact that 54% of the material could be identified to species or family. The cortical surface preservation was generally good, with only 254 (4%) specimens displaying surface cracking, flaking, or general cortical surface damage. A total of 93 specimens exhibited signs of gnawing, evidenced by small parallel striations, indicative of rodent gnawing, but also some small puncture marks, possibly from an avian predator or cat/dog gnawing. Taphonomic markers related to burning were only visible on 25 of the identified specimens. Evidence of digestion was recorded on only two specimens. While these figures are very low, the majority of taphonomic damage was present on the unidentified material, many of which were eroded or burnt, preventing identification.

Butchery was observed on 393 specimens (6.6%). This was the most common taphonomic feature observed. Generally, the butchery marks were in keeping with removal of the elements that provide the least meat, such as the tarsometatarsus and phalanges. Other butchery marks, especially to the sternum, likely represent filleting. The majority of the butchery was on *Gallus gallus* bones, in total 291 specimens. Butchery was recorded on 20 different species, and details of these are presented, where relevant, within the species accounts.

Table 2. Bird representation. The table shows the percentages of bird bones represented within the faunal assemblages for a given area. The NISP figures used to calculate these percentages can be found in Supplementary Table 1 (ST1).

Location (County)	Bird %
Oslo (n = 3)	2
Bergen (n = 7)	3
Tønsberg (n = 4)	1
Alstahaug (n = 1)	3
Røst (n = 1)	65
Borgund (n = 1)	0.3
Dovre (n = 2)	5
Trondheim (n = 1)	3
Finnmark (n = 1)	12

Table 3. Taphonomy identified. The table shows the main Taphonomic markers observed within the Norwegian Medieval assemblages.

Taphonomic marker	No. specimens	Overall %
Butchered	393	6.6%
Modern breaks	66	1.1%
Eroded/weathered	254	4.3%
Gnawed	93	1.6%
Digested	2	0.03%
Concretions	5	0.08%
Charred/Burnt	25	0.4%
Puncture marks	26	0.4%

3.2 Species representation

From the 21 sites that were analysed, 5938 bird bones could be identified to species, genus or family (Table 4), with 55 different species being represented, from 15 different orders. The remaining 5085 specimens were unidentifiable beyond Aves, of these, 2618 bone fragments were identified as probably Aves. Of the remaining 2467 unidentified fragments, 149 were considered to be large birds, 982 fragments were placed into the medium birds category, and only two fragments were placed into the small birds group. The remaining 1334 specimens were placed in the unidentified bird category.

Of the 5938 identifiable specimens examined in this study, a total of 1300 (22%) specimens have had the original identification changed to some degree (Table 5). Only 276 (4.6%) specimens were previously identified a different taxa. In addition, 1024

(17.3%) were either more cautiously or more accurately identified. A further 867 (14.6%) newly identified specimens were also recorded. This leaves 3771 (63.5%) specimens where the previous identification was maintained. The most common issue was the over identification of the *Lagopus* species, where we have adopted a more cautious approach. In addition, Anseriformes are also prone to misidentification, as it is not always possible to identify beyond the tribe. The confidence level of identifying certain gulls and auks to species level has also been a problem with previously identified material, which we have tried to prevent by placing species into broader groups covering a number of morphologically similar species.

Table 4. Species representation. Here the re-examined sites (n = 21) have been grouped by locations, for a full breakdown of species per site see Supplementary Table 2 (ST2). A column of all the species represented on the supplementary sites (n = 33) has also been added, for a full breakdown of species by supplementary site see Supplementary Table 3 (ST3). All figures are based upon Number of Identified Specimens (NISP).

Taxa	1	2	3	4	5	6	7	8	9	Norway re-examined total (n = 21)	Norway previously identified total (n = 33)	Norway Medieval Total (n = 54)
	Oslo sites (n = 3)	Bergen sites (n = 7)	Tønsberg sites (n = 4)	Alstahaug sites (n = 1)	Røst sites (n = 1)	Borgund, Ålesund (n = 1)	Dovre sites (n = 2)	Trondheim sites (n = 1)	Finnmark sites (n = 1)			
Galliformes												
<i>Galliformes</i> sp.	127	14	11	-	-	-	33	36	1	222	131	353
cf. <i>Galliformes</i> sp.	8	-	-	-	-	-	3	-	-	11	1	12
<i>Gallus gallus</i>	1870	739	97	1	-	18	23	109	-	2857	556	3413
cf. <i>Gallus gallus</i>	42	4	1	-	-	2	2	1	-	52	0	52
<i>Lyrurus tetrix</i>	63	26	2	-	-	-	9	3	-	103	18	121
cf. <i>Lyrurus tetrix</i>	6	1	-	-	-	1	-	-	-	8	0	8
<i>Tetrao urogallus</i>	134	6	1	-	-	-	23	12	1	177	72	249
cf. <i>Tetrao urogallus</i>	8	-	-	-	-	-	-	1	-	9	0	9
<i>Lagopus</i> sp.	7	2	1	-	-	1	1083	3	33	1130	31	1161
cf. <i>Lagopus</i> sp.	1	-	-	-	-	-	132	-	-	133	0	133
<i>Lagopus lagopus</i>	-	-	-	-	-	-	28	-	2	30	3	33
<i>Lagopus muta</i>	-	-	-	-	-	-	-	-	-	0	27	27
<i>Bonasa bonasia</i>	4	-	1	-	-	-	-	5	-	10	0	10
cf. <i>Bonasa bonasia</i>	1	-	-	-	-	-	1	-	-	2	0	2
Anseriformes												
<i>Anseriformes</i> sp.	-	1	-	-	-	-	-	-	-	1	20	21
Anserini sp. (<i>Anser/Branta</i> sp.)	6	2	-	-	-	-	-	10	-	18	0	18
<i>Anser</i> sp.	17	7	1	2	-	-	-	1	-	28	8	36

	1	2	3	4	5	6	7	8	9	10	144	526
<i>Anser anser</i>	286	64	16	1	-	5	-	-	-	-	382	-
cf. <i>Anser anser</i>	21	4	-	-	-	-	-	-	-	-	0	25
<i>Anser fabalis</i>	-	-	-	1	-	-	-	-	-	-	1	2
<i>Anser brachyrynchus</i>	-	-	-	-	-	-	-	-	-	-	1	1
<i>Branta bernicla/leucopsis</i>	-	2	-	-	-	-	-	-	-	-	0	1
<i>Cygnus cygnus</i>	7	1	-	-	-	1	-	-	-	-	0	9
cf. <i>Cygnus cygnus</i>	1	-	-	-	-	-	-	-	-	-	0	1
<i>Anatinae</i> sp.	9	1	-	-	-	-	2	1	-	-	0	13
<i>Anas platyrhynchos</i>	1	1	-	-	-	1	-	1	-	-	1	5
<i>Anas crecca</i>	-	1	-	-	-	-	-	-	-	-	0	1
<i>Anatidae</i> sp.	-	-	-	-	-	-	-	-	-	-	0	1
<i>Somateria mollissima/spectabilis</i>	-	-	-	-	-	-	-	-	-	-	0	2
<i>Somateria mollissima</i>	3	40	1	3	-	2	-	-	1	-	14	64
cf. <i>Somateria mollissima</i>	-	1	-	-	-	-	-	-	-	-	1	2
<i>Somateria spectabilis</i>	-	-	-	-	-	-	-	-	-	-	0	1
<i>Clangula hyemalis</i>	-	-	-	-	-	-	4	-	-	-	4	5
<i>Melanitta fusca</i>	1	-	-	-	-	-	-	-	-	-	1	3
<i>Melanitta nigra</i>	-	-	-	-	-	-	-	-	-	-	0	1
<i>Mergus serrator</i>	1	1	-	-	-	-	-	-	-	-	0	2
<i>Bucephala clangula</i>	-	-	-	-	-	-	1	-	-	-	0	1
<i>Mergini</i> sp.	-	-	-	-	-	1	2	-	-	-	0	3
<i>Anas</i> sp.	1	-	-	-	-	-	1	-	-	-	0	2
<i>Aythya</i> sp.	1	-	-	-	-	-	-	-	-	-	0	1
Gaviiformes												
<i>Gavia</i> sp.	-	-	-	-	-	-	-	-	-	-	0	2
<i>Gavia arctica</i>	6	1	-	-	-	-	-	-	-	-	7	8
cf. <i>Gavia arctica</i>	1	-	-	-	-	-	3	-	-	-	0	4
<i>Gavia stellata</i>	-	1	-	-	-	-	-	-	-	-	1	2
Procellariiformes												
<i>Fulmarus glacialis</i>	3	2	-	-	-	2	-	-	-	-	7	8
<i>Puffinus puffinus</i>	-	-	-	-	-	2	-	-	-	-	0	2
Ciconiiformes												
<i>Ciconia nigra</i>	-	1	-	-	-	-	-	-	-	-	0	1
Suliformes: Phalacrocoracidae												
<i>Phalacrocorax aristotelis</i>	-	5	-	-	-	8	-	-	-	-	13	16
<i>Phalacrocorax carbo</i>	-	6	-	-	-	2	-	-	-	-	8	10
Suliformes: Sulidae												
<i>Morus bassanus</i>	-	3	-	-	-	10	-	-	-	-	13	17
Pelecaniformes												
<i>Ardea cinerea</i>	1	3	-	-	-	-	-	5	-	-	2	11

Table 5. Identification changes. This table shows the amount of specimens in each identification category, the final three rows show the amount of previously misidentified specimens. Descriptions for the categories can be found under the methods-faunal analysis section. Figures are based upon Number of Identified Specimens (NISP).

Category	NISP	NISP %
Maintained identification	3771	63.5%
More accurately identified	598	10.1%
More cautiously identified	426	7.2%
Different taxa	276	4.6%
Newly identified	867	14.6%
Total	5938	

3.2.1 Galliformes (Pheasants and Grouse)

Galliforms form the bulk of the avian material recovered from the Medieval sites with 4744 specimens identified within this order (80% of NISP). It was not possible to assign 233 specimens to a taxonomic level beyond Galliformes.

3.2.1.1 Domestic Galliformes

Domestic fowl (*Gallus gallus* var. *domesticus*) is the most common bird species represented in Medieval Norway. In total 2857 specimens were positively identified with a further fifty-two cf. *G. gallus*, forming 49% of the represented Medieval avian specimens. *Gallus gallus* is fairly ubiquitous and present on 17 sites. However, the dominance of this species does vary; whilst it contributes heavily to sites in Oslo, Bergen, Tønsberg and Trondheim, it has little importance on sites in Alstahaug, Ålesund and Dovre, and does not occur on Røst or the Finnmark site of Gæccevajnar'ga.

There is a fairly even distribution of elements with a slight dominance of wing and leg bones and a lack of small, less dense bones. Medullary bone was identified within 42 individuals with varying degree of cavity fill (<50% fill of shaft cavity n = 29, <100% fill of shaft cavity n = 8 and 100% fill of shaft cavity n = 5). In addition, 98 tarsometatarsi lacked a spur, indicating a total of 140 females. It is important to note that, while uncommon, juvenile males sometimes do not show indications of a spur (Serjeantson, 2009). A hundred and twelve tarsometatarsi were identified as male. Fourteen of these only have a spur scar, and not a fully developed spur. Age at death

was based upon the ossification of epiphyses; 2642 (93%) were fully developed adult individuals. Only 26 (1%) specimens were just ossified and classified as sub-adult. Sixty-six (2%) specimens were not ossified and therefore juvenile, whilst 123 (4%) showed no indicators of age.

Butchery marks were identified on 291 (10%) of the *G. gallus* bones, and predominantly found on the femur and tibiotarsus (201 specimens). Specific patterns of butchery observed on these elements were fine diagonal cut marks across the trochanter femoris (Figure 2A), fine transverse cut marks across the distal lateral and medial condyles of the tibiotarsi (Figure 2B), and some heavier chops to the proximal articular facets of the tibiotarsi (Figure 2C). The amount of butchery observed varied greatly; in Bergen 25% (n = 188) of the *G. gallus* bones showed sign of butchery, in Trondheim 10% (n = 12) and in Oslo only 4.5% (n = 86). On all other sites, cut marks were observed on one or two *G. gallus* bones. Pathological markers were recorded on *G. gallus* specimens more than on any other species. However, this was still a relatively small number of the total number of domestic fowl specimens, only 42 (1.5%). The most common pathology was periosteal new bone growth on the mid-shaft of the tarsometatarsus, 20 specimens (48%) fell into this category, predominantly on male (i.e. spurred) individuals (n = 17). Ten (24%) specimens showed indications of periosteal new bone growth around the articular surfaces of long bones, often on the femur. Healed fractures were identified on four (9%) specimens. The remaining eight (19%) specimens showed various pathologies not falling into these three main categories.

3.2.1.2 Wild Galliformes

The wild Galliformes are one of the best represented groups within the Medieval Norwegian avian assemblages with 1602 specimens (27%) identified, representing four different species of galliform. Of the wild Galliformes, the two *Lagopus* species are dominant, with 1293 (22% of the Medieval bird bones). The vast majority of these, 1243 specimens come from the two Dovre sites, Vesle Hjerkinn and Tøftom. The *Lagopus* specimens have been further identified as 1130 specimens into the broader taxonomic group of *Lagopus* sp., 133 specimens as cf. *Lagopus* species and 30 *Lagopus lagopus* specimens. No specimens morphologically matched *L. muta*. Linear measurements of seven *Lagopus* tarsometatarsi show that all seven specimens fall in the *L. lagopus* size range (Figure 3A). Linear measurements for upper limbs showed too much overlap between species to make any accurate identifications (Figure 3B). It appears from current analysis that *L. lagopus* was the most dominant of the *Lagopus* species within the Medieval Norwegian assemblages. It is unclear if any *L. muta* specimens are present in the assemblages. Some specimens appear to be smaller, but due to their fragmentary nature, no meaningful measurements could be taken. Puncture marks possibly caused by avian predators, and often located at the epiphyses (Figure 2D), were recorded for 11 *Lagopus* specimens.

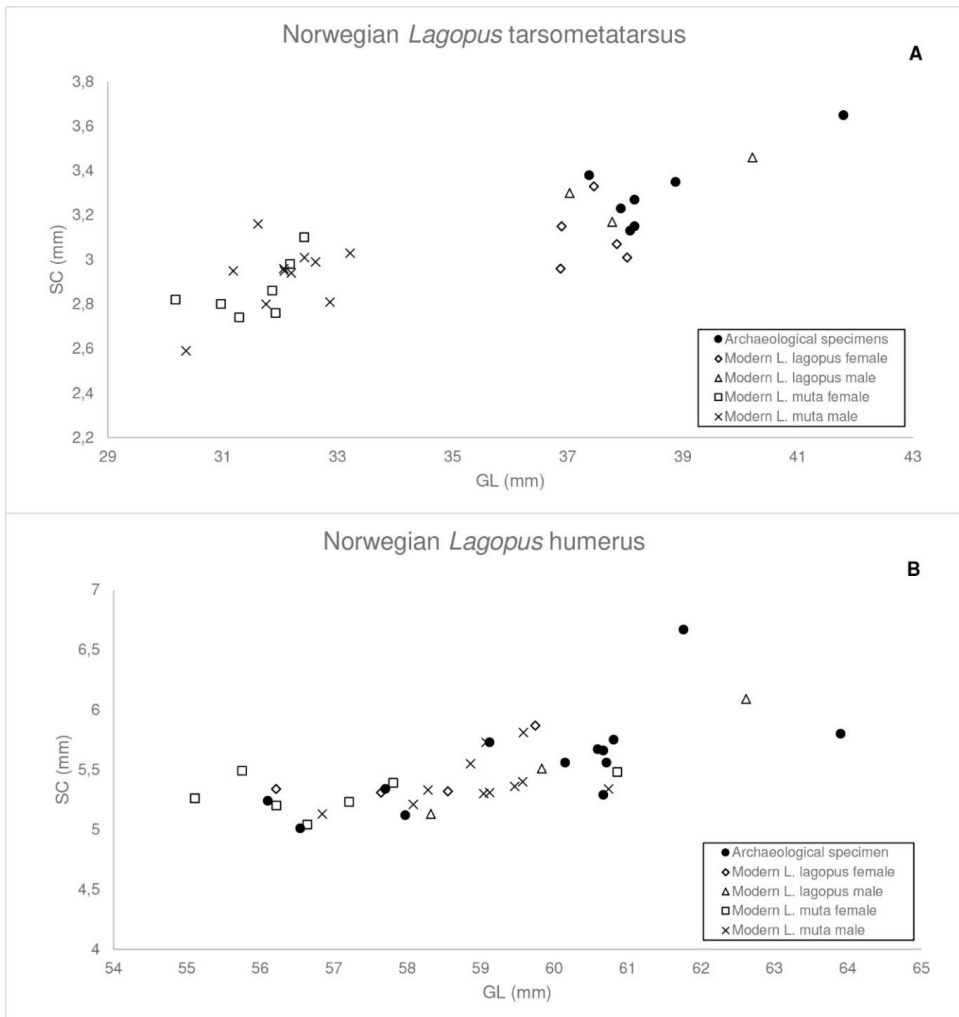


Figure 3. Plotted measurements of *Lagopus tarsometatarsus* and humerus. Greatest length (GL) and smallest breadth of the shaft (SC) of archaeological specimens from Norwegian Medieval sites. The modern measurements are from Norwegian individuals, measured from the Bergen University Museum and Tring Natural History Museum collections.

The second best represented wild galliform is the Western Capercaillie (*Tetrao urogallus*). With 177 specimens confidently identified and a further nine specimens identified to cf. *T. urogallus*, this species accounts for around 3% of the represented Medieval birds. Males dominated the assemblages (122 specimens, 69%) while 50 (28%) elements were identified as female, and five (3%) specimens as indeterminate. Butchery marks were observed on 11 (6%) specimens, predominantly on the wing elements ($n = 7$, 64%). Element representation shows an even distribution, with a very slight bias towards the wing elements. *Tetrao urogallus* has been identified on most sites, however, with varying abundance. It is most dominant on sites in Oslo and Trondheim, making up 5% of their respective assemblages, whilst in Bergen, *T. urogallus* only accounts for 0.5% of the bird bone assemblages.

The Black Grouse (*Lyrurus tetrrix*) is also well represented within the Medieval bird bone material. A total of 103 specimens were identified as *L. tetrrix* and a further eight were classified as cf. *L. tetrrix*, contributing almost 2% to the overall NISP. This species was one of the more common misidentifications, due to its similar size and morphology to *G. gallus*. However, there are a number of clear characteristics that separate these species. In general, *L. tetrrix* is more slender, and its morphology is more pronounced. For instance, the facies articularis scapularis on the coracoid is far more distinct in *L. tetrrix*, along with a much more hooked angulus medialis coracoidei. The humerus in *L. tetrrix* also has distinct features, such as a more prominent condylus ventralis humeri. Butchery marks were observed on four elements, approximately 4% of the *L. tetrrix* bones. No irregular patterns were observed in terms of element representation. This species appears to follow a distribution pattern similar to *T. urogallus*, with a slightly better representation in Bergen, but still less abundant than in Oslo.

The Hazel Grouse (*Bonasa bonasia*) makes up a small amount of the total Medieval avian assemblages, with only 10 specimens and a further two specimens identified as cf. *B. bonasia*, totalling less than 0.2%. The majority of these have been identified from the Oslo and Trondheim sites, with very few occurring within assemblages across the rest of Norway.

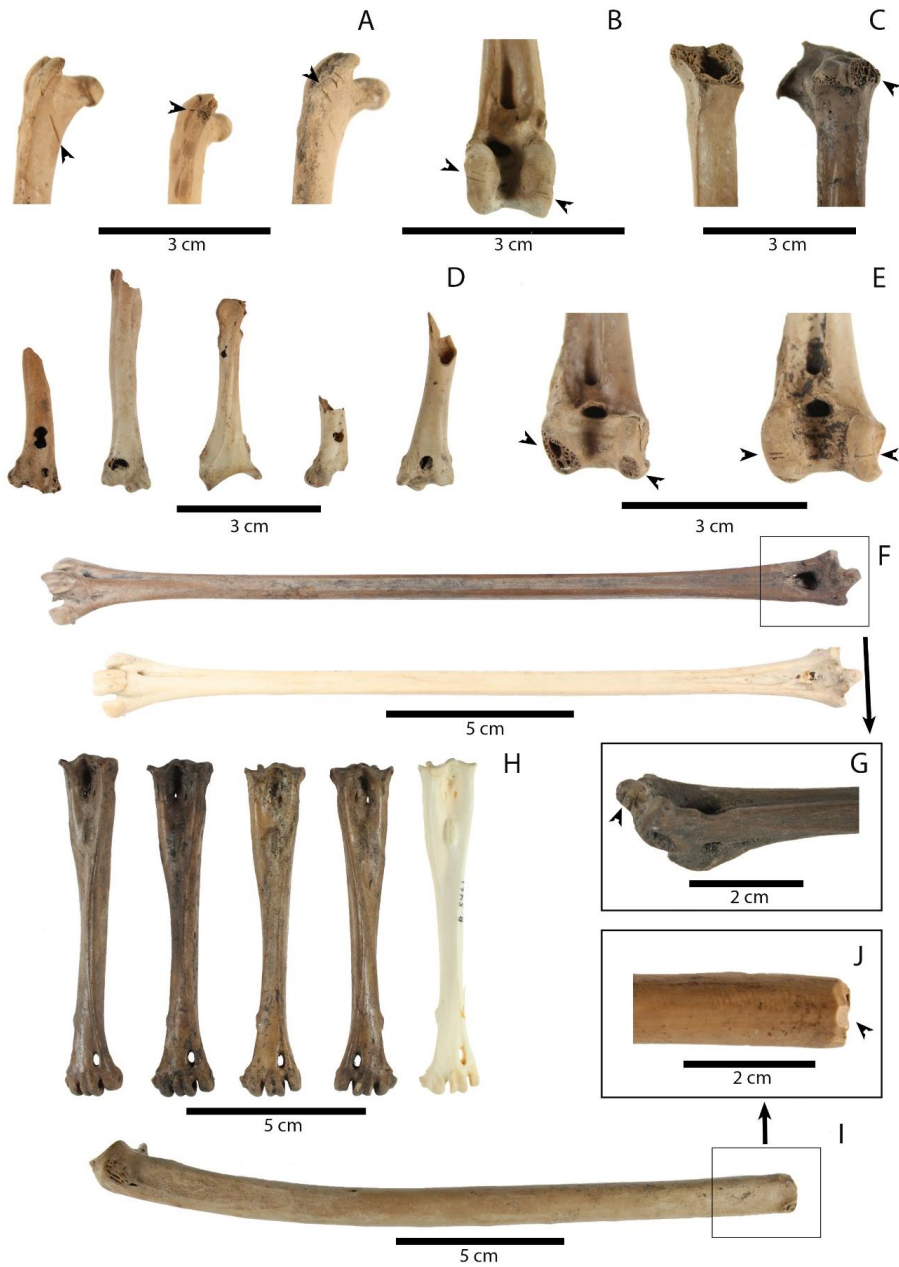


Figure 2. Selected avian remains from Medieval sites in Norway. **A:** Butchery marks on the trochanter of *G. gallus* femora. **B:** Butchery marks on the distal condyles of *G. gallus* tibiotarsus. **C:** Heavy butchery marks on the proximal end of *G. gallus* tibiotarsi. **D:** Puncture marks on *Lagopus* specimens, puncture on the distal humerus on the far right is a

puncture caused by ulna piercing via hyperextension. **E:** Butchery marks on the distal condyles of *A. anser* tibiotarsi. **F:** *Ciconia nigra* worked tarsometatarsus, comparative *C. nigra* specimen from the University Museum of Bergen (BM. 7896). **G:** Close up of the *C. nigra* specimen, showing cut marks to the eminentia intercondylaris. **H:** Four *A. gentilis* tarsometatarsi from Mindets Tomt, Oslo. Showing the large and robust nature of the Medieval specimens in comparison to the largest *A. gentilis* female (B. 5461) in the University Museum of Bergen's comparative collections. **I:** Worked *A. chrysaetos* ulna from Finnegården 3A, Bergen. **J:** Close up of the fine working to the distal shaft of the *A. chrysaetos* specimen.

3.2.2 Anseriformes (Ducks, Geese and Swans)

Anseriformes represent the most diverse order within the Norwegian bird bone material with a minimum of 12 species identified. A total of 550 specimens have been attributed to this order, forming 9% of the Medieval material. The most dominant species in this group is Greylag Goose (*Anser anser*) with 382 (6%) specimens identified. These are likely to be the domestic form (*Anser anser* var. *domesticus*). However, as mentioned in the methods the wild counterpart cannot be ruled out, and this figure may include wild geese as well. A further 25 specimens were classified as cf. *A. anser* and 28 specimens were placed into the *Anser* sp. group. Element representation for *A. anser* showed a very even distribution, even more so than the smaller species. This is expected within larger species where there is a better recovery rate of the smaller skeletal elements. Butchery marks were identified on 37 specimens, just under 10% of the *A. anser* remains (Figure 2E). Pathologies were observed on seven specimens, which mainly consisted of periosteal new bone growth around articular facets. Similarly to *G. gallus*, *Anser anser* mainly occurs on urban sites and not on island and hunting locations. Other Anserinae species identified within the assemblages include a single specimen of Bean Goose (*Anser fabalis*), and two specimens of Brent/Barnacle Goose (*Branta bernicla/leucopsis*). The Whooper Swan (*Cygnus cygnus*) was present in Medieval contexts from Oslo, Bergen and Borgund, with a total of nine specimens and an additional cf. *C. cygnus* specimen. Eighteen specimens could not be identified beyond Anserini.

We identified 83 specimens as belonging to the Anatinae, representing at least eight different species. Fifty specimens, predominantly from Bergen, were assigned to the Common Eider (*Somateria mollissima*). The Mallard (*Anas platyrhynchos*) is only represented by four specimens, found in Oslo, Bergen, Borgund and Trondheim assemblages. Four specimens of Long-tailed Duck (*Clangula hyemalis*) were recovered from Dovre. The Red-breasted Merganser (*Mergus serrator*) was represented by two specimens from Oslo and Bergen. Single specimens of Velvet Scoter (*Melanitta fusca*), Common Teal (*Anas crecca*) and Common Goldeneye (*Bucephala clangula*) were identified from Oslo, Bergen and Dovre respectively. A number of specimens could only be identified to genus level; two specimens to *Anas* sp., a single specimen to *Aythya* sp. In addition, three specimens were attributed to the *Mergini* tribe. A further 13 specimens were not identifiable beyond Anatinae.

3.2.3 Gaviiformes (Loons and Divers)

The Gaviiformes make up a very small percentage of the species represented with only 12 (0.20%) specimens identified, most of them from Oslo. The Black-throated Loon (*Gavia arctica*) was the most common of this order with seven specimens identified. In addition, four cf. *G. arctica* specimens were recorded. The Red-throated Loon (*Gavia stellata*) was the only other Gaviiformes represented in the Medieval material, with a single distal humerus recorded from Bergen.

It is important to note a misidentification of three specimens from Vesle Hjerkin, Dovre (Lie & Fredriksen, 2007). Previously, the humerus, ulna and radius of a *Gavia* species had been identified as Common Loon (*Gavia immer*). However, after close examination and use of both the Bergen and Tring Natural History Museum modern reference collections these specimens have been re-identified as the Black-throated Loon (*G. arctica*). The Common Loon (*G. immer*) breeds in Iceland and predominantly North America, whilst *G. arctica* breeds throughout Norway and Scandinavia (Caboreras et al., 2019a; Caboreras & Garcia, 2019).

3.2.4 Procellariiformes (Petrels and Shearwaters)

These pelagic species are not highly represented. Seven (0.12%) specimens from Oslo, Bergen and Borgund have been identified as Northern Fulmar (*Fulmarus glacialis*). All remains identified were wing elements. In addition to *F. glacialis*, a single carpometacarpus and ulna of Manx Shearwater (*Puffinus puffinus*) were also identified from Borgund. The migratory *P. puffinus* is currently the most frequently found Shearwater species in Norway (Caboneras et al., 2019b).

3.2.5 Ciconiiformes (Storks)

A single Black Stork (*Ciconia nigra*) tarsometatarsus was identified from Dreggsalmenningen, Bergen (Figure 2F; Figure 2G). This specimen represents the only Ciconiiformes species in the Norwegian Medieval bird bone material. Currently *C. nigra* is a vagrant species to Norway. The specimen recovered from Dreggsalmenningen is of particular interest; the foramen vasculare proximale has been worked into a larger hole, the proximal shaft has also been scraped, and fine transverse cut marks can be found just above the distal trochlea (see Figure 3C). It is clear that the specimen had some form of use and was possibly regarded as an important object. Magnus (1555) mentions the importance placed upon this species by people in the Medieval period, this could be the reason for the working of this specimen. The importance placed on the Black Stork may also indicate that this is a trade item rather than an indicator for the presence of *C. nigra* around Bergen.

3.2.6 Suliformes (Cormorants and Gannets)

Suliformes are represented by 34 specimens, from 3 different species, forming 0.55% of the Medieval bird bone assemblage. The most abundant is the European Shag (*Phalacrocorax aristotelis*) with 13 specimens. The Great Cormorant (*Phalacrocorax carbo*) is represented by eight specimens. The Northern Gannet (*Morus bassanus*) is also an abundant species within this order with 13 bones positively identified. However, six of these are from one individual excavated from Borgund. The elements from this individual are representative of the left and right wing. All Suliformes specimens were recovered from Bergen and Borgund. It is highly likely that all of these

animals were a result of fishing by-catch, as these seabirds are likely to get caught in the fishing nets, and both Bergen and Borgund were fishing towns.

3.2.7 Pelecaniformes (Herons)

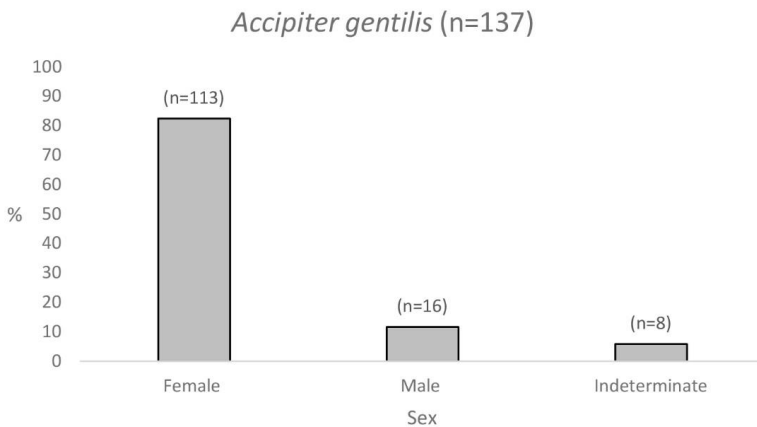
This order is represented by nine specimens identified as Grey Heron (*Ardea cinerea*). Five bone specimens are from one individual (ABG) recovered from Erkebispegården, Trondheim. They are all elements from the left wing. A single tarsometatarsus from Mindets Tomt (Oslo) was a juvenile. A complete humerus from Bryggen, Bergen, shows signs of butchery through hyperextension of the elbow causing the olecranon of the ulna to pierce the distal shaft of the humerus.

3.2.8 Accipitriformes (Hawks and Eagles)

The Accipitriformes are the third best represented order, accounting for almost 4% of the overall species counts. The Northern Goshawk (*Accipiter gentilis*) is the most dominant species within this order with 137 specimens (2.3%). *Accipiter gentilis* has been identified in material from Oslo, Bergen and Trondheim. Seven *A. gentilis* Associated Bone Groups (ABGs) were identified within the material (Table 6). Almost all specimens were fully developed adults, apart from a single juvenile humerus and ABG No. 4, which represents a young adult. Around 83% of the specimens (n = 113) were identified as females (Figure 4), 11% (n = 16) fell into the male size range. For 6% (n = 8), it was not possible to determine the sex. Overall, many of the female specimens from Medieval archaeological sites across Norway were examples of large individuals, often larger than the modern reference *A. gentilis* specimens held within the Bergen University Museum and the Natural History Museum at Tring (Figure 2H; Figure 5).

Table 6. Associated Bone Groups (ABGs) of *Accipiter gentilis*.

Site	Species	ABG details
Bryggen (JS 397)	<i>Accipiter gentilis</i>	ABG No. 10. Adult female partial skeleton. Only the cranium, mandible and sternum represented.
Bryggen (JS 529)	<i>Accipiter gentilis</i>	ABG No. 12. Adult male right wing. Complete humerus, ulna and radius represented.
Mindets Tomt (JS 537)	<i>Accipiter gentilis</i>	ABG No. 8. Adult female partial skeleton. Right sided tarsometatarsus, tibiotarsus and radius. Fragment of the left side of the furcular.
Mindets Tomt (JS 537)	<i>Accipiter gentilis</i>	ABG No. 9. Adult female partial skeleton. Right side of the pelvis fused to a complete synsacrum. A right sided humerus, ulna and tibiotarsus.
Mindets Tomt (JS 537)	<i>Accipiter gentilis</i>	ABG No. 4. Young adult female partial skeleton. All bones are developed but have only just finished ossification. Elements present are left and right femur, tibiotarsus and humerus. Left coracoid and ulna. Right tarsometatarsus and carpometacarpus.
Nordre Felt II (JS 702)	<i>Accipiter gentilis</i>	ABG No. 6. Adult female partial skeleton. Includes left and right pelvis fused to the synsacrum. Left and right femur, partial cranium, left scapula, carpometacarpus and tibiotarsus.
Nordre Felt II (JS 702)	<i>Accipiter gentilis</i>	ABG No. 7. Adult female partial skeleton, found in one context along with humerus and scapula from a second adult female. Includes left and right humerus, left radius, scapula, femur, tibiotarsus and fibula.

**Figure 4.** Representation of male and female *A. gentilis* in Norwegian Medieval contexts.

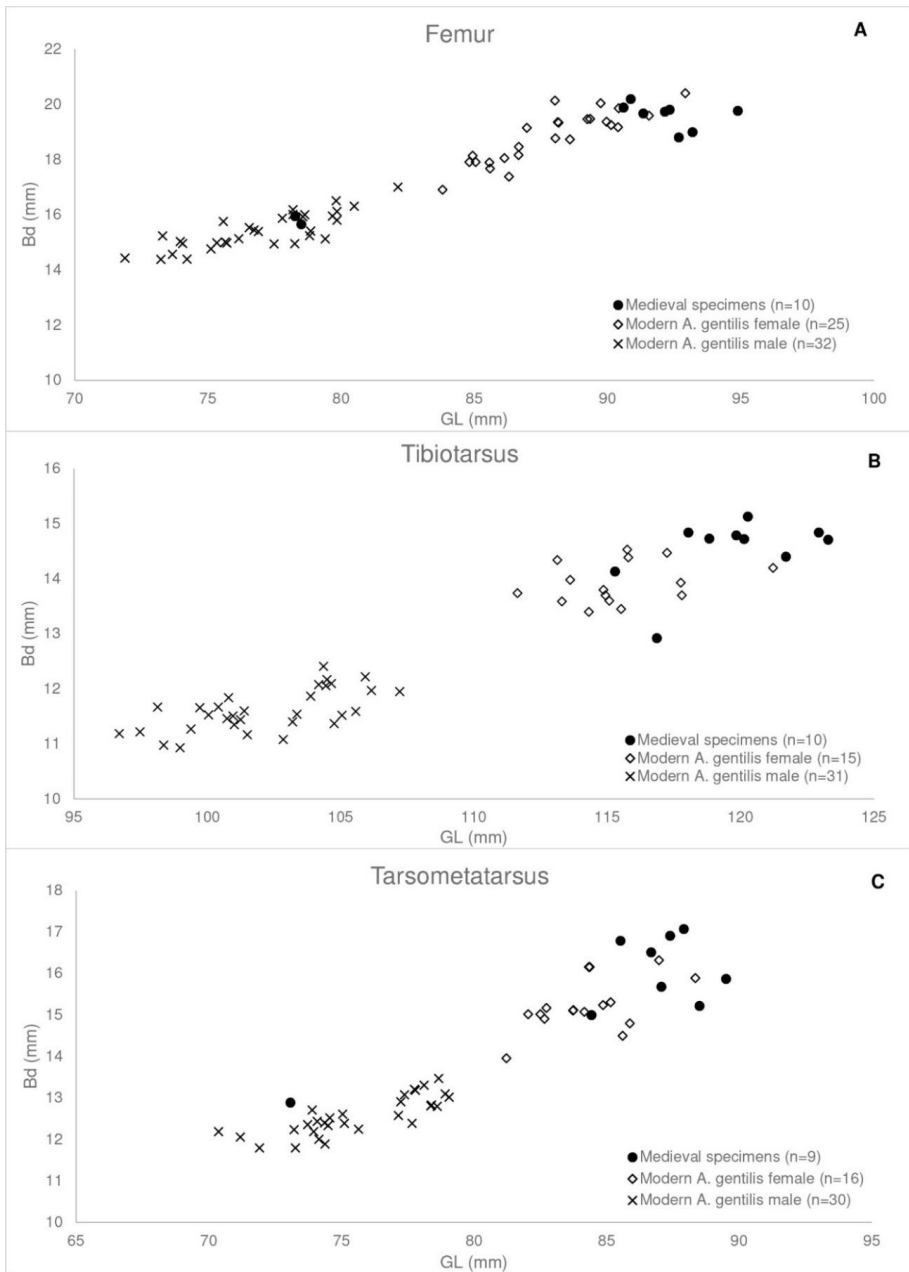


Figure 5. Plotted measurements (Breadth of the distal end (Bd) and Greatest Length (GL)) of modern Norwegian *Accipiter gentilis* specimens and the archaeological specimens from the Norwegian Medieval sites.

Remains of the Eurasian Sparrowhawk (*Accipiter nisus*) were also present within the Oslo and Bergen assemblages but in very few numbers (n = 2, 0.03%). Both specimens were identified as females.

The White-tailed Sea-eagle (*Haliaeetus albicilla*) was identified on eight of the 21 sites, these were all sites from Oslo, Bergen, Borgund and Trondheim. *Haliaeetus albicilla* is represented by 71 specimens and three cf. *H. albicilla* fragments (1.25%). Element representation shows that *H. albicilla* skeletal remains have a strong bias towards wing elements, with very few axial or lower limb remains being found within the assemblages (Figure 6).

The Golden Eagle (*Aquila chrysaetos*) was the third best-represented accipitriform, with eight specimens identified. All eight fragments (three humeri, two ulnae, two radii and one carpometacarpus) preserved are from the wing, similar to *H. albicilla*. These specimens were identified in Oslo, Bergen and Trondheim. Cut marks were observed on two ulnae specimens. One of the ulna has fine cut marks around the olecranon and approximately three more cuts on the underside of the dorsal cotyle. The other specimen, recovered from the Finnegården 3A site in Bergen, is intriguing; a chop to the proximal end has removed the olecranon, with another chop through the distal shaft. The edges of the chopped distal end have been retouched, similar to the retouching observed on the edge of a flint tool (Figure 2I; Figure 2J). Furthermore, scrape marks can be observed running the whole length of the specimen, possibly as a result of removing the feathers.

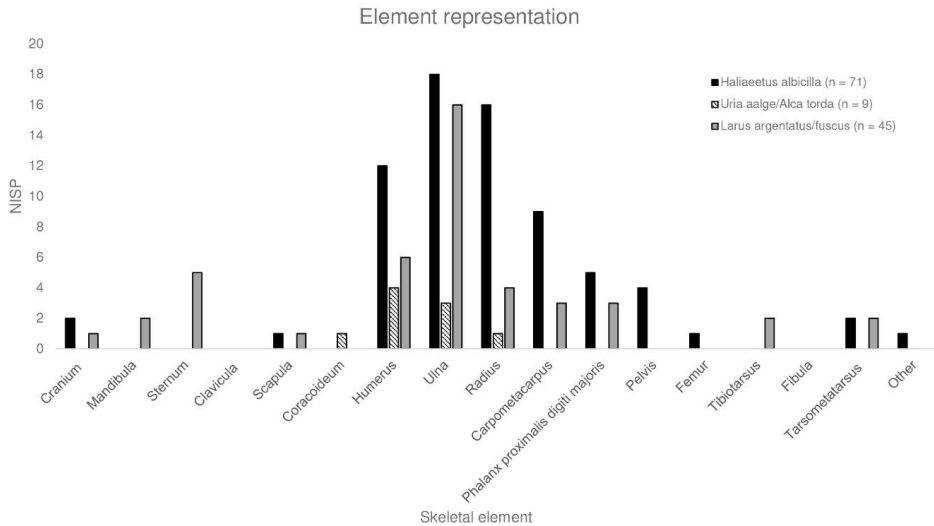


Figure 6. Element representation of *Haliaeetus albicilla*, *Uria aalge/Alca torda* and *Larus argentatus/fuscus*. Showing a dominance of the wing elements. Cf. specimens were not included in this figure.

3.2.9 Falconiformes (Falcons)

Falconiformes are represented by only 10 specimens, 0.17% of the total Medieval bird bones. All of these specimens were found in either Oslo or Bergen. The Gyrfalcon (*Falco rusticolus*) was represented by six specimens, all of these were from Bergen sites. The Peregrine Falcon (*Falco peregrinus*) is represented by two specimens from Bergen. Both specimens belong to a large female, and are probably from the same individual. A further two specimens were recorded within this order. It was not possible to identify them beyond Falconidae, but they fall within the size range of *F. peregrinus* and *F. rusticolus*.

3.2.10 Strigiformes (Owls)

Strigiformes are represented by only two specimens (0.03% of the bird bone assemblage). Both specimens are of the Eurasian Eagle-owl (*Bubo bubo*) and are found only within the Bergen assemblages. The first specimen is a complete ulna from Bryggen and the second a complete tarsometatarsus from Finnegården.

3.2.11 Gruiformes (Cranes)

Three specimens of Common Crane (*Grus grus*) were identified, contributing 0.05% to the Medieval bird bones. Cut marks were observed on a single tibiotarsus shaft from Bryggen, Bergen. The other two specimens were a femur and humerus recovered from the Blomsøy excavations in Alstahaug.

3.2.12 Charadriiformes: Scolopacidae, Alcidae and Laridae

The Charadriiformes is a large and diverse order, and contributed a total of 181 specimens, making up 3% of the identified material.

3.2.12.1 Scolopacidae (*Sandpipers, Snipes and Phalaropes*)

It was only possible to positively identify one species within this family, the Eurasian Woodcock (*Scolopax rusticola*), with five specimens from sites in Oslo. In addition, a single distal radius fragment was identified as Scolopacidae sp. but could not be identified further.

3.2.12.2 Charadriidae (*Plovers*)

The Charadriidae within the Medieval Norwegian material are represented by a single carpometacarpus from Gæccevajnjar'ga, Finnmark. This specimen is assigned to *Pluvialis apricaria/squatarola*. Morphologically, the carpometacarpus of these two species cannot be separated from each other. The Eurasian Golden Plover (*Pluvialis apricaria*) breeds in Norway and migrates south in the winter (Wiersma et al., 2019a). Whilst the Grey Plover (*Pluvialis squatarola*) does not breed in Norway, it occurs during migration (Wiersma et al., 2019b), and its presence in Medieval times should not be ruled out. We therefore refer this specimen to *Pluvialis apricaria/squatarola*.

3.2.12.3 Alcidae (*Auks*)

In total 57 specimens were identified to the Alcidae family, contributing 1% to the overall Medieval identified count. Many of these were identified on the island of Røst, but with a number identified from Oslo, Bergen, Borgund and Finnmark. Skeletal remains of Common Murre (*Uria aalge*), Thick-billed Murre (*U. lomvia*) and Razorbill

(*Alca torda*) are similar in size and morphology. Furthermore, these three species are often found in mixed colonies in northern Norway. To prevent over-identification of any one species, 11 specimens have been grouped as *Uria aalge/lomvia/Alca torda*. The majority of these specimens were from Borgund. Current *Uria lomvia* only breed in easternmost Finnmark and winter in the Barents sea (Nettlehip et al., 2019). This makes the Bergen and Borgund specimens more likely to be *Uria aalge* or *Alca torda*. Nine specimens from the Oslo sites (Mindets Tomt, Oslogate 7 and Nordre Felt II) were grouped as *Uria aalge/Alca torda*, with a further four cf. *Uria aalge/Alca torda* specimens from Nordre Felt II. All of the specimens within this group are wing elements (Figure 6). Remains of the Atlantic Puffin (*Fratercula arctica*) are more distinct than the Murre and Razorbill species, making it easier to distinguish them. A total of 30 specimens were identified, most of them from Røst. However, the odd specimen was identified in Oslo, Bergen, Borgund and Finnmark. The only other Alcidae species which we were able to identify was a Black Guillemot (cf. *Cepphus grylle*) specimen, represented by a single femur from Bergen.

3.2.12.4 Laridae (Gulls, Terns and Skimmers)

In total 116 bones were assigned to Laridae. The Great Black-backed Gull (*Larus marinus*) is the largest of the gull species, and 18 specimens were identified from sites in Oslo, Bergen, Alstahaug and Borgund. Wing bones were the dominant elements here. As with the Alcidae, there are a number of similar sized and morphologically similar Laridae species which are residents in Norway. Consequently, remains of European Herring Gull (*Larus argentatus*) and Lesser Black-backed Gull (*Larus fuscus*) could not be separated and have been placed into one group. This group was the most numerous, with 45 specimens. Once again, these are predominantly wing bone elements (Figure 6). Other species of Laridae were also identified but in smaller numbers. Three specimens of Black-legged Kittiwake (*Rissa tridactyla*) with an additional two cf. *Rissa tridactyla* specimens. The Mew Gull (*Larus canus*) was represented by two specimens, and a further two cf. specimens, from Bergen sites. One specimen of a *Sterna* species was identified from Dovre. A single ulna from Oslo was identified as cf. *Sterna hirundo* (Common Tern). Forty-two specimens were placed into

the wider Laridae sp. category, 40 of these were from a single context at the Finnegården 3A, Bergen. This assemblage consisted of 20 tarsometatarsi, 19 tibiotarsi and one maxilla fragment. The epiphyseal ends were missing from every specimen, with crenulated edges indicative of gnawing, making it difficult to identify to species. However, they most likely fall into the *Larus argentatus/fuscus* category. The missing epiphyseal ends has also been observed in Greenland, and has been interpreted as being chewed by humans (Gotfredsen, 1997).

3.2.13 Columbiformes (Pigeons and Doves)

Pigeons and doves are not common in the archaeological material for the Medieval period in Norway, with just seven specimens (0.1%). The Common Woodpigeon (*Columba palumbus*) is represented by six specimens from sites across Oslo. In addition, a single ulna specimen from Tønsberg has been identified to *Columba livia/oenas*. It is highly likely that this specimen represents a Stock Dove (*C. oenas*) which is currently a breeding visitor to south-eastern Norway (Baptista et al., 2019). In addition, there is little evidence to suggest the presence of *Columba livia* in Norway prior to the Post-Medieval period.

3.2.14 Passeriformes

A total of 155 specimens from five different families were identified to this order, accounting for 2.6% of the identified counts. The results for this order have been separated into families. Four specimens could not be identified beyond Passeriformes. In addition, a further three specimens were only identifiable to Sturnidae/Turdidae sp.

3.2.14.1 Corvidae (Crows and Jays)

A total of 105 specimens (1.8%) were recorded within this family, representing four different species. Corvidae have been found exclusively within the urban sites. Fifty-two specimens have been identified as *Corvus corone*. Based upon the current geographical range, it is likely that the *C. corone* specimens are of the subspecies *Corvus corone cornix* (Hooded Crow). It should be noted that it is very difficult to osteologically separate Crows from Rooks (*Corvus frugilegus*). However, breeding

pairs of Rooks in Norway are not that numerous (Madge, 2019). Therefore, we have assumed that the Medieval specimens are most likely to be *Corvus corone cornix*, but *Corvus frugilegus* cannot be ruled out. The Common Raven (*Corvus corax*) is also well represented, with 36 specimens. The Eurasian Jackdaw (*Corvus monedula*) was identified in the material with eight specimens and a further two cf. *Corvus monedula*. The Eurasian Magpie (*Pica pica*) was the least common species in the Corvidae family with seven specimens. A very small number of sub-adult and juvenile specimens have been recorded for the Corvidae, most of them are *P. pica* specimens.

3.2.14.2 Turdidae (Thrushes)

Thirty-nine specimens (0.7%) were assigned to this family. The majority of specimens were recovered from Vesle Hjerkin, with some additional specimens from Oslo. Whilst attempts have been made to separate these species, six specimens were identified no further than *Turdus* sp., 11 specimens have been placed into the small *Turdus* sp. group, and a further 20 specimens fell into the large *Turdus* sp. group. It was only possible to identify two specimens confidently to species, both specimens were humeri and were identified with the aid of Jánossy (1983) to Fieldfare (*Turdus pilaris*). These specimens were recovered from Vesle Hjerkin.

3.2.14.3 Sturnidae (Starlings)

A single specimen, a distal tibiotarsus from Vesle Hjerkin, was assigned to the Common Starling (*Sturnus vulgaris*).

3.2.14.4 Motacillidae (Pipits and Wagtails)

A single humerus of the Meadow Pipit (*Anthus pratensis*) was recorded from Vesle Hjerkin.

3.2.14.5 Passeridae (Sparrows)

Passeridae are represented by a single House Sparrow (*Passer domesticus*) carpometacarpus and a cf. *P. domesticus* humerus, both from Oslo.

3.3 Site type distribution

The Medieval assemblages can be split into four main site types; urban, rural, monastic and hunting. The full NISP figures and percentages per site type are presented in Figure 7, for full information on site type see Table 1. There are 15 urban sites represented in the re-examined material. These towns and cities are predominantly in the southern part of Norway, as no Medieval urban sites are known north of Trondheim. A minimum of 48 different species from a diverse number of avian families are represented within the urban material. The assemblages are dominated by domestic species with *G. gallus* and *A. anser* collectively forming 74% of the NISP. The wild Galliformes formed just over 6% of the species represented on urban sites. Accipitriformes are present exclusively on urban and monastic sites, and contributed 5% to the urban bird bone assemblages.

Rural sites are defined as small rural communities and farms, and the majority of these are found in northern Norway. The avian assemblages from the four rural assemblages re-examined here show a different pattern than the urban sites; only 21 species were represented within these four sites, and domestic species form only 2% of the avian material identified. Wild Galliformes are well accounted for (89%). This high percentage is mainly due to the number of *Lagopus* specimens identified from Vesle Hjerkin, although this number may be inflated by the fact that Vesle Hjerkin had a hunting lodge attached.

Only one monastic assemblage has been examined, the Erkebispegården site in Trondheim. The Erkebispegården site is best described as a high status site, characterised by ecclesiastical practices. We compared the Erkebispegården with other monastic sites within Norway, but many of the non-native introductions which were found in the Post-Medieval period are more likely linked with the high status of the site rather than the religious practices. The vast majority of the bird bone material from the Erkebispegården is associated to Post-Medieval contexts, and not considered here. The Medieval assemblage from this site is relatively small. In terms of species representation, this monastic site falls between urban and rural sites. The assemblage contained only 15 different species, which is relatively high considering the small

assemblage size. Domesticates form 47% of the assemblage. The number of corvids (18%) identified on this site is higher than on all other site types.

The only hunting site represented in the re-identified material is Tøftom, in the Dovre region. The main focus on this site was reindeer hunting (Lie & Fredriksen, 2007). The assemblage size here is very small, making it difficult to discern any patterns. Wild Galliformes form 93% of the assemblage and likely were the target species. Domesticates are not represented at all, and in this respect it is similar to rural sites.

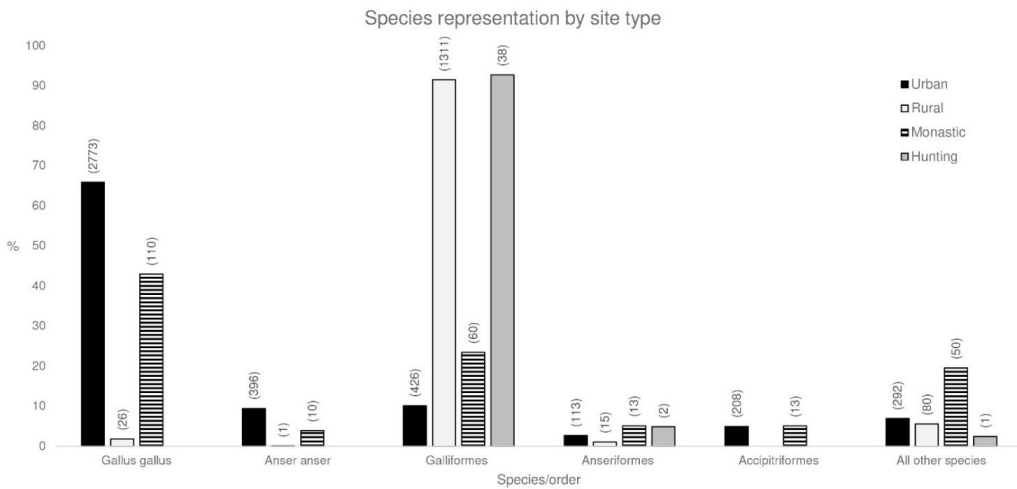


Figure 7. Species representation by site type. The four main site types for Medieval Norway are represented here (Urban, rural, hunting and monastic). Percentages are based on the NISP figures for each site type, in order to compare and identify site specific patterns. The NISP figures are placed in brackets within the figure.

4. Discussion

Our re-examination of bird remains in Norwegian Medieval faunal assemblages identified a minimum of 55 different species from 16 different orders. This is the first time data on avian remains from Norwegian Medieval faunal assemblages has been amalgamated, and it forms the first representation of avian species in Medieval Norway. Furthermore, our work identifies patterns of avian exploitation and highlights the importance of birds in Medieval Norwegian societies.

4.1 Patterns in wild bird species

We adopted a cautious approach in identifying specimens. As a result, less species may be represented, but these paint a more accurate representation of the Medieval avifauna for Norway. In addition to the re-identification of material from archaeological sites, a large amount of new data has been recorded for the material, highlighting the need to closely re-examine existing collections, particularly when they include species prone to misidentification. When considering the distribution of birds in Medieval assemblages, we have to work under the assumption that the species representation within the bird bone assemblages is the result of anthropogenic bias. In addition to humans selecting for or against certain species, trade and fishing bycatch can cause displacement of species outside of their natural habitat. Furthermore, recovery bias also causes distortions in species representation, particularly when methods like sieving have not been implemented methodically. Consequently, the absence of certain species from the archaeological record does not mean they were not present, or possibly even abundant, within the Norwegian avifauna, and we should treat any absences with caution.

Despite these caveats, we found no evidence to suggest that the Medieval Norwegian avifauna differed from the current one, as all wild species identified in the Medieval assemblages are still extant within Norway today. In most cases, their occurrences in Medieval locations overlap with their modern ranges. This was somewhat unexpected, given that the Medieval period experienced significant climatic oscillations (Ahmed et al., 2013; Zawiska et al., 2017), and saw the rise of urban

centres. Climatic changes were expected to be reflected by the presence of species well outside their current ranges or by species currently absent from Norway. The rise of urban centres may have resulted in habitat destruction and increased hunting pressure, and potential extinction of species. However, our data do not show any evidence for these scenarios. That is not to say that Medieval climatic oscillations and an increasing human population did not impact the Norwegian bird fauna. The lack of precise dating for a number of sites and the concomitant binning of species in broad time periods obscures any links between the temporal occurrence of a species and the timing of climatic oscillations. In addition, the anthropogenic bias on most of our sites means that the presence, absence or abundance of species in an assemblage does not necessarily translate to population status in the wild.

Although the current Norwegian avifauna can be traced back to at least the Medieval period, we recorded a few species that were either unexpected or observed in higher or lower quantities than predicted based upon their current range and abundance. The Black Stork (*Ciconia nigra*) breeds in the Western Palearctic but not as far north as Scandinavia. However, *C. nigra* does occur as a vagrant in Norway (Elliott et al., 2019). Generally, this species avoids dense woodlands and forests, as well as areas of human activity. However, slightly higher summer temperatures of around 1–2 °C warmer than the mean millennial temperature during the Medieval warm period (Zawiska et al., 2017) could have encouraged northwards dispersal of *C. nigra*. There is evidence of *C. nigra* breeding in Sweden from at least c. 1450 CE up to the middle of the twentieth century, with only the occasional breeding pair being recorded in recent times (Ericson & Tyrberg, 2004). Magnus (1555) mentions *C. nigra* as linked to the Norse god Odin, which suggest that this bird may have had a special status. This makes the Dreggsalmenningen (Bergen) specimen even more intriguing, but currently this is the only record of *C. nigra* in the archaeological record for all periods in Norway.

Wild Galliformes are in decline across Scandinavia (Alsaker, 2017; Gregersen & Gregersen, 2009), although the reasons behind this are not fully understood. Both *Tetrao urogallus* and *Lyrurus tetrix* occur throughout most of modern Norway, although their densities are higher east of the Norwegian watershed in eastern Norway and Sweden (Gjershaug et al., 1994; Haftorn, 1971). Increased precipitation and a lack

of old forests is thought to drive this pattern (Alsaker, 2017; Gregersen & Gregersen, 2009). Occurrences of these two species in Medieval sites overlap with their modern ranges, but both *T. urogallus* and *L. tetrix* are more abundant in eastern sites (Oslo and Trondheim) than in western Norway (Bergen). This suggests that current patterns in the distribution and abundance of these two wild galliforms may be older than previously thought. Another example of a species that appears to have maintained a similar range since Medieval times is *Corvus monedula*. Although only a few specimens have been retrieved from the Medieval period, all were recovered from Oslo or Trondheim sites. This overlaps with its current distribution, which is restricted to south eastern Norway and a small area around Trondheim (Madge & de Juana, 2019).

Although several Norwegian seabird populations are currently in decline (Fauchald et al., 2015), it has been suggested that certain species of seabirds were more abundant in Medieval times. For instance, the Black-legged Kittiwake (*R. tridactyla*) was more abundant in Sweden during the Medieval period, and this was attributed to a good “Herring period” in the southwest Baltic (Ericson & Tyrberg, 2004). Although we identified a number of species of seabirds in Norwegian Medieval assemblages, gaviiforms, procellariiforms, suliforms, pelecaniforms and charadriiforms are only present in low abundances. For the Northern Gannet, *Morus bassanus*, prehistoric data indicate that it was rather abundant in Norway from 6000–5000 BP (Montevicchi & Hufthammer, 1990), but similarly to other marine species, *M. bassanus* has only been found in small numbers in the Medieval period. The species continued to decline during the Post-Medieval period and went extinct in Norway, only to reappear in the 1940s (Barrett & Folkestad, 1996). Our data therefore do not support the notion of high seabird abundances in Medieval times. Whether this reflects actual low population abundances, possibly related to a decline in fish stocks in southern Norway since 1000 CE onwards due to increased fishing activities in the North Atlantic (Barrett et al., 2004), or reflects a preference for other wild and domestic species remains unclear. It is worth noting here that during the Norse periods on the Western Isles of Scotland, there was a marked decrease in the exploitation of seabirds, and an increase in domesticates and land fowl exploitation (Best & Mulville, 2014). This suggests a preference away from seabirds, and a similar shift might have occurred in Norway as

well. The Great Auk (*Pinguinus impennis*) is notably absent from Medieval contexts. The latest archaeological specimen from Norway dates to 1500 BP (not calibrated) (Hufthammer, unpublished data). The absence of any *P. impennis* specimens from Medieval contexts implies it was already in heavy decline during this time, and it is likely that the Great Auk had abandoned former breeding sites in Norway prior to the Medieval period (Hufthammer, 1982). This pattern is echoed in the Scottish Isles, where the dominance of Great Auk remains in Bronze Age and Iron Age assemblages is heavily diminished or absent by the Norse periods (Best & Mulville, 2014).

Interestingly, several groups of birds which are ubiquitous today, particularly near urban centres, such as passerines, Laridae and Corvidae, are poorly represented within the Medieval archaeological record. In the case of the passerines, this is likely due to a recovery bias, as the lack of sieving means that smaller bones have not been sampled. In addition, smaller bones are less likely to survive compared to the larger bones. However, that being said, a number of small fish bones have been recovered from almost all of the sites, which suggests that passerines may not have been in demand. The practice of trapping thrush species has been mentioned by historical sources (Magnus, 1555; Nilsson, 1858; Lloyd, 1867), but this is likely to have happened mostly on the rural and hunting sites (for which we have limited data) rather than in the urban centres. The dispersal of gulls and corvids into urban areas may have lagged behind the emergence and expansion of large urban centres and these species may not have been established within towns at this point. Swedish data suggests that certain gull species, particularly *L. argentatus*, were almost exclusively marine species prior to c.1900, but are now frequently breeding inland (Ericson & Tyrberg, 2004). Alternatively, the absence of corvids and gulls could indicate a taboo against eating these birds. Gulls were not considered particularly inedible, as evidenced by a quote from Bjørnstad (1972) “The meat of the year-old birds being particularly delicious, as indeed it is for all year-old gulls”. However, Christian laws forbade the consumption of ‘unclean’ species and although it is not known if this included birds as well, it could explain the lack of Laridae within the archaeological material. The complete absence of *Larus* species from the high status/monastic site of Erkebispegården would support this.

4.2 Domesticates

Domesticates are the largest group of birds represented in the Norwegian Medieval bird bone assemblages. Although the definition of a domestic species varies, we here follow the species mentioned within Serjeantson (2009). The introduction of domestic fowl into Scandinavia is not fully understood. Current evidence suggests that introduction appears to be slightly later than Central Europe. In Sweden the earliest evidence dates to the 1st century BCE (Lepiksaar, 1977). Domestic fowl are not abundant in Sweden and Denmark until the Late Iron Age into the Viking Age (Tyrberg, 2002; Ericson & Tyrberg, 2004; Gotfredsen, 2013; Gotfredsen, 2014). Prior to this, domestic fowl are not dominant within assemblages; rather, they are seen as high status commodities. Current evidence places the introduction of *G. gallus* in Finland to the 8th century CE (Ukkonen & Mannermaa, 2017; Wessman et al., 2018). For northern Scotland and the Scottish Isles the introduction of domestic fowl is later than the rest of Britain (Serjeantson, 1988). Zooarchaeological work conducted on the Orkney Islands and the Hebrides dates the introduction of *G. gallus* to possibly the Iron Age, but more likely the Norse period (c. 1100–1300 CE) (Serjeantson, 2014). Best and Mulville (2014) have identified a similar date for the Western Isles.

Barrett et al. (2007) claim that the presence of early domestic fowl in Viking Age Kaupang dating to the early 9th century CE constitutes evidence for early domestic fowl in Norway. It is possible that the single *G. gallus* specimens from Iron Age sites at Viklem, Sør-Trøndelag and Sør-Dalaheller, Kristiansund (Unpublished data from the Natural History archive, University Museum of Bergen) are earlier but they have not been re-examined or C14 dated. However, a lack of avian assemblages dating to the Iron Age and early Viking Age makes it difficult to assess the presence and abundance of domestic fowl before the Medieval period. Regardless, current evidence seems to suggest a slightly delayed introduction in both Norway and Finland, with domestic fowl not being abundant until the Medieval period.

Sites with more refined dating give an indication of how quickly *Gallus gallus* became established in Norway. The site of Bibliotekstomten in Trondheim has *G. gallus* present in its early phases dated to 900–ca.1125 CE (Lie, 1989, Unpublished report, see SMF1). Another Trondheim site, Televerkstomten, records a single *G.*

gallus specimen from early 1100 CE contexts, with the abundance of *G. gallus* not increasing until the later part of 1100 CE (Marthinussen, 1992, Unpublished thesis, see SMF1). In addition, early Medieval evidence of *G. gallus* is recorded in Oslo at Mindets Tomt (contexts dating to 1025–1125/1150 CE (Lie, 1988)) and Oslogate 4 (contexts dating to 1000–ca.1150 CE (Lie, 1991)). The Borgund sites may represent another early introduction of *G. gallus*, as there are a number of Viking Age contexts with domestic fowl. However, further analysis of the stratigraphy on this site is necessary, along with C14 dates for the *G. gallus* specimens. From Dreggsalmenningen, Bergen, *G. gallus* is present in the earliest phases dated to ca.1170–1300 CE and becomes more abundant in the second phase dated to 1300–1332 CE (Undheim, 1985, Unpublished report, see SMF1). All of these dates point towards a presence of domestic fowl on most urban sites during the early Medieval period.

Gallus gallus is the most dominant species within the Medieval assemblages. On urban sites domestic fowl overall account for 66% of the avian representation. This is in stark contrast to rural sites, where domestic fowl represent only 2% of the assemblages. However, an increased abundance of *G. gallus* specimens is found on the supplementary rural sites, where they account for 38% of the assemblage. It is possible that a proportion of these are misidentified, given the high number of *L. tetrrix* specimens that were previously recorded as *Gallus gallus*. The dominance of domestic species on urban sites and a focus on wild resources on rural sites is a common trend across Norway, this likely reflects a focus on imports and domesticates within the towns and a reliance upon local resources on rural sites. It is most likely that the larger populations within towns would have needed a steady supply of food, leading to a reliance on domesticates, a pattern mirrored in the mammalian fauna identified in towns. In addition, the hunting possibilities around towns would not have been as easily accessible as on the rural sites.

The Norwegian material suggests the primary focus on domestic fowl was the production of eggs, as indicated by the low percentages of immature birds. This suggests that domestic fowl was not intensely exploited, and birds were allowed to reach full maturity. Alternatively, the lack of evidence for immature *G. gallus* may be due to taphonomic processes, whereby the more porous juvenile bones are simply not

surviving. In England, a rise in the number of immature specimens in the Medieval periods has been associated with meat exploitation (Maltby & Wilkinson, 1979; Serjeantson, 2009). As domestic fowl became established in Britain during the Roman period, it is likely they were viewed as a precious commodity and exploited mostly for eggs. Chickens may have been only consumed when they were older or by higher status households. We propose that the later introduction, and presumed lack of juvenile *G. gallus* into Norway reflects a similar role of domestic fowl in Norwegian Medieval society as that seen in Roman Britain.

The identification of domestic geese from their wild counterparts is almost impossible osteologically, with very few morphological characters separating the two. In the case of the Norwegian Medieval material we are assuming that the majority of the geese identified are domesticated. This is based on the higher abundance of *A. anser* found within assemblages in comparison to previous periods. Prior to the Medieval period sites rarely have more than one *A. anser* specimen recorded, and these sites are often located along the coast where the current distribution of wild *A. anser* can be found. In contrast, the Medieval specimens are almost exclusively found within urban contexts, which is outside of their natural habitat. In addition, the specimens appear slightly larger and more robust in size than their wild counterparts. The presence of pathologies on a small percentage of the *Anser anser* specimens also adds support to the idea that these represent domesticated individuals. A similar percentage and types of pathologies were only observed in the other domesticated species, *Gallus gallus*. Evidence suggests that the introduction of domesticated geese into much of Scandinavia is dated to the Iron Age. This introduction has been identified in Sweden through a massive increase in subfossil *A. anser* remains from the Iron Age onwards (Ericson & Tyrberg, 2004). In Denmark, domestic geese were present during the Roman Iron Age, specifically around 200–250 CE, and have been identified within high status graves (Gotfredsen, 2013). However, it is unlikely that domestic geese were common during this period. It is not until the Viking Age and the Early Medieval period that domestic geese occur on numerous sites and are generally the second most dominant species after *G. gallus* (Gotfredsen, 2014). Evidence from the Scottish Isles

indicates a pattern similar to that of *Gallus gallus*, in that geese were introduced during the Norse period (Best & Mulville, 2014).

Our data for Norway show a distribution of *A. anser* focused on the larger urban sites of Oslo, Bergen, Tønsberg and Trondheim. Very few specimens have been identified outside of these large towns. The urban location of these specimens indicates that these specimens represent domesticated *Anser anser*. Based on current evidence we propose that a Medieval introduction of *A. anser* to Norway seems most likely. *Anser anser* has been identified from late 1100 CE contexts at Televerkstomten, Trondheim, but is not abundant on this site until 1300 CE (Marthinussen, 1992, Unpublished thesis, see SMF1). Similarly, *A. anser* is recorded in phase 2 at Bibliotekstomten, Trondheim (only a broad date is given for phases 1–3 of 900–ca.1125 CE, (Lie, 1989, Unpublished report, see SMF1)). The site of Oslogate 4, Oslo, shows an introduction of *A. anser* on the site between the first half to the middle 1200s, whilst *G. gallus* is present from 1000 CE onwards (Lie, 1991). There is currently no definitive osteological method for separating the domestic from the wild and we realise that the specimens we have identified as domestic geese may include wild specimens. However, we believe the evidence is strong enough to suggest the presence of domestic *A. anser* in Medieval Norway.

On a number of sites *A. anser* and *G. gallus* are both present in the earliest phases, but with *Anser anser* not becoming abundant until later, it is possible that these earlier specimens are wild *Anser anser* and not the domesticated form. The site of Mindets Tomt in Oslo shows the presence of both *G. gallus* and *A. anser* in phase 1 dating to 1025–1125/1150 CE (Lie, 1988). The same is the case for Dreggsalmenningen, Bergen, where both domesticates are present in the earliest phases dating to ca.1170–1300 CE (Undheim, 1985, unpublished report, see SMF1). The identification of only two sub-adult *A. anser* specimens would suggest a pattern of exploitation similar to that of domestic fowl, whereby secondary products are being exploited. Historical evidence does not mention egg production for geese. Instead, they were prized for their fat, often used in cooking and also as a remedy to many ailments (Magnus, 1555). With the evidence at hand, we suggest a slightly later introduction of *A. anser* than *G. gallus*. More precise dating of these specimens will show if this is

indeed the case. However, it is not until the mid-late Medieval period in Norway that both domestic fowl and geese become abundant.

In contrast to geese, ducks are distinctly lacking in the assemblages. Tyrberg (2002) also notes a lack of domesticated duck from Swedish Medieval periods. However, there are some sites in Sweden where domestic ducks are abundant during the early Medieval period, only to be later replaced by domestic geese. This high number of ducks is also seen at Novgorod, Russia, where a dominance of Mallard/domestic duck has been observed (Hamilton-Dyer, 2002). This pattern differs from Norway, where *G. gallus* and *A. anser* were the dominant domesticates, assuming the *Anser anser* specimens are indeed domesticated. The lack of ducks is reflected in historical sources, in particular Olaus Magnus (1555), who refers to ducks as “cold and coarse in taste” and preferring woodland birds to water birds, a statement which is supported by our findings.

The practice of falconry in Medieval Norway is well documented (Lie, 2018). At current, the earliest zooarchaeological evidence for falconry practice in Norway dates to 900 CE, from the Gokstad burials (Hufthammer, 2019). Iconographic evidence from Norway may point to an earlier use of falcons (Lie, 2018). Our data identify the favoured species used in Norwegian Medieval falconry; the Northern Goshawk, the Eurasian Sparrowhawk, the Gyrfalcon and the Peregrine Falcon. There is little evidence for the use of Golden Eagle and White-tailed Sea-eagle as falconry birds (Prummel, 1997; Cherryson, 2001). However, historical sources do not mention their use in Norway (Lie, 2018), and the dominance of wing elements suggests a different use for these larger species. The dominance of wing elements is an interesting and common pattern. It likely results from the extraction of feathers, which have many uses such as arrow fletching’s and decorations amongst others (Bovy, 2002).

The most striking pattern observed within the avian assemblages, is the dominance of the Northern Goshawk (*Accipiter gentilis*) above all other birds of prey. This species accounts for 95% of the falconry species represented (not including *H. albicilla* and *A. chrysaetos*). Due to the persecution of this species in the last century (Heggøy & Øien, 2014), it is possible that it was more abundant during the Medieval period than today. The dominance of females shows a clear selection of large

individuals for use as hunting birds. Further analysis also identified seven ABGs within this species, more than any other for the Norwegian Medieval material. The deposition of these species as a whole or partial bird possibly indicates greater respect shown to falconry birds.

In contrast to the abundance of Northern Goshawk, the lack of Gyrfalcon and Peregrine Falcon remains was unexpected, given that they were highly prized (Serjeantson, 2009; Lie, 2018). However, current population figures show a higher abundance of *Accipiter* species than *Falco*, this suggests that *Falco* species may have been less abundant, harder to access and/or trap. Whilst the *Falco* species were highly sort after, *A. gentilis* and *A. nisus* could be owned by a range of people from low nobility to wealthy commoners (Wood & Fyfe, 1955). It has been suggested the practice of falconry within Norway was not reserved for the upper classes of society as it was in many other countries, such as England (Thorsen, 2007; Iversen, 2013), but was rather seen as a means by which to supply subsistence. Despite this the practice of trapping birds would have been more efficient, and we presume this was the main hunting technique employed. Recent work has investigated the heavy exportation of falconry birds from Norway (Lie, 2018), which could have lowered the abundance of *Falco* species found within the Norwegian archaeological record.

Falconry species are limited to sites in Oslo, Bergen and Trondheim. The presence of these species within Oslo and Bergen could represent birds which were to be traded with Europe. Some of the individuals identified were from high status and monastic sites, whilst others, such as those found in Bryggen, could have been used by lower classes. At the site of Mindets Tomt, Oslo, a higher abundance of *A. gentilis* in the earlier phases (1025–1225 CE) was observed, with a decrease in numbers in later phases (Lie, 1988). Whether this represents an increase in exportation of falconry birds after 1225 CE or simply a decrease in its popularity is unclear.

Indirect evidence of possible falconry practice can be found at Vesle Hjerkin. Although no falconry species were identified from this assemblage, this site is dominated by *Lagopus* remains, and a number of *Turdus* specimens (a typical prey of falconry species). These species may have been snared and trapped, a practice well documented within Norway (Magnus, 1555; Nilsson, 1858; Lloyd, 1867; Collett et al.,

1921). However, the small number of specimens which display puncture marks indicative of an avian predator may be evidence for the use of falconry. Whilst discussing the presence of falconry prey, it is worth mention that the remains of Grey Heron and Common Crane have been documented as highly prized falconry prey (Sykes, 2014). This is something to consider, especially for the Grey Heron, which has only been found on sites in Oslo, Bergen and Trondheim, all locations with strong falconry evidence. Our re-examination of birds of prey from the Medieval contexts has strengthened the evidence for falconry within Norway, by adding sex and metric data, as well as ABG information to the observations following the key zooarchaeological indicators for falconry as outlined by Prummel (1997). Our current work on falconry species adds zooarchaeological evidence for falconry in Norway to the recently conducted work by Lie (2018) on the historical records of falcon catching in Norway.

Previous work has identified a number of species that are non-native, such as *Pavo cristatus* and *Perdix perdix*, but we have found these to be erroneous. Our re-examination of a previously identified *Pavo cristatus* specimen from Mindets Tomt was, in fact, Western Capercaillie, and we have found no Indian Peafowl in Medieval Norway. Historical sources support, the absence of *P. cristatus*, noting how rare and highly prized Indian Peafowl were (Magnus, 1555). We have subfossil *P. cristatus* from the Gokstad burials (Hufthammer, 2019), dating to the Viking period, after these specimens, *P. cristatus* does not re-appear in the archaeological record until the Post-Medieval period. The Post-Medieval specimens are from Revierstredet, Oslo and Erkebispegården, Trondheim (dating to 1640–1672 CE). There is also a possible *P. cristatus* specimen from Post-Medieval contexts at Kontraskjæret, Oslo but DNA analysis is needed to rule out other larger Galliformes.

There were a number of species which we presumed were introduced into Norway during the Medieval period. However, our work found that the earliest evidence for these non-native species dates to the Post-Medieval period, and were identified from the Erkebispegården site. Currently these specimens are the best evidence we have for their introduction into Norway. Common Pheasant (*Phasianus colchicus*), has been identified in period 11, which dates to 1708–1783 CE (Hufthammer, 1999). The timing of the introduction of *P. colchicus* into Norway is

uncertain. In Sweden, the Common Pheasant was introduced in the 16th century (Ericson & Tyrberg, 2004). The identification of Turkey (*Meleagris gallopavo*) from period 11, dating to 1708–1783 CE (Hufthammer, 1999) also forms our earliest evidence for the introduction of this species to Norway. The Grey Partridge (*Perdix perdix*) was identified from period 9 (1537–1660 CE) (Hufthammer, 1999). *Perdix perdix* was only introduced to southern Norway for hunting purposes (Collett et al., 1921). All of the previously identified *P. perdix* specimens dating to the Medieval period were re-identified as Hazel Grouse (*Bonasa bonasia*), a similar-sized species native to Norway. Given *P. perdix* is easy to misidentify the Post-Medieval specimens must be viewed with caution. DNA analysis is needed to confirm these identifications, especially given that *P. perdix* was not established in Sweden until the 18th century (Ericson & Tyrberg, 2004).

The establishment of feral pigeons within Norway and Scandinavia is poorly understood, and consequently little attention has been given to these species, and where the first populations came from. In Sweden, there are three Medieval sites which may indicate the keeping of *C. livia* (Ericson & Tyrberg, 2004). However, these are not conclusive. By the 17th–18th century Tyrberg (2002) claims that domestic pigeons were introduced to Sweden, supported by finds of *C. livia* from Gothenburg. Olaus Magnus (1555) mentions dovecotes within Scandinavia, but they were not common. In Norway, our research has shown that there is no Medieval evidence for *C. livia*. Rock Doves appear in the Post-Medieval Period 11 contexts (1708–1783 CE) from the Erkebispegården (Hufthammer, 1999), with nine specimens, and we interpret these as kept pigeons. These specimens currently represent the strongest evidence for pigeon keeping within Norway. Michaelsen and Refvik (2003) mention the Utstein monastery as a possible source for the Rennesøy colony, with kept *C. livia* released after the reformation in 1537 CE. However, there is no specific evidence of pigeons being kept at the Utstein monastery. Despite the absence of *C. livia* from Medieval contexts, it is possible that with more avian assemblages from monastic sites we may identify Medieval kept pigeons. If this is the case, the release of kept pigeons from monastic sites after the reformation, may have been the source for feral populations.

It is clear that the Erkebispegården was a site of great importance and may have been the site of many non-native bird species introductions. The high status of this site and its excellent trade links make it very possible. The addition of more high status sites to the Norwegian archaeological record would assist in understanding more about these species introduction to Norway.

4.3 Supplementary Norwegian data

In addition to the material of the 21 sites which were re-examined in this study, a further 33 Medieval sites were included, but not re-examined (Supplementary Table 3). These additional sites are mostly small assemblages and contain 2226 specimens, of which 1229 could be identified beyond Aves (Table 4; Supplementary Table 3). Broadly speaking, the species present and their abundance follow the same patterns observed in the re-examined assemblages. However, eight species have been previously identified within these supplementary sites that have not been recorded in our re-analysis of the 21 main sites, but all remain extant within Norway.

A specimen from Bibliotekstomten, Trondheim has previously been identified as Pink-footed Goose (*Anser brachyrhynchus*). *Anser brachyrhynchus* breeds on Svalbard, and only occurs for short periods of the year on mainland Norway, during migration (Carboneras & Kirwan, 2019a). There are important staging areas for *A. brachyrhynchus* near Trondheim, and it is possible that this was also the case during the Medieval period. However, we would need more specimens from the area to confirm this. It is also worth bearing in mind that given the difficulty in osteologically separating the Anserini species, this specimen may have been misidentified. There is evidence that *A. brachyrhynchus* is spending more time on the Norwegian stop-over sites due to climate change (Bauer et al., 2008), and it is possible that with climate fluctuations during the Medieval period, extended or shortened periods spent at staging sites would have occurred.

A femur of a Common Scoter (*Melanitta nigra*) was identified from the Alstahaug 1992 site. *Melanitta nigra* occurs all year round in Norway, breeding inland and wintering on the coast (Carboneras & Kirwan, 2019b). The identification of

Anseriformes is notoriously difficult and as such the identification of the two species mentioned above needs to be confirmed by re-examination.

Additional species recorded in the supplementary sites are the Eurasian Buzzard (*Buteo buteo*), the Rough-legged Buzzard (*Buteo lagopus*), the Osprey (*Pandion haliaetus*), the Eurasian Oystercatcher (*Haematopus ostralegus*) and the Common Swift (*Apus apus*). It was possible to locate and confirm both *P. haliaetus* identifications. Given the sizeable population of Eurasian Oystercatchers in Norway (Hockey et al., 2019), their presence in the Medieval material is sparse.

It is also worth mentioning here that, although no *Lagopus muta* were positively identified in the re-examined material, 27 specimens were identified in the supplementary material. Based on our data from the re-examined assemblages, the more abundant *Lagopus* species within Medieval contexts for Norway has been *Lagopus lagopus*. It is therefore likely that the abundance of *L. muta* in the supplementary material results from overly confident identifications. As a result, the abundance of *L. muta* within the supplementary sites should be regarded with caution.

When the supplementary material is compared with the re-examined material based upon site type, the general patterns remain the same. The supplementary sites are made up of 18 urban (NISP = 790), 10 rural (NISP = 363), four monastic (NISP = 67) and a single hunting site (NISP = 9). The addition of more rural sites within the supplementary material results in an increased importance in domesticates on rural sites, within the supplementary sites *G. gallus* forms 38% of the assemblages, compared to the 2% in the re-examined assemblages. It is possible that some of the *G. gallus* identifications on rural sites are misidentified, given the discrepancy between re-identified rural sites and the supplementary sites. In addition, our re-examination found that wild Galliformes were often misidentified as domestic fowl. Domestic goose is also increased from 0.1% to 13%. As the NISP figures on these additional sites are not substantial these figures do not change the patterns overall inferred from the re-examined material. However, we believe that the slight increase in domesticates on rural sites is likely to give a more accurate representation of species abundance, whilst wild species remain the most important on rural sites, domesticates are still fairly well represented on the majority of rural sites.

5. Conclusion

Our re-examination and compilation of bird bone assemblages from Medieval Norway found no evidence to suggest that the Medieval bird fauna differed from the modern one. Although certain groups of birds have been found in low numbers from Medieval sites, this may not reflect actual low population abundance in Medieval times. The most common birds in Medieval assemblages are Galliformes. In urban sites these are mostly domestic fowl, whereas on rural sites wild species dominate. Our data indicates an introduction of domestic fowl in the early Medieval period and a slightly delayed introduction of domestic geese, with both species becoming more abundant during the mid to late Medieval period. This appears to be later than other Scandinavian countries. Interestingly, species that are now ubiquitous in urban areas, such as pigeons, corvids and gulls are mostly absent from Medieval urban centres. In addition, we found a bias towards the use of female *Accipiter gentilis* in falconry, while *Falco* species may have been exported. For the majority of non-native species found in Norway today, our data suggests that these were introduced during Post-Medieval times.

Our work has identified a number of exciting research avenues that warrant future research. The timing of the arrival of domestic bird species, mostly *G. gallus* and *A. anser* in Norway and their role(s) in Scandinavian society are still poorly understood. Further analyses of their earliest occurrences and their subsequent spread will shed light on when, how and why domesticates reached Norway. Furthermore, the clear size difference between medieval *A. gentilis* and modern ones suggests the effects of human selection for large individuals for falconry in Medieval Norway. Analyses of older *A. gentilis* material, as well as material from a wider geographic range is needed to better interpret these trends in body size. Lastly, the absence of several groups of birds that were expected to be present during Medieval times merits further investigation to see if this is indeed an effect of the rise of urban centres in the last few centuries, or if this represents an ecological shift in species habitats.

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7. Competing interests

The authors have no competing interests to declare.

8. References

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Supplementary Material File 1 (SMF1): Unpublished report references. Available within the University Museum of Bergen's Natural History Archives (Curated by Anne Karin Hufthammer)

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Supplementary Table 1 (ST1)

ST1. This table shows the Number of Identified Specimens (NISP) for the birds in Medieval Norway. The NISP figures do not include unidentified fragments. The total is calculated from the total mammal, fish and birds identified on a site. The sites of Vågsalmenning, Kroken 3, Finnegården 3A and Bryggen Gullskoen have not previously been identified and as such, there is no mammal or fish data available for comparison. The figures from this table were used to produce the percentages represented in Table 2, within the manuscript. The numbers in brackets next to the site name is the University Museum of Bergen's JS number, this is a catalogue ID given to an assemblage, allowing the material to be easily retrieved and tracked back to site details.

Mindets Tomt (537)	Oslogate 7, Gamlebyen (599)	Nordre Felt II, Gamlebyen (702)	Bryggen (397,401,406,492,529,540)	Dreggsalmenningen (630)	Vågsalmenning (1152)	Kroken 3 (1168)	Finnegården 3A (1237)	Bryggen Gullskoen (1280)	Bryggessporden (1750)	Storgaten 35 (563)	Storgaten 24-26 (637)	Tunsberghus (660)	Baglergaten 2-4 (664)	Blomsøy (151)	Husen (308)	Tøftom (710)	Vesle Hjerkin (712)	Erkebispgården Medieval Phases (845)	Gæccevaþnar' ga (715)	Borgund (344, 357, 374, 410, 411, 430, 431, 432, 1699)			
Birds	1052	175	1640	911	61	3	3	3	78	18	18	23	81	13	25	17	12	26	41	1352	256	43	108
TOTAL	53384	9927	57161	14516	9483	3	3	3	78	18	18	9915	5916	3885	405	1645	366	40	13019	16432	8423	351	35860

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
<i>Lagopus lagopus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	27	-	2	-	30
<i>Lagopus muta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Bonasa bonasia</i>	-	1	3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	5	-	-	10
cf. <i>Bonasa bonasia</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2
Anseriformes																						
Anseriformes sp.	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Anserini sp. (<i>Anser/Branta</i> sp.)	1	1	4	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	10	-	-	18
<i>Anser</i> sp.	10	4	3	5	1	-	-	-	1	-	-	1	-	-	2	-	-	-	1	-	-	28
<i>Anser anser</i>	139	14	133	61	2	-	-	1	-	-	12	-	2	2	1	-	-	-	10	-	5	382
cf. <i>Anser anser</i>	6	-	15	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25
<i>Anser fabalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
<i>Anser brachyrhynchus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Branta bernicla/leucopsis</i>	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Cygnus cygnus</i>	6	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	9
cf. <i>Cygnus cygnus</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Anatinae</i> sp.	-	1	8	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	13
<i>Anas platyrhynchos</i>	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	4
<i>Anas crecca</i>	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Anatidae</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Somateria</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>mollissima/spectabilis</i>																						
<i>Somateria mollissima</i>	1	-	2	38	-	-	-	2	-	-	-	-	-	1	3	-	-	-	-	1	2	50
cf. <i>Somateria mollissima</i>	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Somateria spectabilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Clangula hyemalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	4
<i>Melanitta fusca</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Melanitta nigra</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Mergus serrator</i>	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Bucephala clangula</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
<i>Mergini</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	3

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21			
<i>Anas</i> sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2		
<i>Aythya</i> sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
Gaviiformes																								
<i>Gavia</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	
<i>Gavia aretica</i>	2	1	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	
cf. <i>Gavia arctica</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	4	
<i>Gavia stellata</i>	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
Procellariiformes																								
<i>Fulmarus glacialis</i>	-	-	3	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	7
<i>Puffinus puffinus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
Ciconiiformes																								
<i>Ciconia nigra</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
Suliformes:																								
Phalacrocoracidae																								
<i>Phalacrocorax aristotelis</i>	-	-	-	2	2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	8	13
<i>Phalacrocorax carbo</i>	-	-	-	4	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	8
Suliformes: Sulidae																								
<i>Morus bassanus</i>	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10(7)	13
Pelecaniformes																								
<i>Ardea cinerea</i>	1	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5(5)	9
Accipitriformes																								
<i>Accipiter gentilis</i>	49(19)	4	54(18)	25(6)	3	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	137
<i>Accipiter nisus</i>	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Buteo buteo</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Buteo lagopus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Haliaeetus albicilla</i>	8	-	14	22	6	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	11	-	6	71
cf. <i>Haliaeetus albicilla</i>	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
<i>Pandion haliaetus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Aquila chrysaetos</i>	2	-	-	4	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	8

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
<i>Larus marinus</i>	2	-	2	6	3	-	1	1	-	-	-	-	-	-	2	-	-	-	-	-	1	18	
<i>Larus canus</i>	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	
cf. <i>Larus canus</i>	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	
<i>Rissa tridactyla</i>	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3
cf. <i>Rissa tridactyla</i>	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Sterna</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
cf. <i>Sterna hirundo</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Columbiformes																							
<i>Columba palumbus</i>	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
<i>Columba livia/oenas</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Apodiformes																							
<i>Apus apus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Passeriformes: Corvidae																							
Corvidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
<i>Corvus corax</i>	10	-	11	3	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2	-	8	36	
<i>Corvus monedula</i>	2	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	8	
cf. <i>Corvus monedula</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	
<i>Corvus corone</i>	13	2	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	34(13)	-	-	52	
<i>Pica pica</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	5	-	-	7	
Passeriformes: Turdidae																							
<i>Turdus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	6
<i>Turdus pilaris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2	
Large <i>Turdus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	19	-	-	-	20	
Small <i>Turdus</i> sp.	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	11	
Passeriformes: Sturnidae																							
Sturnidae/Turdidae sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	3
<i>Sturnus vulgaris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	
Passeriformes: Motacillidae																							
<i>Anthus pratensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
Passeriformes: Passeridae																						
Passeriformes sp.	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	4	
<i>Passer domesticus</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
cf. <i>Passer domesticus</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
Total identified	1052	175	1640	911	61	3	3	78	18	23	81	13	25	17	12	26	41	1352	256	43	108	5938
Unidentified Large Bird	13	1	91	2	-	-	-	-	-	-	-	-	5	-	2	-	-	28	6	-	1	149
Unidentified Medium Bird	21	10	172	16	3	-	-	4	-	1	10	8	1	10	2	1	7	683	16	17	-	982
Unidentified Small Bird	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2
Unidentified Bird	3	10	421	4	-	-	-	-	1	14	1	2	7	5	-	1	4	782	72	7	-	1334
Bird?	9	1	2491	11	-	-	-	5	-	2	8	15	-	24	-	-	37	-	11	4	-	2618
Total unidentified	46	22	3175	33	3	0	0	9	1	19	19	25	13	39	4	2	48	1493	105	28	1	5085
Total	1098	197	4815	944	64	3	3	87	19	42	100	38	38	56	16	28	89	2845	361	71	109	11023

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33						
Passeriformes: Turdidae																																							
<i>Turdus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1		
<i>Turdus pilaris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
Large <i>Turdus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	
Small <i>Turdus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	
Passeriformes: Sturnidae																																							
Sturnidae/Turdidae sp.																																							
<i>Sturnus vulgaris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Passeriformes: Motacillidae																																							
<i>Anthus pratensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	
Passeriformes: Passeridae																																							
Passeriformes sp.																																							
<i>Passer domesticus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	
c.f. <i>Passer domesticus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	
Total identified	9	37	13	236	19	169	10	14	41	7	12	5	52	1	32	40	19	9	2	1	36	12	26	7	5	20	1	2	141	114	115	6	16	1229	-	-	-	0	
Unidentified Large Bird																																							
Unidentified Medium Bird																																							
Unidentified Small Bird																																							
Unidentified Bird	-	1	51	62	-	407	-	6	9	-	-	-	5	-	-	8	-	-	-	-	49	4	79	2	1	5	-	-	220	70	17	1	-	-	-	-	997		
Bird?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	
Total unidentified	0	1	51	62	0	407	0	6	9	0	0	0	5	0	0	8	0	0	0	0	49	4	79	2	1	5	0	0	220	70	17	1	0	-	-	-	997		
Total	9	38	64	298	19	576	10	20	50	7	12	5	57	1	32	40	27	9	2	1	85	16	105	9	6	25	1	2	361	184	132	7	16	2226	-	-	-	0	

Paper II

RESEARCH PAPER

More than food; evidence for different breeds and cockfighting in *Gallus gallus* bones from Medieval and Post-Medieval Norway

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Abstract

Domestic fowl (*Gallus gallus* var. *domesticus*) can now be found in every continent across the globe (except Antarctica), and have become a dominant part of our diets. For Scandinavia, there is lack of knowledge regarding the timing of arrival and subsequent spread of chickens throughout the region. Domestic fowl were abundant throughout Norway by the mid-late Medieval period. Historical sources shed little light on the role of chickens in past Norwegian societies. Here we describe chicken remains from Medieval and Post-Medieval assemblages in Norway and identify osteological features and patterns that signal different roles for chickens in the past. Our data show that by the Medieval period there were at least two different-size breeds present, including a crested ornamental breed. In addition, we see clear evidence for the removal of spurs for the practice of cockfighting. Our evidence suggests a more complex role for domestic fowl than just a food source. The presence of multiple breeds and the evidence for cockfighting can be linked to the trade networks coming into Bergen and Oslo at this time, and highlight the socio-cultural aspects of chicken husbandry.

Keywords: Domestic fowl, Cockfighting, Breeds, Chickens, Scandinavia, Medieval

1. Introduction

Domestic fowl (*Gallus gallus* var. *domesticus*) can now be found in every continent across the globe (except Antarctica), and have become a dominant part of our diets (Robinson et al., 2015). Many papers have focused on the spread of *Gallus gallus* out of its native distribution in Asia (Xiang et al., 2014, 2015; Perry-Gal et al., 2015; Peters et al., 2015; Eda et al., 2016; Pitt et al., 2016), yet the routes of its expansion across the world are still not fully understood. From the current archaeological evidence, domestic fowl were a relatively late introduction to much of Scandinavia, with Sweden and Denmark providing the earliest examples, around the 1st century BCE and 1st century CE respectively (Lepiksaar, 1977; Tyrberg, 2002; Ericson and Tyrberg, 2004; Gotfredsen, 2013; Gotfredsen, 2014). In Finland, the earliest evidence for domestic fowl dates to the 8th century CE (Ukkonen and Mannermaa, 2017; Wessman et al., 2018). For Norway, the earliest remains of *G. gallus* appear in the late Viking Age (Barrett et al., 2007). However, domestic fowl are very rare at this point and it is not until the beginning of the Medieval period (1030 CE) that *G. gallus* appears more frequently within the archaeological record, with their abundance increasing in the mid to late Medieval period (1300 CE) (Walker et al., 2019).

The emergence and spread of domestic fowl, along with the development of the species to many different breeds, reflects the distinct interactions between humans and chickens and the roles that domestic fowl play in societies, ranging from a food source to entertainment and icons of religion. Individual breeds have often gone on to become important components of a country or regions heritage, with legislation in place to protect and safeguard many breeds. To date, there has been little focus on the spread and role(s) of *G. gallus* in Norway. Nowadays, around 40 Scandinavian domestic fowl breeds are recognised (DAD-IS, 2019), with the Jærhøns the only recognised ‘traditional’ Norwegian breed.

Historical sources mentioning domestic fowl in Norway are scarce. The keeping of poultry was not legislated for in Norway, likely due to their low value and the relatively small space required to keep them (Leslie-Jacobsen, H.F. 2019. pers. comm.).

The lack of historical sources highlights the importance of investigating the archaeological material further. A better understanding of the introduction, husbandry practices and human interactions with this species will lead to a more clear insight into past Norwegian societies and the reasons why domestic fowl came to be one the most dominant bird species in Norway. In this study, we describe osteological features of *G. gallus* from Medieval and Post-Medieval assemblages in Norway that suggest different societal role(s) for some of the earliest Norwegian domestic fowl.

2. Methods

2.1 Sites

The *Gallus gallus* bone specimens included in this study are from 20 sites across Norway, and mostly from Southern Norway (Figure 1; Table 1). Eighteen sites date to the Medieval period (1030–1537 CE), and two sites are Post-Medieval (Revierstredet and Kontraskjæret) (1537–1700 CE). In addition, a number of the Medieval assemblages also had Post-Medieval contexts which were included here as well. In total, our study includes 2857 *G. gallus* bone specimens from Medieval contexts, and a further 398 from Post-Medieval contexts. For site selection, recording protocols and analyses, we refer to Walker et al. (2019).

Table 1. Norwegian sites that contain *Gallus gallus* bones. The table includes all the sites which have been investigated in this study. The table gives the sites name, the number of identifiable specimens (NISP) for *G. gallus*, the avian NISP for the site (for the Post-Medieval Erkepispegården and Televerkstomten sites, we have only included the tarsometatarsi which have had the spur removed and one skull specimen, these are marked *), the location of the site, the specific dates for a site, the JS number assigned to the site (a catalogue number given by the University Museum of Bergen), and any references to previous zooarchaeological reports and contextual dating sources. In many cases, the reports have not been published, these can be found listed in the unpublished sources reference list in the supplementary material (SMF1).

Site name	<i>G. gallus</i> NISP	Avian NISP	Location	Date range of site	JS Number	Site references
Mindets Tomt	603	1052	Oslo	1025 – 1350 CE	537	Archive Natural History, University Museum of Bergen. (Lie, 1988)
Oslogate 7, Gamlebyen	122	175	Oslo	1150 – 1600 CE	599	Archive Natural History, University Museum of Bergen. (Lie, 1979)
Nordre Felt II, Gamlebyen	1145	1640	Oslo	Medieval	702	Archive Natural History, University Museum of Bergen.
Bryggen	661	911	Bergen	Medieval	397,401,406,492,529, 540	Archive Natural History, University Museum of Bergen.
Dreggsalmenningen	30	61	Bergen	1170 – 1527 CE	630	Archive Natural History, University Museum of Bergen. (Undheim, 1985, unpublished report, see SMF1)
Kroken 3	2	3	Bergen	Medieval	1168	Archive Natural History, University Museum of Bergen. (Dunlop, unpublished report, see SMF1)
Finnegården 3A	22	78	Bergen	Medieval	1237	Archive Natural History, University Museum of Bergen. (Golembnik, 1993, unpublished report, see SMF1)
Bryggen Gullskoen	15	18	Bergen	Medieval	1280	Archive Natural History, University Museum of Bergen.
Bryggesporden	9	23	Bergen	Medieval	1750	Archive Natural History, University Museum of Bergen. (Bejersbergen et al., 2018, unpublished report, see SMF1)
Storgaten 35	58	81	Tonsberg	Before 1200 – 1400 CE	563	Archive Natural History, University Museum of Bergen. (Eriksson, 1975, unpublished report, see SMF1)
Storgaten 24-26	7	13	Tonsberg	Mid/late 1200 – 1350 CE	637	Archive Natural History, University Museum of Bergen. (Lindh, 1984, unpublished report, see SMF1)
Tunsberghus	22	25	Tonsberg	1200 – 1500 CE	660	Archive Natural History, University Museum of Bergen.
Baglergaten 2-4	10	17	Tonsberg	c.1200 – c.1400 CE	664	Archive Natural History, University Museum of Bergen. (Brendalsmo, 1986, unpublished report, see SMF1)
Blomsøy	1	12	Alstahaug	Medieval	151	Archive Natural History, University Museum of Bergen.
Vesle Hjørkinn	23	1352	Dovre	Medieval	712	Archive Natural History, University Museum of Bergen. (Lie and Fredriksen, 2007)
Borgund	18	108	Ålesund	Medieval	344,357,374,410,411, 430,431,432,1699	Archive Natural History, University Museum of Bergen.
Erkebispegården (Medieval contexts)	109	256	Trondheim	c.1250 – 1537 CE (Phases 4 – 7)	845	Archive Natural History, University Museum of Bergen. (Hufthammer, 1999, Nordeide, 2000)
Erkebispegården (Post-Medieval contexts)	4*	Unknown	Trondheim	c.1537 – after 1700 CE (Phases 8 – 11)	845	Archive Natural History, University Museum of Bergen. (Hufthammer, 1999, Nordeide, 2000)
Televærkstomten	1*	Unknown	Trondheim	c.900 – 1850 CE	632	Archive Natural History, University Museum of Bergen. (Marthinussen, 1992, unpublished thesis, see SMF1)
Kontraskjæret	313	721	Oslo	1624 – 1686 CE	628	Archive Natural History, University Museum of Bergen.
Revierstredet	80	238	Oslo	1624 – c.1730 CE	600	Archive Natural History, University Museum of Bergen. (Lie, 1981)

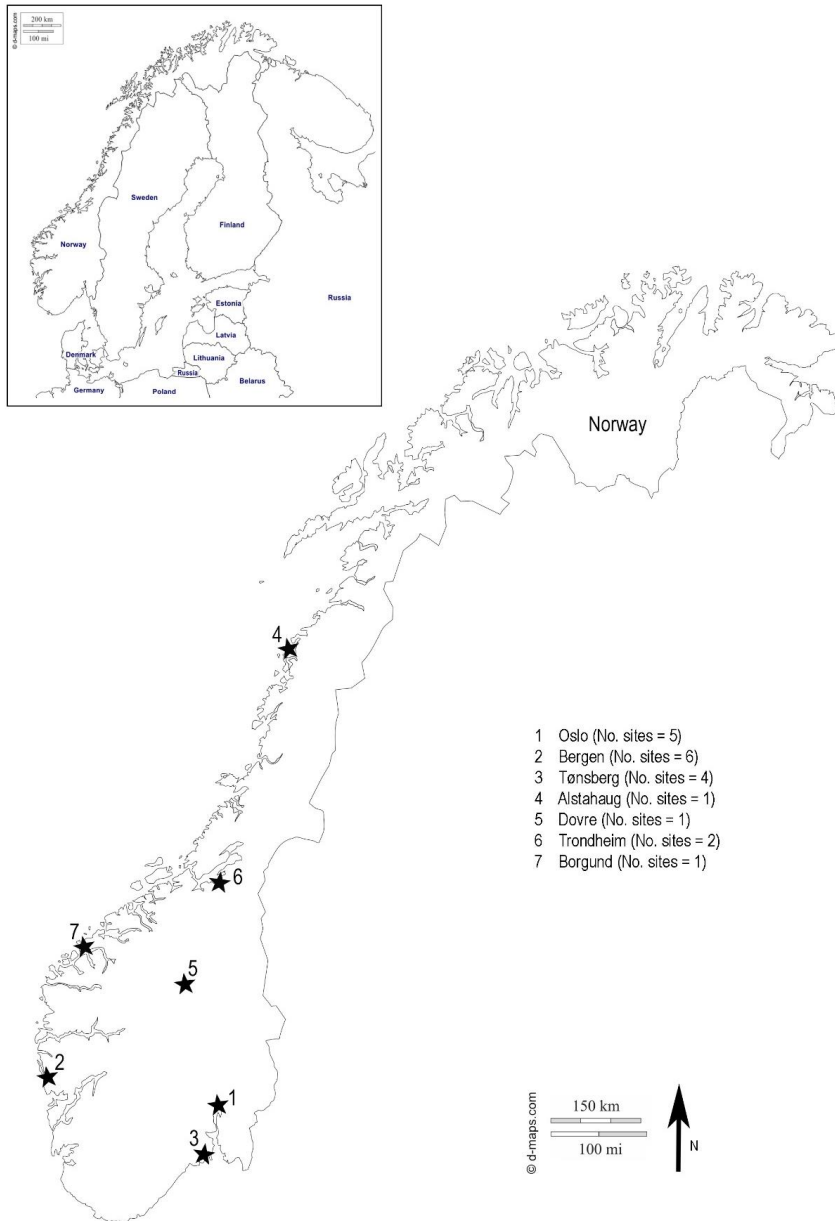


Figure 1. Location of sites included within this study. The number of sites examined under each locality is included in the legend. Table 1 includes details of the sites studied.

2.2 Size variation

Four archaeological assemblages were selected for size variation analyses, these were chosen based upon the reliable dating and in the case of the Medieval assemblages, the large number of domestic fowl bones present. The sites included were the Medieval contexts of Mindets Tomt, Oslo (1175–1350 CE) and Bryggen, Bergen (Medieval, specific dates are difficult to locate), and two Post-Medieval sites, Kontraskjæret, Oslo (1624–1686 CE) and Revierstredet, Oslo (1624–c.1730 CE). Measurements were based upon Von den Driesch (1976), and taken with digital callipers to the nearest 0.1 mm. Only complete long bones from adult specimens were considered in this analysis. Tarsometatarsi were sexed based on the presence/absence of a spur or spur scar.

It is worth noting at this point how we define the term breed within archaeology and its use within this article. We follow Clutton-Brock (1979), who identifies a breed as “a group of animals that has been selected by man to possess a uniform appearance that is inheritable and distinguishes it from other groups of animals within the same species”. Moreover, using the term ‘breed’ does not imply we are referring to the sort of uniformity dictated by modern poultry exhibitors and 'British Poultry Standards', rather we are referring to different types of chickens.

3. Results

3.1 Size variation

Our analyses of *Gallus gallus* bone specimens from Medieval and Post-Medieval assemblages from Bergen and Oslo revealed intra-site size variation that suggests the presence of different-sized populations of chickens (Figure 2 and Supplementary data (SMF2 and SMF3)).

The tarsometatarsi from the Medieval site of Mindets Tomt, Oslo (Figure 2A) range in size from 60 mm to 86 mm and indicate the presence of two groups of chickens. The first group consists of smaller *G. gallus* with tarsometatarsi of around 60–76 mm in

length (similar in size to modern-day Bantams), with female tarsometatarsi ranging in size between 60–72 mm, and male tarsometatarsi ranging between 72–76 mm. A second group indicates larger individuals, with female tarsometatarsi at 74–84mm and male tarsometatarsi ranging between 80–86 mm. In both groups, there is size overlap between male and female tarsometatarsi. A similar pattern was observed in the Medieval material from Bryggen, Bergen (Figure 2B), whereby we see a smaller group with females between 56–72 mm, and males between 70–76 mm, and a larger group with females measuring between 74–86 mm and males ranging from 78–90mm.

For the Post-Medieval site of Kontraskjæret, Oslo (Figure 2C), the tarsometatarsi show a pattern similar to that of the Medieval sites of Mindets Tomt and Bryggen with a smaller and larger group of chickens. However, female tarsometatarsi in the smallest group range between 66–72 mm, which indicates a slight size increase from the small group of females found in the Medieval period. A second group of larger females was identified between 74–84 mm. There were relatively few males on the site of Kontraskjæret and they fall towards the larger end of the females at 80–82 mm. The Post-Medieval site of Revierstredet, Oslo (Figure 2D), also displays a group of small chickens, similar in size to those at Kontraskjæret, with females at 66–72 mm and corresponding males at 78–84 mm. No second group of larger females was identified on this site, but the site records two very large male tarsometatarsi ranging between 98–104 mm. This size is not seen on the Medieval sites.

Measurements of the femora of Medieval Mindets Tomt (Figure 2E) and Bryggen (Figure 2F) show a pattern suggestive of two size classes, similar to that seen in the tarsometatarsus. Although the femora could not be sexed, the presence of medullary bone in one refitted specimen from Bryggen indicates the presence of at least one larger female which corresponds with the larger female group identified in the tarsometatarsi. The post-Medieval site of Kontraskjæret (Figure 2G) generally follows the patterns seen in the tarsometatarsi but with the presence of a much smaller specimen, which is likely to represent a small female. In addition, a much larger femur was identified at 100–102 mm. Such a large-sized individual was not seen in the tarsometatarsi of Kontraskjæret, but a large individual was also identified in the Post-Medieval Revierstredet assemblage.

The pattern in femur size for Revierstredet (Figure 2H) is very similar to that of the tarsometatarsus.

The patterns described here for the tarsometatarsi and femora for both the Medieval and Post-Medieval sites, i.e. the presence of two size classes of chickens and a shift towards larger individuals in Post-Medieval material, are also observed in the size-frequency distributions for the humerus, coracoid, ulna and tibiotarsus (See SMF2 and SMF3).

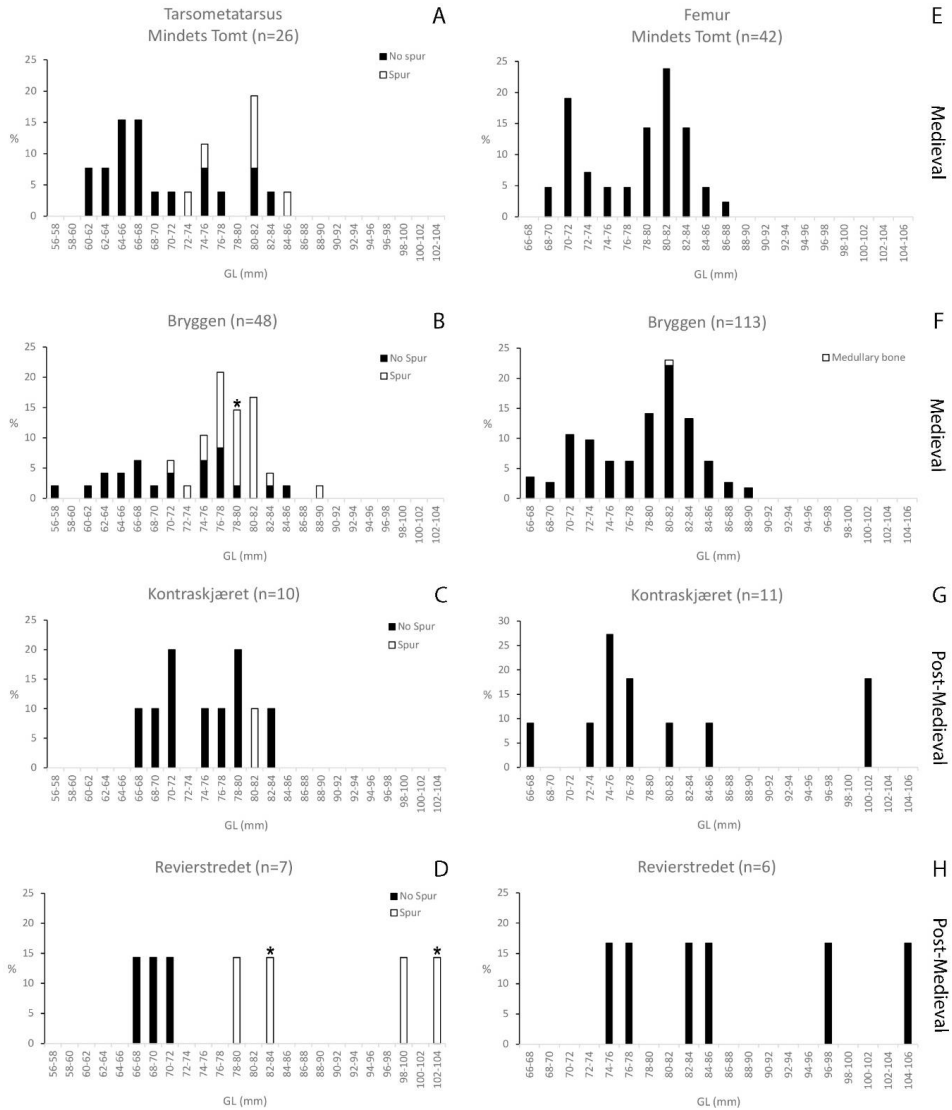


Figure 2. Frequency distributions of the Greatest Length (GL) for *G. gallus* tarsometatarsi (A-D) and femora (E-H) from Medieval (A, B, E, F) and Post-Medieval (C, D, G, H) sites. The * represents a single specimen which has had the spur deliberately removed (B and D).

3.2 Cranial morphology

Two crania were found to display an abnormal morphology. One specimen (Figure 3A-B) is from the Erkebispegården site, Trondheim, and was found in contexts to the north of the site outside the first quartermaster's complex. This specimen dates to 1690–1720 CE (Nordeide, 2000). The other specimen (Figure 3C-D) is from Kontraskjæret, Oslo, and dates to 1624–1686 CE (date taken from the Natural History Museum archives). All other *G. gallus* cranial remains (n = 26) from sites across Norway display a regular cranial morphology (Figure 3E-F).

The cranial morphology of the two unique specimens displays a slightly vaulted frontal lobe with perforations. These perforations on the Erkebispegården cranium (Figure 3A) are rather uniform in size, whereas on the Kontraskjæret cranium (Figure 3C) they are more irregular in size. The Kontraskjæret cranium also displays a more vaulted frontal lobe, and appears to indicate a more extreme form of cerebral herniation.



Figure 3. Post-Medieval crania of *G. gallus*. **A:** cranial view of vaulted *Gallus gallus* cranium from Erkebispegården. **B:** lateral view of vaulted *G. gallus* cranium from Erkebispegården. **C:** cranial view of vaulted *G. gallus* cranium from Kontraskjæret. **D:** lateral view of vaulted *G. gallus* cranium from Kontraskjæret. **E:** cranial view of non-vaulted *G. gallus* cranium from Kontraskjæret. **F:** lateral view of non-vaulted *G. gallus* cranium from Kontraskjæret.

3.3 Deliberate removal of spurs

Of the 258 tarsometatarsi recorded for this study, (see site data, Table 1), 128 specimens display a spur or spur scar. These specimens were assigned as males all of which were fully developed adults. In sixteen tarsometatarsi the spurs had been removed either partially or completely (Table 2, Figure 4 and SMF4).

Table 2. Tarsometatarsi with full or partial spur removal from Norwegian Medieval and Post-Medieval assemblages.

Site	Specimen	Date	Description	Interpretation	Photo
Erkebispegården, Trondheim (ID 7872)	Left adult tarsometatarsus, distal epiphysis missing (75% complete).	1672 – c.1720 CE (Nordeide, 2000)	Removal of the spur close to the shaft (5 mm from the base of the spur). An additional cut mark at the base of the spur and slightly on the shaft. The edges of the cut surface are slightly rounded, indicating that this is not a fresh cut.	Removal of spur, possibly to attach an artificial spur. The rounded edges of the remaining spur stump may indicate healing of the bone.	Fig. 4C, 4D
Erkebispegården, Trondheim (ID 7523)	Right adult tarsometatarsus, Complete.	1640 – 1672 CE (Nordeide, 2000)	Removal of the spur very close to the shaft (almost flush with the shaft). The edges of the cut surface are slightly rounded, indicating that this is not a fresh cut.	Removal of spur, possibly to attach an artificial spur. However, more of a stump is usually left. The rounded edges of the remaining spur stump may indicate healing of the bone.	SMF3 A,B
Erkebispegården, Trondheim (ID 7738)	Left adult tarsometatarsus, with the cotyla medialis and trochlea metatarsi II missing (75% complete).	1500 – 1532 CE (Nordeide, 2000)	Removal of approximately half of the spur, with the other half being broken off. The cut is located 12.5 mm from the base. The surface indicates a fresh cut. A small cut mark was also identified on the cotyla lateralis. A pathological lesion is also present just below the spur and above the trochlea metatarsi II.	The spur has been de-tipped, possibly for 'naked heel' fighting. The lesion may have been a result of a previous fight. Alternatively, the spur may have been de-tipped to prevent in fighting, which may have also caused the lesion. The fresh nature of the tip removal suggests that it took place just before the cockerel's death or after.	Fig. 4N, 4O
Erkebispegården, Trondheim (ID 7468)	Right adult tarsometatarsus, with the cotyla medialis missing (95% complete).	1500 – 1532 CE (Nordeide, 2000)	Diagonal cut through the spur near to the shaft (7 mm from the base of the spur), leaving a triangular stump. The edges of the cut surface are slightly rounded, indicating that this is not a fresh cut.	Removal of the spur to attach an artificial spur. Alternatively, the diagonal chop may have been to sharpen the spur for 'naked heel' fighting. The rounded edges of the remaining spur stump may indicate healing of the bone.	Fig. 4A, 4B
Erkebispegården, Trondheim (ID 7678)	Right adult tarsometatarsus, with the cotyla medialis and lateralis removed (75% complete).	1640 – 1672 CE (Nordeide, 2000)	Diagonal cut through the spur near to the shaft (6 mm from the base of the spur), leaving a triangular stump. The edges of the cut surface are slightly rounded, indicating that this is not a fresh cut. A post-mortem cut has removed the cotyla medialis and lateralis.	Removal of the spur to attach an artificial spur. Alternatively, the diagonal chop may have been to sharpen the spur for 'naked heel' fighting. The rounded edges of the remaining spur stump may indicate healing of the bone. The removal of the cotyla medialis and lateralis appears to be a separate event to the spur removal as there is healing present on the spur stump.	SMF3 C,D

Site	Specimen	Date	Description	Interpretation	Photo
Televærkstomten, Trondheim (ID 8967)	Left adult tarsometatarsus, complete.	c.1650 – 1700 CE (Marthinussen, 1992, unpublished thesis, see SMF1)	Diagonal cut on the spur near the shaft (8.8 mm from the base of the spur), leaving a stump. A small additional cut mark on the spur near the base.	Removal of the spur to attach an artificial spur.	Fig. 4E, 4F
Bryggen, Bergen (ID 7349)	Left adult tarsometatarsus, complete.	1476 – 1702 CE (Hansen et al., 2017)	Diagonal cut through the spur near to the shaft (6.9 mm from the base of the spur), leaving a stump. The edges of the cut surface are slightly rounded, indicating that this is not a fresh cut.	Removal of the spur to attach an artificial spur. The rounded edges of the remaining spur stump may indicate healing of the bone.	Fig. 4H, 4I
Mindets Tomt, Oslo (ID 5238)	Left adult tarsometatarsus, slight erosion/rodent gnawing of the cotyla medialis and lateralis (75% complete).	c.1225 – 1250 CE (Petter Molaug, pers. comm.)	Diagonal cut on the spur near the shaft (8 mm from the base of the spur), leaving a stump. The gnawing on the spur masks whether the cut is fresh or older.	Removal of the spur to attach an artificial spur.	Fig. 4G
Mindets Tomt, Oslo (ID 4318)	Left adult tarsometatarsus, with the cotyla medialis and lateralis removed (75% complete).	c.1250 – 1275 CE (Petter Molaug, pers. comm.)	Removal of the spur tip, with a diagonal cut through the spur (15.2 mm from the base of the spur). The edges of the cut are slightly rounded, indicating that this is not a fresh cut. A post-mortem cut has removed the cotyla medialis and lateralis.	The spur has been de-tipped, possibly for 'naked heel' fighting. Alternatively, the spur may have been de-tipped to prevent in fighting. The rounded edges of the remaining spur stump may indicate healing of the bone. The removal of the cotyla medialis and lateralis appears to be a separate event to the spur removal as there is healing present on the spur stump.	SMF3 E,F
Gamlebyen, Nordre Felt II, Oslo (ID 2343)	Right adult tarsometatarsus, with slight damage to the cotyla medialis (95% complete)	Late 1200 – 1352 CE (Petter Molaug, pers. comm.)	Removal of the spur tip, with a diagonal cut through the spur (12.8 mm from the base of the spur). The surface indicates a fresh cut.	The spur has been de-tipped, possibly for 'naked heel' fighting. Alternatively, the spur may have been de-tipped to prevent in fighting. The fresh nature of the tip removal suggests that it took place just before the cockerels death or after.	Fig. 4L, 4M
Gamlebyen, Nordre Felt II, Oslo (ID 2958)	Right adult tarsometatarsus, only a short section of the shaft remains, both epiphysis missing (25% complete)	1300 – c.1352 CE (Petter Molaug, pers. comm.)	Removal of the spur close to the shaft (6.7 mm from the base of the spur). There appears to be at least two cuts to the spur creating a triangular stump. The surface of the stump does not appear to be a fresh cut.	Removal of the spur to attach an artificial spur. Alternatively, given the shape of the remaining stump possibly the spur was sharpened for 'naked heel' fighting.	SMF3 G

Site	Specimen	Date	Description	Interpretation	Photo
Kontraskjæret, Oslo (ID 6094)	Right adult tarsometatarsus, only a short section of the shaft remains, both epiphysis missing (25% complete)	1624–1686 CE (Archive, Natural History Museum Of Bergen)	Removal of approximately half of the spur (12.4 mm from the base of the spur). The cut surface is fairly smooth and may represent a fresh cut. Two additional cuts were observed on the spur.	The spur has been de-tipped, possibly for 'naked heel' fighting. Alternatively, the spur may have been de-tipped to prevent in fighting. The fresh nature of the tip removal suggests that it took place just before the cockerels death or after. This specimen is very similar to Moreno-Garcia and Pimenta (2010) specimen from Portugal which also has the additional cuts on the spur.	Fig. 4P
Kontraskjæret, Oslo (ID6808)	Left adult tarsometatarsus, only the shaft remains, both epiphysis missing (50% Complete)	1624–1686 CE (Archive, Natural History Museum Of Bergen)	Removal of the spur close to the shaft (5 mm from the base of the spur). The surface of the stump is not smooth and does not indicate a fresh break. In addition, the edges are rounded.	Removal of the spur to attach an artificial spur. The rounded edges of the remaining spur stump may indicate healing of the bone.	SMF3 H,I
Revierstredet, Oslo (ID 5577)	Left adult tarsometatarsus, complete, large individual.	1624 – c.1670 CE (Lie, 1981)	Removal of the spur close to the shaft (5.4 mm from the base of the spur). A small additional cut mark can be seen on the spur stump. The surface doesn't look completely fresh, but no sign of rounded edges.	Removal of the spur to attach an artificial spur. This is the largest specimen and the most compelling evidence for cockfighting.	Fig. 4J, 4K
Revierstredet, Oslo (ID 5367)	Right adult tarsometatarsus, complete.	1624 – c.1670 CE (Lie, 1981)	Removal of the spur close to the shaft (4.3 mm from the base of the spur). Not a straight cut, slightly rounded edges to the cut surface.	Removal of the spur to attach an artificial spur. Slight rounded edges to the cut surface could indicate healing.	SMF3 J,K
Revierstredet, Oslo (ID 5404)	Right adult tarsometatarsus, with the cotyla medialis and lateralis missing (75% complete).	1624 – c.1670 CE (Lie, 1981)	Removal of the spur very close to the shaft (2.5 mm from the base of the spur). Slightly rounded edges to the cut surface.	Removal of spur to possibly attach an artificial spur. However, more of a stump is usually left. The rounded edges of the remaining spur stump may indicate healing of the bone.	SMF3 L,M

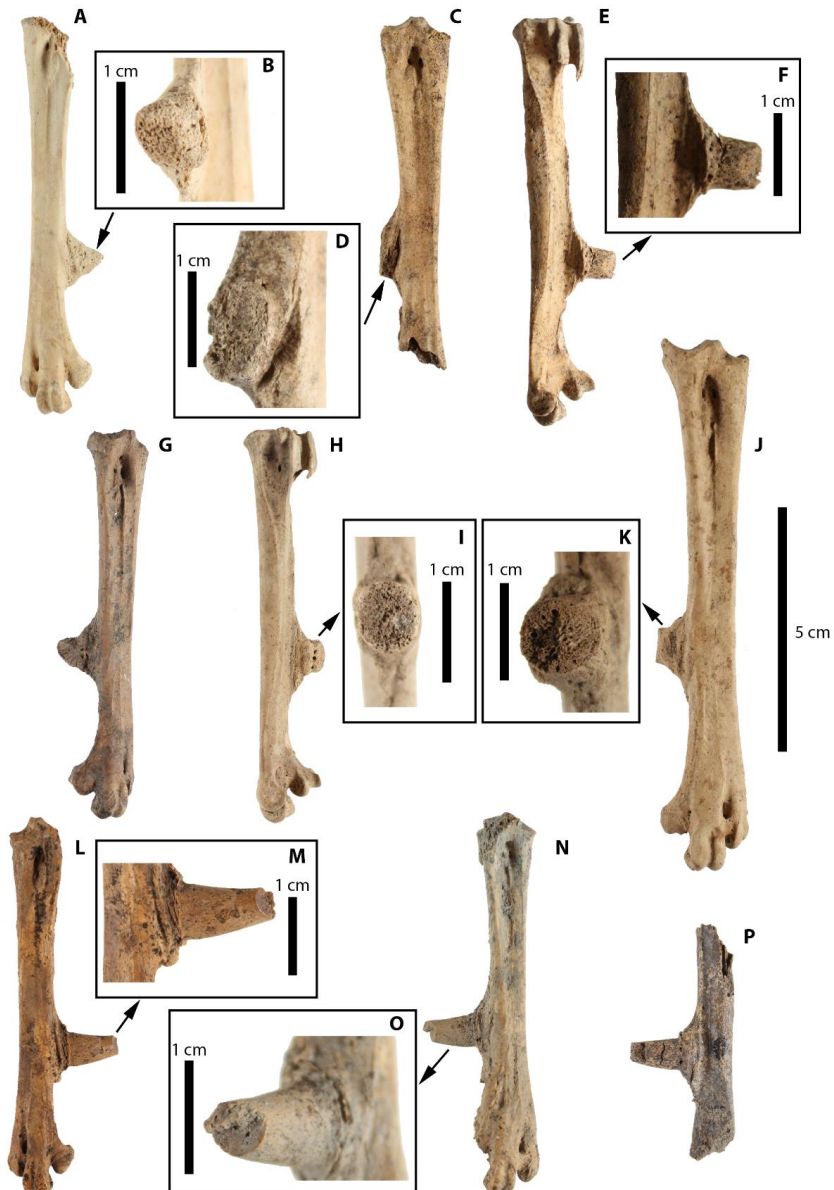


Figure 4. Selected tarsometatarsi with the spurs deliberately removed. **A:** ID7468 from Erkebispegården. **B:** Close up of ID7468. **C:** ID7872 from Erkebispegården. **D:** Close up of ID7872. **E:** ID8967 from Televerkstomten. **F:** Close up of ID8967. **G:** ID5238 from Mindets Tomt. **H:** ID7349 from Bryggen. **I:** Close up of ID7349. **J:** ID5577 from Revierstredet. **K:** Close up of ID5577. **L:** ID2343 from Nordre Felt II. **M:** Close up of ID2343. **N:** ID7738 from

Erkebispegården. **O**: Close up of ID7738. **P**: ID6094 from Kontraskjæret. Further details on these specimens can be found in Table 2. Images for seven additional specimens with deliberate spur removal from Norway can be found in the supplementary material (SMF4).

4. Discussion

4.1 Evidence for chicken breeds

The introduction of *G. gallus* to Norway is poorly understood. Domestic fowl are present in most urban sites by the early Medieval period, and are the overall dominant bird species in the middle-late Medieval assemblages (Walker et al., 2019), but it is not known exactly when domestic fowl arrived in Norway or where they originated from. The measurements of the Medieval material presented here shows a large size range for most elements but without a clear bi-modal pattern. A bi-modal pattern whereby the males and females group separately has previously been interpreted as evidence for a single breed (Boessneck et al., 1979; Reichstein and Pieper, 1986), whereas a less clear grouping could be suggestive of more than one breed. Sexual dimorphism in modern chickens generally results in males being 10–20% larger than females (Woldekiros et al., 2019; Benecke, 1989; Reichstein and Pieper, 1986). In the Medieval Site of Eketorp, Sweden (Boessneck et al., 1979) and Viking Age-Early Medieval site of Haithabu, Germany (Reichstein and Pieper, 1986), males and females could be clearly separated based on size, and sexual dimorphism of the tarsometatarsi averaged 18% (Reichstein and Pieper, 1986). At the site of Sagalassos in Turkey (500–700 CE), size variation exceeded the range for sexual dimorphism and a minimum of three different breeds were identified (De Cupere et al., 2005).

It is unclear if the degree of sexual dimorphism is similar in Scandinavian chicken breeds, as little has been done to investigate them. A male and female specimen of a Finnish landrace breed of *G. gallus*, the Alho-breed, held within the University Museum of Bergen's natural history collections, displays an average size difference of 9%. In certain elements, such as the scapula and pelvis there was only a 2% size increase in the

male specimen, but the male never exceeded a 20% size increase. The variation in bone length in the chicken assemblages of Mindets Tomt and Bryggen exceeds 20% (see SMF5 for minimum and maximum size range comparison), and even exceeds that of Eketorp, Haithabu and Sagalassos for most elements. We therefore argue that more than one breed of *G. gallus* is present in the Medieval period in Norway.

The size-frequency histograms for the two Post-Medieval sites, Kontraskjæret and Revierstredet, show similarly large variations in bone length, also suggesting the presence of more than one breed in Post-Medieval Norway. Additionally, a shift towards larger sizes in females can be observed, a pattern seen in many domestic species during the Post-Medieval period (Grau-Sologestoa and Albarella, 2018). The presence of very large male birds is intriguing. This may represent the introduction of a larger breed of domestic fowl in the Post-Medieval period. Alternatively, they could represent caponised males. Capons are males which are castrated, which results in a much larger individual. There are multiple reasons for why this may have been done. Some have reported that the meat is more tender, while it is also possible that these larger males were used for blood sport.

Unfortunately, historical sources make little difference to our knowledge of Medieval and Post-Medieval chickens. Magnus (1555) mentions two different coloured cockerels, “red roosters rather than those of other colours – most of them are white”. It should be noted that Olaus Magnus was writing about the Medieval period in the 16th century, and was based in Rome at the time, rather than in Scandinavia. However, as one of the few sources available, it adds weight to the hypothesis of the presence of multiple chicken breeds in Medieval Norway. Whether the smaller breed was part of the initial introduction to Norway whilst the larger breeds were a later introduction and restricted to urban locations needs further investigation.

4.2 Evidence for crested breeds

In addition to the size variation of the post-cranial bones from Medieval and Post-Medieval Norway, cranial morphology also suggests the presence of different breeds of *Gallus gallus*. Two skulls were identified (Figure 3) having unique morphological features linked with cerebral herniation. This is an inherited disorder in *G. gallus* and has rarely been reported in archaeological material. Currently, archaeological examples have been found in Britain (Brothwell, 1979), Germany (Teegen, 2008), Austria (Pucher, 1991), Hungary (Gál et al., 2010), and now Norway. Cerebral herniation within domestic fowl has become a cultivated mutation and is linked to a more elaborate crest, as evident in a number of modern breeds such as the Polish, Silkie and Houdan chickens (Gál, 2013). The two Norwegian specimens display a slight cranial vaulting along with the perforations in the neuro-cranium, which is less extreme than seen in modern crested breeds, and we interpret this as these individuals having a smaller and less elaborate crest, possibly similar to that of a modern day crested bantam.

The two crania presented here currently represent the only archaeological evidence for crested breeds within Norway, and, to the best of our knowledge, the only archaeological specimens in Scandinavia. We therefore consider it unlikely that such a crested breed was being developed in Norway. It is more likely that the crested breed identified here was imported from somewhere else. The specimens date to the Post-Medieval period, a period of increased Norwegian shipping (1690–1720 CE) (Stenersen and Libæk, 2007). The increased trade may have led to the introduction of new breeds of domestic fowl.

4.3 Evidence for cockfighting

The large percentage of adult male tarsometatarsi ($n = 128$, 49% of 258 specimens from 19 sites) in combination with the deliberate removal of spurs in 16 tarsometatarsi indicates that there was a reason for retaining a large stock of adult cockerels. There may have been a cultural significance placed upon cockerels whereby they were prized

and kept. The cockerel is often more elaborate in its plumage than the female hen and could have been kept for aesthetic reasons or as a practical bird with its territorial and aggressive nature and loud call. The removal of the spurs may have been to prevent infighting between males, when more than one male was being kept per flock. However, in these cases, it is more common for only half the spur to be removed for this purpose (Alison Foster, pers. comm.). Very few of the archaeological specimens show such a removal of half the spur. Most spurs were removed closer to the shaft, de-tipped and possibly sharpened. These particular patterns of spur removal match those seen in specimens from other countries that are interpreted as cockfighting (Ehrlich et al., this issue; Moreno-Garcia and Pimenta, 2010; Thys and Van Neer, 2010; Johnstone, 2007; West, 1982). A cockfighting scenario would also explain the age data, whereby all of the 128 male tarsometatarsi analysed were fully grown adults, an unprecedented amount. In modern day chicken husbandry, males are often surplus to requirements and slaughtered before reaching full maturity. Although the sizes of the Medieval male specimens varies (See figure 2B and 2D), it is unlikely that only large cockerels were used in cockfighting; providing the fighting birds are equally matched in weight it is unlikely we would see a bias towards one size category. We therefore think that the practice of cockfighting in late Medieval to Post-Medieval Norway best explains the patterns in tarsometatarsi observed above. This indicates that domestic fowl in Norway, during the Medieval and Post-Medieval period had a more complex purpose than just meat and eggs. Sykes (2012) highlights that the spread of domestic fowl was closely linked to complex socio-cultural reasons, and we believe the Norwegian material supports this. The lack of mentions of cockfighting in Norway in the historic literature as well as the lack of artificial spurs, however, remains intriguing.

There are two common styles of cockfighting, these are ‘naked heel’ and artificial spur fights. In the ‘naked heel’ cockfights, the cockerel’s original spur is sharpened, but remains intact. In the artificial spur fights the original spur is removed close to the shaft, leaving a stump, in order to attach an artificial spur. These two styles are fairly distinct as they leave different osteological evidence, and we believe both types of cockfighting are represented in the Norwegian material. Cockfighting is and was a male-dominated

blood sport (Sykes, 2012). This is important to take into account when looking at the Norwegian examples. In total, 16 examples have so far been identified from seven different sites, located in Trondheim, Oslo and Bergen. The context in which some of our specimens were recovered can be interpreted as male dominated areas. The specimens from the Erkebispegården (Trondheim) were found in contexts related to the military phase of the site. Bergen and Oslo were large trading ports during both the Medieval and Post-Medieval period and it is possible that trading ships from countries with a strong cockfighting culture would have introduced the sport into these cities. The Bryggen specimen was found in the Germanic area of Bryggen and part of the Hanseatic leagues trading zone, once again a male-dominated area. In addition, this would have been a place with many non-natives, bringing in foreign influences. It is possible that cockfighting was only practiced by the non-natives. Trading networks between Western Europe and East Asia, where cockfighting has traditionally been very popular, may have facilitated the import of cockfighting to Scandinavia.

Cockfighting is an ancient blood sport with a long tradition in many countries. Whilst it is now banned in much of Europe it continues in countries across the globe. Despite the spread and popularity of cockfighting, we could not find any mention of cockfighting in Norway or Scandinavia in the literature. Cockfighting in this region is not mentioned by Magnus (1555), nor is it mentioned in Finsterbusch's (1929) 'Cockfighting all over the World'. Despite this, the number of tarsometatarsi with spurs removed from Norway currently represents the largest collection of tarsometatarsi with the spur deliberately removed from any country. There are a small number of examples of tarsometatarsi where the spur has been removed or sharpened from Europe (Ehrlich et al., this issue; Moreno-Garcia and Pimenta, 2010; Thys and Van Neer, 2010; Johnstone, 2007; West, 1982). It is possible that when tarsometatarsi with this alteration to the spur are found, they were recorded as butchery. Alternatively, fighting birds may have held a higher significance and were not placed with other domestic waste and as a result are not so regular within the archaeological assemblages.

5. Conclusion

Although the how and when of the introduction of chickens into Norway remains unclear, our data show that by the Medieval period there were at least two different-sized breeds present, including a crested ornamental breed. In addition, we have evidence for the practice of cockfighting in Medieval and Post-Medieval Norway. It is clear that domestic fowl were not necessarily first seen as just food, but also served entertainment and possibly ritualistic purposes. The presence of multiple breeds and the evidence for cockfighting can be linked to the trade networks coming into Bergen and Oslo at this time, and highlight the socio-cultural aspects of chicken husbandry.

6. Data availability statement

The supplementary files for this publication are available on Mendeley Data: Walker and Meijer (2019) (See DOI: 10.17632/rt3dxx3bv2.2) The files found within the Mendeley data repository are outlined below.

6.1 Additional files

The additional files for this article can be found as follows:

Supplementary Material File 1 (SMF1). Unpublished sources reference list. This is predominantly grey literature archaeological and zooarchaeological reports. DOI: <http://dx.doi.org/10.17632/rt3dxx3bv2.2#file-f5d325c7-9fd7-4c08-bee2-e32763f4f211>

Supplementary Material File 2 (SMF2). Shows the frequency distributions of the Greatest Length (GL) for *Gallus gallus* humeri and coracoid from two Medieval and two Post-Medieval sites DOI: <http://dx.doi.org/10.17632/rt3dxx3bv2.2#file-b1507ba0-7e61-42c3-b4e7-c23e616394e2>

Supplementary Material File 3 (SMF3). Shows the frequency distributions of the Greatest Length (GL) for *Gallus gallus* ulnae and tibiotarsi from two Medieval and two Post-Medieval sites. DOI: <http://dx.doi.org/10.17632/rt3dxx3bv2.2#file-681948d6-f0b9-4ef0-9280-47dc939085b2>

Supplementary Material File 4 (SMF4). Is a photo plate showing additional tarsometatarsi with the spurs deliberately removed from Norwegian archaeological specimens. DOI: <http://dx.doi.org/10.17632/rt3dxx3bv2.2#file-b6ecdd82-548a-458e-b07d-2bb74e960e94>

Supplementary Material File 5 (SMF5). Minimum and maximum Greatest Length (GL) measurements for select elements. DOI: <http://dx.doi.org/10.17632/rt3dxx3bv2.2#file-c00bf446-7794-47bc-a937-2f6c5d89aa4b>

7. Competing interests

The authors have no competing interests to declare.

8. Funding sources

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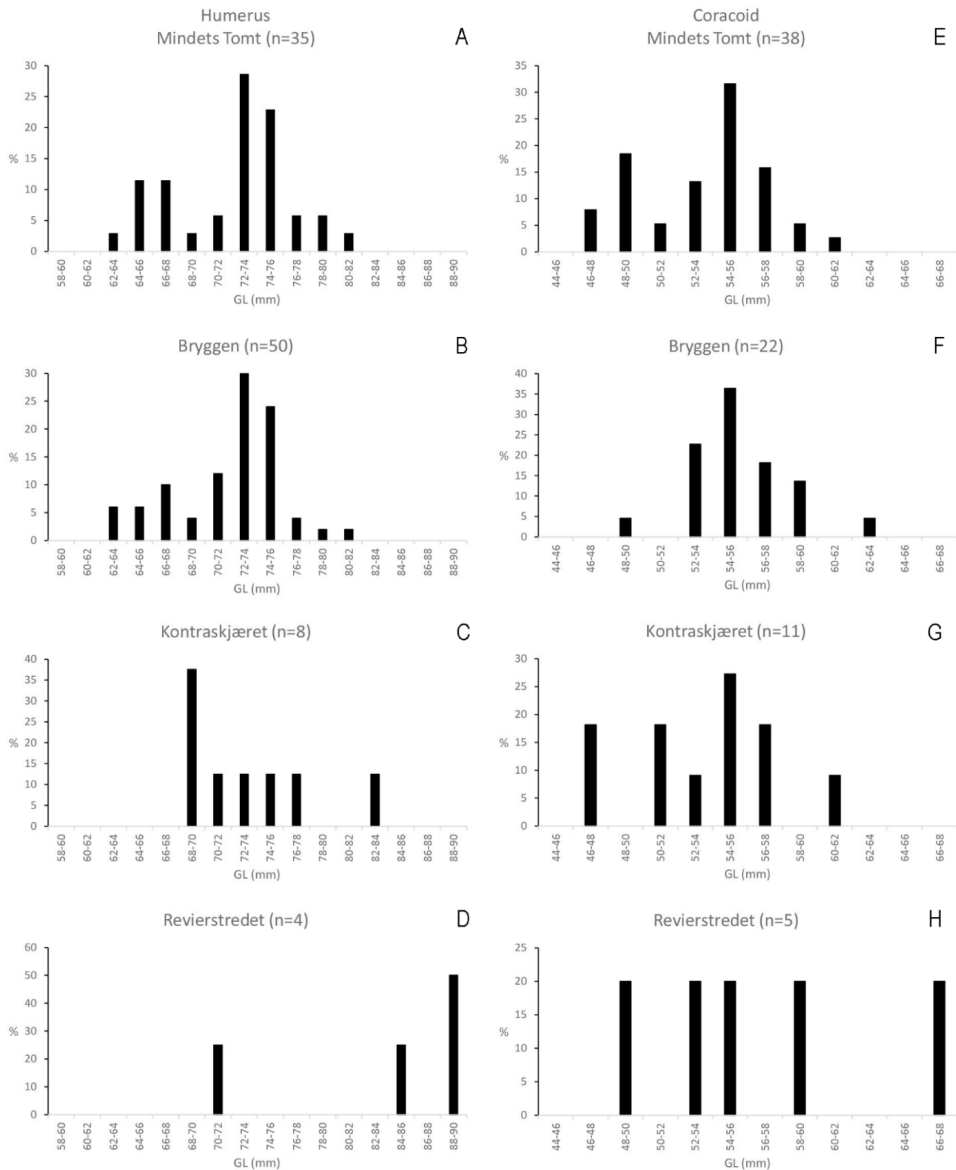
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Supplementary Material File 1 (SMF1)

SMF1. Unpublished report references. Available within the University Museum of Bergen's Natural History Archives (Curated by Anne Karin Hufthammer)

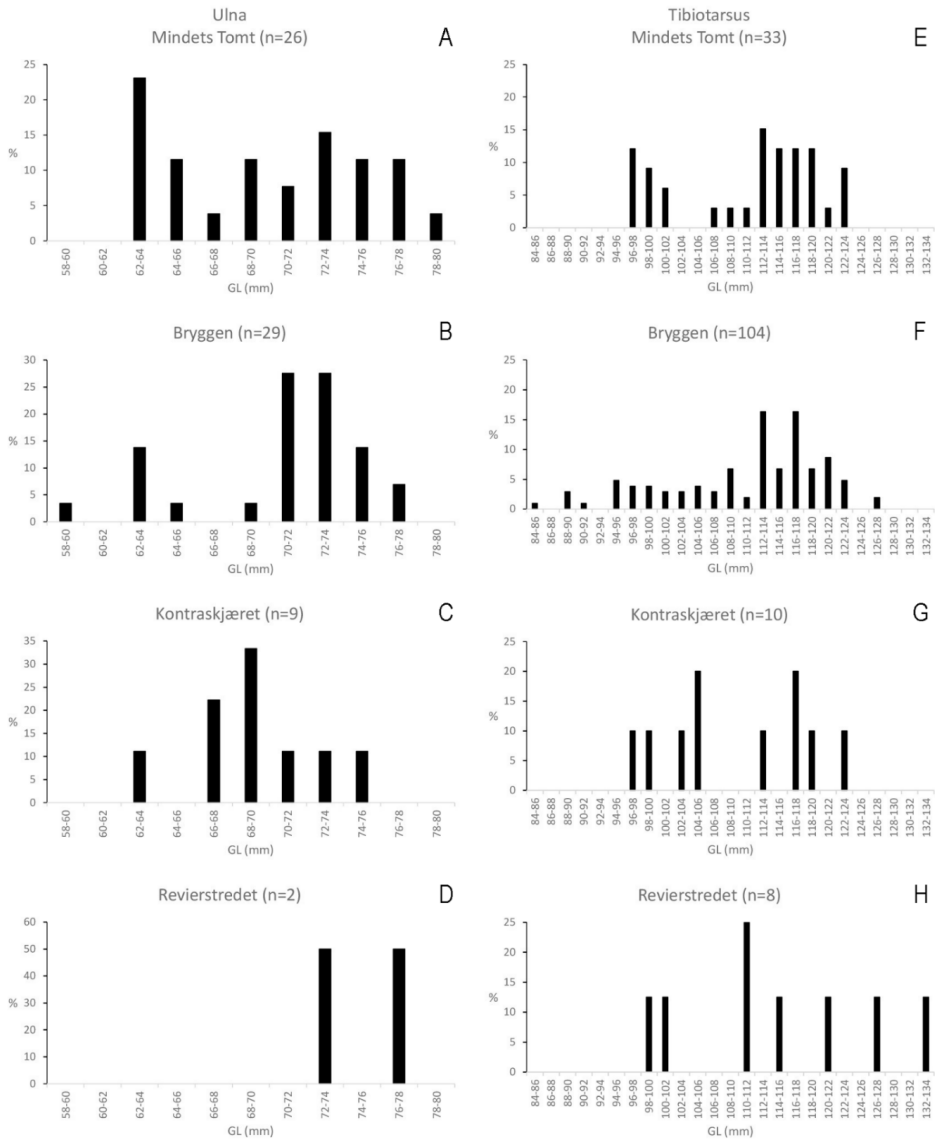
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Supplementary Material File 2 (SMF2)



SMF2. Frequency distributions of the Greatest Length (GL) for *G. gallus* humeri (A-D) and coracoid (E-H) from Medieval (A, B, E, F) and Post-Medieval (C, D, G, H) sites.

Supplementary Material File 3 (SMF3)



SMF3. Frequency distributions of the Greatest Length (GL) for *G. gallus* ulnae (A-D) and tibiotarsi (E-H) from Medieval (A, B, E, F) and Post-Medieval (C, D, G, H) sites.

Supplementary Material File 4 (SMF4)



SMF4. Remaining seven tarsometatarsi with the spurs deliberately removed from Norwegian archaeological assemblages. **A:** ID7523 from Erkebispegården. **B:** Close up of ID7523. **C:** Medial aspect of ID7678 from Erkebispegården. **D:** Anterior aspect of ID7678 from Erkebispegården. **E:** ID4318 from Mindets Tomt. **F:** Close up of ID4318. **G:** ID2958 from Nordre Felt II. **H:** Posterior aspect of ID6808 from Kontraskjæret. **I:** Medial aspect of ID6808 from Kontraskjæret. **J:** ID5367 from Revierstredet. **K:** Close up of ID5367. **L:** ID5404 from Revierstredet. **M:** Close up of ID5404. Further details on these specimens can be found in the main manuscript in Table 2. Images for the nine other examples of deliberate spur removal from Norway can be found in the main manuscript (Figure 4).

Supplementary Material File 5 (SMF5)

SMF5. Minimum and maximum Greatest Length (GL) measurements for select elements. A comparison between Norwegian sites and three other sites where size variation has been examined. Data for Sagalassos, Turkey taken from De Cupere et al. (2005); Eketorp III, Sweden taken from Boessneck et al. (1979); Haithabu, Germany taken from Reichstein & Pieper (1986). All measurements are in mm.

	n	Coracoid	n	Humerus	n	Ulna	n	Femur	n	Tibiotarsus	n	Tarso- metatarsus
Mindets Tomt	(38)	46-62	(35)	62-82	(26)	62-80	(42)	68-88	(33)	96-124	(26)	60-86
Bryggen	(22)	48-64	(50)	62-82	(29)	58-78	(113)	66-90	(104)	84-128	(48)	56-90
Kontraskjeret	(11)	46-62	(8)	68-84	(9)	62-76	(11)	66-102	(10)	96-124	(10)	66-84
Revierstredet	(5)	48-68	(4)	70-90	(2)	72-78	(6)	74-106	(8)	98-134	(7)	66-104
Sagalassos	(75)	46-60	(39)	60-78	(49)	58-78	(33)	68-82	(26)	94-124	(111)	60-90
Eketorp III	(102)	44-56	(54)	60-75	(70)	56-73	(79)	62-81	(35)	90-114	(58)	56-80
Haithabu	(85)	46-59	(218)	60-79	(143)	58-77	(336)	63-86	(197)	89-122	(112)	57-84

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Paper III

RESEARCH PAPER

Size variation in mid-Holocene North Atlantic Puffins indicates a dynamic response to climate change

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Abstract

Seabirds are one of the most at-risk groups, with many species in decline. In Scandinavia, seabirds are at a heightened risk of extinction due to accelerated global warming. Norway is home to a significant portion of the European Atlantic Puffin (*Fratercula arctica*) populations, but Norwegian populations have declined significantly during the last decades. In this paper we use biometric data from modern and archaeological *F. arctica* specimens to investigate patterns in body size variation over time of this iconic species. We aimed to set out a baseline for our archaeological comparison by firstly investigating whether modern subspecies of *F. arctica* are reflected in the osteological characters and are enough to distinguish subspecies from the bones alone. We then investigated if archaeological remains of *F. arctica* differ in size from the modern subspecies. Our results show that the subspecies *Fratercula arctica naumanni* was distinctly larger than the other subspecies. However, *Fratercula arctica arctica* and *Fratercula arctica grabae* were difficult to separate based on size. This generally supports ornithological observations. Post-Medieval *F. arctica* bones from Måsøy were similar to modern *F. a. arctica* populations. The mid-Holocene remains from Dollsteinhola overlaps with the modern size ranges of *F. a. arctica* and *F. a. grabae* but are generally shorter and more robust. Dollsteinhola is located close to the borders of the modern breeding ranges of both *F. a. arctica* and *F. a. grabae*. We consider it therefore likely that given the mid-Holocene climatic oscillations, breeding ranges of the two subspecies shifted north or south accordingly. However, this does not

explain the different proportions of the *Dollsteinhola* specimens. Our data provide the first evidence for shifting distributions in ancient Atlantic Puffins and represent the first osteological analysis of *Fratercula arctica* subspecies.

Keywords: *Fratercula arctica*, Holocene, Osteology, Palaeontology, Seabirds

1. Introduction

Seabirds are one of the most at-risk bird groups with approximately half of all seabirds species in decline (Croxall et al., 2012; Dias et al., 2019; IUCN, 2020), and 110 species (31%) regarded as threatened by the IUCN red list. Seabirds in Scandinavia are at the limits of their distribution, and at a heightened risk of extinction due to further warming in northern biomes as a result of Arctic amplification (Pithan & Mauritsen, 2014). Monitoring of seabird communities along the Norwegian coast (Fauchald et al., 2015) found declining populations across all major ecological groups, with several species, including the iconic Atlantic Puffin (*Fratercula arctica* (Linnaeus, 1758)), having declined more than 50% in the last 25 years.

The Atlantic Puffin is an iconic species, recognised for its distinct appearance, and one of the six Alcidae species breeding in Norway. The vast majority (c.80%) of the European Atlantic Puffin population is found in Iceland and Norway. In addition, Norwegian *F. arctica* constitute 25-30% of the global population (Barrett et al., 2006). Monitoring studies (Fauchald et al., 2015) indicate that the once large populations of Atlantic Puffin in the Norwegian Sea have been significantly reduced from 1.6 million pairs in 1980 to 600 000 at present, likely as a result of environmental and anthropogenic changes.

To understand the responses of modern species to environmental change, it is crucial to understand the responses of ancient species to past environmental perturbations. Organisms may adapt to environmental oscillations by changes in body size, which in turn is linked to a number of life history traits. Only a handful of studies have looked at body size variation of Scandinavian bird species through time. For the

Common Eider (*Somateria mollissima*), Ericson (1987) found that there was stasis in body size between 7000 BCE and 1000 CE, with a subsequent decrease in average size between 1000–1900 CE. This decrease was likely linked to changes in levels of food competition (Ericson, 1987). A study by Hufthammer (1982) on the extinct Great Auk (*Pinguinus impennis*) showed that lower limb bones were larger in the past, a pattern particularly evident in material older than 5000 years BP and attributed to changes in climatic conditions.

There are three recognised subspecies of the Atlantic Puffin. The nominate subspecies *Fratercula arctica arctica* breeds in Iceland, Norway (from the Runde colony northwards (Haftorn, 1971)), Bear Island, southern Novaya Zemlya, south-west Greenland and eastern North America. *Fratercula arctica naumanni* (Norton, 1901) is geographically distributed above the Arctic Circle in north-west and eastern Greenland, Spitsbergen and northern Novaya Zemlya. *Fratercula arctica grabae* (Brehm, 1831) occupies more southern climes and occurs in Britain, Ireland, Faroes, Channel Islands, France and Norway (from Utvær southwards (Haftorn, 1971)) (Cramp, 1988; Lowther et al., 2020). Ornithological studies have sought to distinguish between the three subspecies through weight, bill length, bill depth and wing length (Myrberget, 1962; 1963; Pearson, 1968; Corkhill, 1972; Petersen, 1976; Harris, 1979). These studies have found that subspecies can be loosely separated on size alone. *Fratercula arctica naumanni* is the largest, with *F. a. grabae* being the smallest, and *F. a. arctica* falling in between. Despite the differences, there is considerable overlap between the subspecies, especially between the nominate *F. a. arctica* and *F. a. grabae*. Protein studies (Moen, 1991) show low genetic variation between *F. a. arctica* and *F. a. grabae*, and has led many to question the validity of Atlantic Puffin subspecies (Sangster et al., 2005; Harris & Wanless, 2011). A recent study on population structure of the Atlantic Puffin using whole genome data (Kersten et al., 2020) identified four population clusters that disagrees with the traditional view of three subspecies. This suggests that Atlantic Puffin taxonomy is more complicated than previously assumed.

Studies based on body weights and external measurements have given an important insight into size differences between populations of *F. arctica*. These studies

have identified a north-south clinal pattern (Myrberget, 1963; Pethon, 1967) with body size increasing at higher latitudes, which is likely influenced by environmental factors, like ocean temperature and food quality (Moen, 1991; Harris & Wanless, 2011). It would therefore be expected that at times when environmental conditions differed from the present day, we would see differences in the body size of *F. arctica* populations.

Although *Fratercula arctica* is regularly found in the archaeological record of coastal Norwegian sites (predominantly north of Bergen), there are few osteological studies on their remains. Olsen's (1967) work on Neolithic sites along the Varangerfjord in northern Norway (See Fig. 1) is the main piece of osteological work on *F. arctica*. The study found that *F. a. arctica* was the only subspecies present on the site and that it was slightly larger than modern *F. a. arctica* populations. This led to the conclusion that conditions in the Varangerfjord were colder during the Stone Age. A similar study by Lahtiperä (1979) found that Atlantic Puffin remains from Grunnfjord farm, a 16th–18th Century site in northern Norway (See Fig. 1), displayed a homogenous population of *F. a. arctica*. Unlike Olsen's (1967) study, the material from Grunnfjord Farm was regarded as the same size as modern *F. a. arctica* populations. To further explore past and present variation in Atlantic Puffin body size and its link to environmental conditions, we measured skeletal specimens of modern *F. arctica* and archaeological *F. arctica* remains from two Norwegian sites. Specifically, we aimed 1) to investigate whether modern subspecies of *F. arctica* (from ornithological observations) are reflected in the osteological characters, and are enough to distinguish subspecies from the bones alone, and 2) to determine if archaeological remains of *F. arctica* differ in size from the modern populations in relation to climatic change and other factors.

2. Methods

2.1 Modern comparative material

Modern puffin specimens examined for this study are part of the Osteological collections at the Bergen Natural History Museum and were inspected on site by SJW and HJMM. Additional specimens at the Natural History Museum of Denmark were examined by SJW, while specimens at Natural History Museum of Geneva and the Natural History Museum at Tring were examined by A. Cibois and J. White, respectively. All specimens, with the exception of 3, were measured by SJW. We measured seven skeletal elements (coracoid, humerus, ulna, carpometacarpus, femur, tibiotarsus and tarsometatarsus) from 75 modern Atlantic Puffin specimens using digital calipers. Measurements followed the conventions set out in Von den Driesch (1976). Additional measurements were taken from Kraft (1972) (See **S1 Text** for details on how measurements were taken). In order to compare size of the bones between the 3 subspecies of *F. arctica*, it was integral to select modern specimens confidently identified to subspecies. We therefore only used specimens that had been identified to subspecies upon collection (often on diagnostic external characters such as living weights, bill length, bill depth and wing length), and the location and time of year of collection of the specimen were cross-checked with the subspecies breeding range. Specimens from the Faroe Islands that were labelled as *F. a. arctica* were considered as *F. a. grabae* in this study (Museum numbers; NHMD 223250, NHMD 223251, NHMD 223252, NHMD 223258, NHMD 223263). In addition, a specimen of *F. a. arctica* from Bore, Rogaland (Fig. 1) was also considered as *F. a. grabae* (B 3052). Finally, a specimen labelled as *F. a. arctica* from Spitsbergen was regarded as *F. a. naumanni* (BM 10341). These seven specimens (NHMD 223250, NHMD 223251, NHMD 223252, NHMD 223258, NHMD 223263, B 3052 and BM 10341) were changed due to their geographic origin during the breeding season, all were found outside of the nominate breeding range and were therefore highly likely to belong to one the subspecies.

Any subspecies specimens that were collected outside their temporal and geographic breeding range (breeding colonies occupied between late March - Mid August/early September (Harris & Wanless, 2011)) were not included in this study. Forty-four specimens fell into this category and were not included. This prevents uncertainty over the inclusion of migratory birds, as the migration patterns of Atlantic Puffin cause mixed colonies of the subspecies during the winter months. Through our subspecies cross-check we were able to use 48 specimens of the nominate *Fratercula arctica arctica*, 11 specimens of subspecies *Fratercula arctica grabae* and 16 of subspecies *Fratercula arctica naumanni*. These 75 specimens have been measured from the natural history collections held at the University Museum of Bergen, the Natural History Museum of Denmark, the Natural History Museum of Geneva and the Natural History Museum at Tring (See Appendix 1). Both complete and partial specimens were included within this study, covering the majority of the Atlantic Puffins breeding range. The specimens were collected from Norway and Spitsbergen (n = 38), Greenland (n = 19), Iceland (n = 10), Faroe Islands (n = 7) and Scotland (n = 1) (See Fig. 1). In order to be thorough and to check for any effects of sexual dimorphism, sex was recorded for all modern specimens. We found that males were on average between 0.3 – 2.8% larger than females. However, there was also a large overlap between the sexes. Given this and the relatively low percentage of sexual dimorphism, we decided to group males and females for comparisons with archaeological material, which also likely represents a mix of males and females.

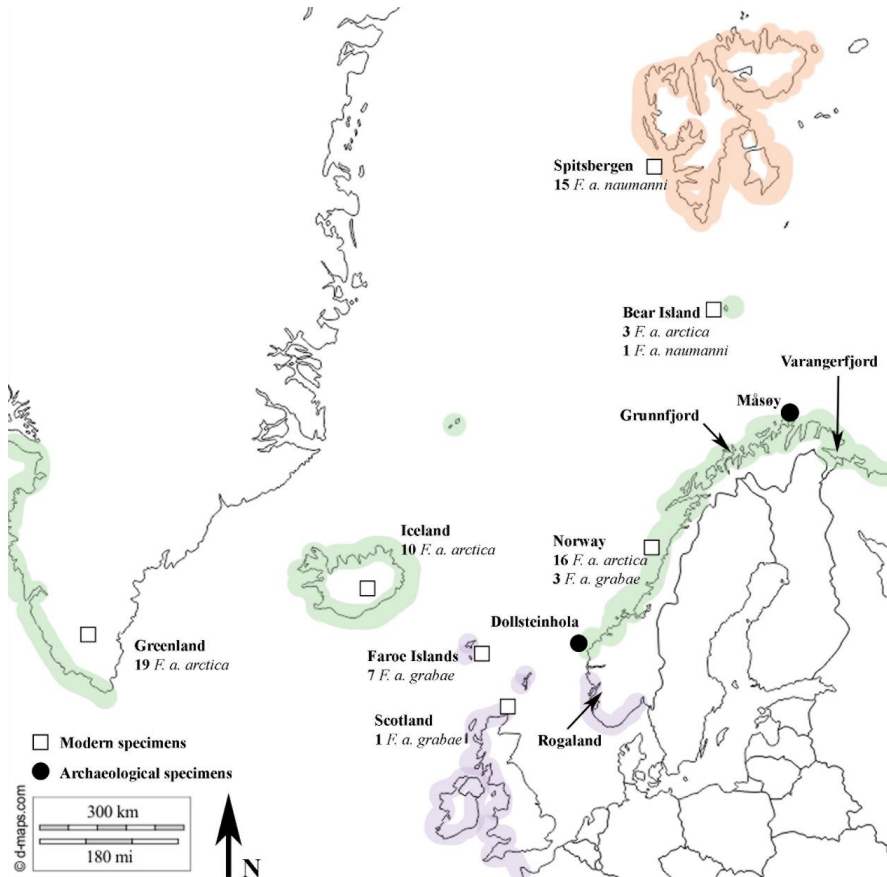


Fig 1. Map of archaeological sites (Dollsteinhola and Måsøy) and the locations of the comparative *Fratercula arctica* specimens. The sites investigated by Olsen (1967) and Lahtiperä (1979) are also indicated on the map. The known breeding distribution of all three subspecies is clearly indicated on the map (purple; *F. a. grabae*, green; *F. a. arctica* and orange; *F. a. naumanni*), data on breeding distributions is taken from Dementev and Gladkov (1951). Reprinted from d-maps (2020) under a CC BY licence, with permission from [d-maps], original copyright [2020].

2.2 Archaeological material

Morphologically *Fratercula arctica* can be separated from other closely related Alcidae species based on a number of characteristics and the use of an extensive comparative collection. Morphological characters specific to *F. arctica*, such as a distinct facies articularis sternalis of the coracoid, and the tarsometatarsus being much shorter and more robust than some of the similar sized Alcids were utilised in this study (Additional characters and comparisons with other Auks can be found in Olsen (1967)). Certain skeletal elements, such as the coracoid, humerus, tibiotarsus and tarsometatarsus, are more diagnostic than others. All archaeological material was reidentified using the extensive modern comparative collections held at the University Museum of Bergen. We made sure to use only specimens that could be confidently assigned to *Fratercula arctica*. In total 380 archaeological specimens were included within this study, 227 from the site of Dollsteinhola and 153 from Måsøy.

The cave site of Dollsteinhola (stored under number JS 706 in the University Museum of Bergens collections) is located on the west coast of Norway on Sandøya Island in the county Møre and Romsdal at a latitude of 62°N (See Fig. 1). Over 70,000 bones were recovered from the site, representing 124 bird species (Lie, 1989). Dollsteinhola has a wide date range of between c.6600 – 3600 BP (Lie, 1989). This date range encompasses a short period of the late Mesolithic and into the Neolithic, and there is also some evidence of Bronze Age material at the site. The older material at this site is non-anthropogenic and represents a natural deposited assemblage, however, by the Bronze Age it is an anthropogenic assemblage. In terms of climatic change, Dollsteinhola is of great interest, representing a mid-Holocene (7.3 – 4.8 BP) assemblage, a period where higher summer temperatures were around 1.5 – 2.0°C warmer than present (Snowball et al., 2004; Seppä et al., 2009; Balascio & Bradley, 2012; Bjune et al., 2004; 2005). According to the temperature curve for the west coast of Norway (Bjune et al., 2005) the post-glacial warm period lasted until 4000 years BP. The younger material from Dollsteinhola dates to the late-Holocene (4.8 BP – present), a period of decreasing summer temperatures (Snowball et al., 2004; Seppä et al., 2009;

Balascio & Bradley, 2012) and higher levels of precipitation (Nichols et al., 2009). This indicates that some of the later specimens from this site would have been from a colder and wetter period.

Måsøy (stored under number JS 673 in the University Museum of Bergen's collections) is located in the county of Troms and Finnmark in the far north of Norway, at a latitude of 71°N (See Fig. 1). The bone material from Måsøy is from a Post-Medieval midden and has been dated to 1620 – 1770 CE (Geffen et al., 2011), representing an anthropogenic assemblage from the Little Ice Age (LIA). The Little Ice Age was a period of increased glacial activity in the late Holocene and temperature reconstructions reveal oscillating warm and cold periods across the Northern Hemisphere (Svarva et al., 2018). For northern Norway, the coldest period was reconstructed for the 17th century (Kirchhefer, 2001).

2.3 Data analysis

We first explored differences in size between groups using descriptive statistics. All data were tested for normality by looking at the variances and the Shapiro-Wilk test for normality. To statistically test for differences in size between the 3 modern subspecies, and between the modern subspecies and the archaeological material, we used one-way ANOVA's. We considered p-values ≤ 0.05 statistically significant. All analyses were performed using the analytical program PAST 4.03 (Hammer et al., 2001).

3. Results

3.1 The data

Data tables presenting the mean measurements in millimetres along with the variance and number of specimens for the coracoid, humerus, ulna, carpometacarpus, femur, tibiotarsus and tarsometatarsus are given in Tables 1-7.

Table 1. Coracoid data. Mean measurements (in mm) and the variance for the coracoid of modern *F. a. arctica*, *F. a. grabae* and *F. a. naumanni*, and archaeological specimens from Dollsteinhola and Måsøy. Abbreviations: Lm, medial length, Bb, basal breadth, BF, breadth of the facies articularis sternalis. The number of specimens is presented in the second column, any deviations are indicated in brackets next to the mean values.

Taxon	No. specimens	Lm	Standard deviation	Bb	Standard deviation	BF	Standard deviation
<i>F. a. arctica</i>	48	35.40	1.36	12.78	0.94	10.01	0.67
<i>F. a. grabae</i>	10	34.57	1.94	12.55	0.57	9.51	0.51
<i>F. a. naumanni</i>	16	38.44 (n=15)	0.67	13.86	0.73	10.95	0.64
Dollsteinhola	39	34.40 (n=35)	1.59	13.64 (n=1)	0	10.21 (n=36)	1.11
Måsøy	28	35.47 (n=24)	0.71	12.59 (n=3)	0.23	9.82 (n=26)	0.52

Table 2. Humerus data. Mean measurements (in mm) and the variance for the humerus of modern *F. a. arctica* and subspecies *F. a. grabae* and *F. a. naumanni*, and archaeological specimens from Dollsteinhola and Måsøy. Abbreviations: GL, greatest length, Bp, breadth of the proximal end, SC, smallest breadth of the corpus, Bd, breadth of the distal end, KB, smallest depth of the distal shaft. The number of specimens is presented in the second column, any deviations are indicated in brackets next to the mean values.

Taxon	No. specimens	GL	Standard deviation	Bp	Standard deviation	SC	Standard deviation	Bd	Standard deviation	KB	Standard deviation
<i>F. a. arctica</i>	48	65.21 (n=45)	1.70	15.07	0.68	3.21 (n=46)	0.17	6.95 (n=44)	0.28	3.97 (n=44)	0.20
<i>F. a. grabae</i>	11	62.74	3.03	14.18	0.76	3.14	0.29	6.76	0.41	3.85	0.41
<i>F. a. naumanni</i>	16	69.66 (n=14)	1.71	16.00	0.50	3.46	0.16	7.37	0.25	4.29	0.21
Dollsteinhola	32	63.38 (n=14)	2.11	14.54 (n=25)	0.43	3.27 (n=22)	0.26	6.92 (n=19)	0.26	3.95 (n=20)	0.22
Måsøy	37	68.96 (n=1)	0	15.15 (n=13)	0.80	3.33 (n=7)	0.19	6.98 (n=25)	0.33	4.05 (n=25)	0.19

Table 3. Ulna data. Mean measurements (in mm) and the variance for the ulna of modern *F. a. arctica* and subspecies *F. a. grabae* and *F. a. naumanni*, and archaeological specimens from Dollsteinhola and Måsøy. Abbreviations: GL, greatest length, Dip, diagonal of the proximal end, Bp, breadth of the proximal end, Tp, depth of the proximal end, SC, smallest breadth of the corpus, Did, diagonal of the distal end. The number of specimens is presented in the second column, any deviations are indicated in brackets next to the mean values.

Taxon	No. specimens	GL	Standard deviation	Dip	Standard deviation	Bp	Standard deviation	Tp	Standard deviation	SC	Standard deviation	Did (mm)	Standard deviation
<i>F. a. arctica</i>	27	50.76	1.19	8.15	0.39	6.84	0.33	6.17	0.27	2.96	0.13	7.45	0.32
<i>F. a. grabae</i>	6	50.92	2.56	8.77	0.71	6.57	0.16	6.78	0.73	3.26	0.60	7.47	0.26
<i>F. a. naumanni</i>	16	55.02 (n=13)	1.25	8.82 (n=12)	0.48	7.37 (n=12)	0.24	6.71 (n=12)	0.21	3.25	0.18	8.09	0.17
Dollsteinhola	18	49.46 (n=17)	2.44	7.98	0.49	6.77	0.40	6.13	0.35	2.96 (n=16)	0.29	7.33 (n=17)	0.32
Måsøy	28	51.65 (n=24)	0.97	8.20 (n=26)	0.41	6.92 (n=26)	0.30	6.30 (n=25)	0.24	3.06 (n=26)	0.14	7.53 (n=26)	0.25

Table 4. Carpometacarpus data. Mean measurements (in mm) and the variance for the carpometacarpus of modern *F. a. arctica* and subspecies *F. a. grabae* and *F. a. naumanni*, and archaeological specimens have also been included from Dollsteinhola and Måsøy. Abbreviations: GL, greatest length, Bp, breadth of the proximal end, Did, diagonal of the distal end, HS, height of the symphysis. The number of specimens is presented in the second column, any deviations are indicated in brackets next to the mean values.

Taxon	No. specimens	GL	Standard deviation	Bp	Standard deviation	Did	Standard deviation	HS	Standard deviation
<i>F. a. arctica</i>	27	34.15	0.90	8.02	0.42	5.04	0.29	3.89	0.23
<i>F. a. grabae</i>	6	34.26	1.60	8.30	0.43	5.01	0.18	4.12	0.58
<i>F. a. naumanni</i>	16	37.12	0.81	8.64	0.33	5.54	0.34	4.18	0.24
Dollsteinhola	27	32.84 (n=25)	1.42	8.00	0.39	5.31 (n=25)	0.38	3.67 (n=24)	0.40
Måsøy	23	34.85 (n=21)	0.77	8.17 (n=22)	0.30	5.21 (n=22)	0.34	3.89 (n=22)	0.22

Table 5. Femur data. Mean measurements (in mm) and the variance for the femur of modern *F. a. arctica* and subspecies *F. a. grabae* and *F. a. naumanni*, archaeological specimens from Dollsteinhola and Måsøy. Abbreviations: GL, greatest length, Bp, breadth of the proximal end, Dp, depth of the proximal end, SC, smallest breadth of the corpus, Bd, breadth of the distal end, Dd, depth of the distal end. The number of specimens is presented in the second column, any deviations are indicated in brackets next to the mean values.

Taxon	No. specimens	GL	Standard deviation	Bp	Standard deviation	Dp	Standard deviation	SC	Standard deviation	Bd	Standard deviation	Dd	Standard deviation
<i>F. a. arctica</i>	47	39.66	1.56	7.88	0.41	5.24	0.30	2.96 (n=46)	0.17	7.12	0.38	6.12 (n=46)	0.38
<i>F. a. grabae</i>	8	38.27	2.41	7.32	0.46	5.18	0.29	2.87	0.14	6.80	0.44	5.60	0.60
<i>F. a. naumanni</i>	16	41.97	1.14	8.37	0.38	5.63	0.26	3.15	0.18	7.53	0.29	6.55	0.23
Dollsteinhola	12	37.46	1.25	7.63	0.40	4.92	0.25	2.98	0.16	7.05	0.40	5.95	0.33
Måsøy	14	39.76 (n=9)	0.85	7.70 (n=10)	0.41	5.12 (n=9)	0.30	3.08	0.17	7.16 (n=11)	0.26	6.13 (n=11)	0.19

Table 6. Tibiotarsus data. Mean measurements (in mm) and the variance for the tibiotarsus of modern *F. a. arctica* and subspecies *F. a. grabae* and *F. a. naumanni*, and archaeological specimens from Dollsteinhola and Måsøy. Abbreviations: La, axial length (defined as, from the tuberculum centrale to the distal border of the trochlea tibiotarsi), Dip, diagonal of the proximal end (defined as, from the condylus medialis femoralis to the crista lateralis), Bp, breadth of the proximal end, SC, smallest breadth of the corpus, Bd, breadth of the distal end, Dd, depth of the distal end. The number of specimens is presented in the second column, any deviations are indicated in brackets next to the mean values.

Taxon	No. specimens	La	Standard deviation	Dip	Standard deviation	Bp	Standard deviation	SC	Standard deviation	Bd	Standard deviation	Dd	Standard deviation
<i>F. a. arctica</i>	27	62.90	1.56	8.45	0.41	5.84 (n=26)	0.35	3.22	0.19	5.73	0.27	6.02	0.28
<i>F. a. grabae</i>	6	63.55	3.66	9.11 (n=5)	0.50	5.69 (n=4)	0.44	3.14	0.32	5.74	0.31	5.60	1.15
<i>F. a. naumanni</i>	16	68.29	1.98	9.10	0.27	6.47 (n=15)	0.22	3.48	0.25	6.28	0.26	6.37	0.23
Dollsteinhola	15	61.37 (n=8)	1.89	8.43 (n=12)	0.31	5.88 (n=12)	0.20	3.25	0.21	6.04 (n=11)	0.38	5.85 (n=11)	0.24
Måsøy	15	63.34 (n=2)	1.34	8.6 (n=11)	0.31	5.99 (n=11)	0.36	3.41 (n=12)	0.21	5.93 (n=5)	0.29	5.93 (n=5)	0.29

Table 7. Tarsometatarsus data. Mean measurements (in mm) and the variance for the tarsometatarsus of modern *F. a. arctica* and subspecies *F. a. grabae* and *F. a. naumanni*, and archaeological specimens from Dollsteinhola and Måsey. Abbreviations: GL, greatest length, Bp, breadth of the proximal end, SC, smallest breadth of the corpus, Bd, breadth of the distal end. The number of specimens is presented in the second column, any deviations are indicated in brackets next to the mean values.

Taxon	No. specimens	GL	Standard deviation	Bp	Standard deviation	SC	Standard deviation	Bd	Standard deviation
<i>F. a. arctica</i>	24	27.84 (n=23)	0.97	6.43	0.32	3.57 (n=23)	0.30	6.96 (n=21)	0.28
<i>F. a. grabae</i>	3	29.71	1.85	6.24 (n=2)	0.23	3.49 (n=2)	0.01	6.83 (n=2)	0.24
<i>F. a. naumanni</i>	15	30.03	1.23	7.09	0.31	3.86	0.19	7.43	0.27
Dollsteinhola	84	27.21 (n=70)	1.77	6.22 (n=72)	0.36	3.57 (n=83)	0.29	6.74 (n=69)	0.37
Måsey	8	28.51 (n=6)	0.79	6.56 (n=6)	0.27	3.63 (n=7)	0.19	7.14	0.22

3.2 Size differences between subspecies

Table 8. P-values for the one-way ANOVA for modern subspecies. Summary of the p values from the one-way ANOVA results for all 7 elements investigated in this paper of modern *F. a. arctica*, *F. a. grabae* and *F. a. naumanni*. All p-values below 0.05 are regarded as statistically significant. For the full ANOVA results and details of normality testing see supplementary file (S2 Appendix).

A		Coracoid ANOVA results											
		<i>F. a. arctica</i>			<i>F. a. naumanni</i>								
		Lm	Bb	BF	Lm	Bb	BF						
<i>F. a. grabae</i>		0.185	0.721	0.071	<.001	<.001	<.001						
<i>F. a. arctica</i>					<.001	<.001	<.001						
B		Humerus ANOVA results											
		<i>F. a. arctica</i>				<i>F. a. naumanni</i>							
		GL	Bp	SC	Bd	KB	GL	Bp	SC	Bd	KB		
<i>F. a. grabae</i>		<.001	<.001	0.554	0.133	0.292	<.001	<.001	<.001	<.001	<.001		
<i>F. a. arctica</i>							<.001	<.001	<.001	<.001	<.001		
C		Ulna ANOVA results											
		<i>F. a. arctica</i>						<i>F. a. naumanni</i>					
		GL	Dip	Bp	TP	SC	Did	GL	Dip	Bp	TP	SC	Did
<i>F. a. grabae</i>		0.969	0.014	0.128	<.001	0.026	0.991	<.001	0.970	<.001	0.904	1	<.001
<i>F. a. arctica</i>								<.001	<.001	<.001	<.001	<.001	<.001
D		Carpometacarpus ANOVA results											
		<i>F. a. arctica</i>				<i>F. a. naumanni</i>							
		GL	Bp	Did	HS	GL	Bp	Did	HS				
<i>F. a. grabae</i>		0.963	0.258	0.961	0.218	<.001	0.184	<.001	0.893				
<i>F. a. arctica</i>						<.001	<.001	<.001	0.009				
E		Femur ANOVA results											
		<i>F. a. arctica</i>						<i>F. a. naumanni</i>					
		GL	Bp	Dp	SC	Bd	Dd	GL	Bp	Dp	SC	Bd	Dd
<i>F. a. grabae</i>		0.064	0.002	0.832	0.329	0.073	0.002	<.001	<.001	<.001	<.001	<.001	<.001
<i>F. a. arctica</i>								<.001	<.001	<.001	<.001	<.001	<.001
F		Tibiotarsus ANOVA results											
		<i>F. a. arctica</i>						<i>F. a. naumanni</i>					
		La	Dip	Bp	SC	Bd	Dd	La	Dip	Bp	SC	Bd	Dd
<i>F. a. grabae</i>		0.756	0.002	0.644	0.759	1	0.108	<.001	0.997	<.001	0.009	<.001	0.002
<i>F. a. arctica</i>								<.001	<.001	<.001	0.002	<.001	0.046
G		Tarsometatarsus ANOVA results											
		<i>F. a. arctica</i>				<i>F. a. naumanni</i>							
		GL	Bp	SC	Bd	GL	Bp	SC	Bd				
<i>F. a. grabae</i>		0.028	0.700	0.898	0.788	0.897	0.003	0.152	0.015				
<i>F. a. arctica</i>						<.001	<.001	0.005	<.001				

The results of the one-way ANOVA (Table 8) show that on the whole comparisons between *F. a. arctica* and *F. a. grabae* were not statistically significant. However, the greatest length of the humerus (Table 8B) and the greatest length of the tarsometatarsus (Table 8G) did identify a significant difference between them, along with a number of other measurements (See Table 8). The comparisons between *F. a. grabae* and *F. a.*

naumanni (Table 8) show that almost all measurements are statistically different. A small number of measurements showed no difference (Table 8C, 8D, 8F and 8G). Finally, comparisons between *F. a. arctica* and *F. a. naumanni* show that all measurements are statistically significant.

3.3 Size differences between modern and archaeological material

Comparisons of the modern subspecies with the archaeological specimens from Dollsteinhola and Måsøy, and between the two archaeological populations are presented in Table 9. The ANOVA results show that the subspecies *F. a. naumanni* is significantly different to the archaeological specimens at Dollsteinhola and Måsøy (Table 9). The comparison between the nominate *F. a. arctica* and Dollsteinhola shows that the length measurements of the coracoid, humerus, carpometacarpus and femur were all significantly different (Table 9A, 9B, 9D and 9E). Comparisons between *F. a. arctica* and Måsøy showed that they were not statistically different in any measurement. The subspecies *F. a. grabae* showed few statistical differences when compared to the Dollsteinhola population, the carpometacarpus was the most notable difference (Table 9D). Similarly, there were very few differences detected between *F. a. grabae* and the Måsøy specimens. Finally, comparisons between the two archaeological sites indicated significant differences in the greatest length of the upper limb bones (Table 9A, 9C and 9D) and the femur (Table 9E). Other measurements tended not to be significantly different.

Table 9. P-values for the one-way ANOVA for modern subspecies compared to archaeological populations. Summary of the p-values for one-way ANOVA results for all 7 elements investigated in this paper. Comparison of modern *F. a. arctica*, *F. a. grabae* and *F. a. naumanni* with the archaeological material from Dollsteinhola and Måsøy. All p-values below 0.05 are regarded as statistically significant. For the full ANOVA results and details of normality testing see supplementary file (**S3 Appendix**).

A		Coracoid ANOVA results					
		Dollsteinhola			Måsøy		
		Lm	Bb	BF	Lm	Bb	BF
<i>F. a. grabae</i>		0.997		0.092	0.374	1	0.820
<i>F. a. arctica</i>		0.008		0.774	1	0.981	0.851
<i>F. a. naumanni</i>		<.001		0.017	<.001	0.088	<.001
Dollsteinhola					0.023		0.297

B		Humerus ANOVA results									
		Dollsteinhola					Måsøy				
		GL	Bp	SC	Bd	KB	GL	Bp	SC	Bd	KB
<i>F. a. grabae</i>		0.858	0.522	0.413	0.612	0.788		0.233	0.329	0.233	0.111
<i>F. a. arctica</i>		0.018	0.009	0.734	0.994	0.993		0.994	0.594	0.994	0.642
<i>F. a. naumanni</i>		<.001	<.001	0.058	<.001	<.001		<.001	0.641	<.001	0.015
Dollsteinhola								0.955	0.971	0.955	0.544

C		Ulna ANOVA results											
		Dollsteinhola						Måsøy					
		GL	Dip	Bp	TP	SC	Did	GL	Dip	Bp	TP	SC	Did
<i>F. a. grabae</i>		0.307	0.004	0.706	<.001	0.064	0.838	0.849	0.055	0.130	0.012	0.335	0.984
<i>F. a. arctica</i>		0.070	0.744	0.951	0.988	1	0.627	0.278	0.995	0.880	0.609	0.508	0.816
<i>F. a. naumanni</i>		<.001	<.001	<.001	<.001	0.005	<.001	<.001	0.002	<.001	0.005	0.072	<.001
Dollsteinhola								<.001	0.528	0.529	0.401	0.649	0.141

D		Carpometacarpus ANOVA results							
		Dollsteinhola				Måsøy			
		GL	Bp	Did	HS	GL	Bp	Did	HS
<i>F. a. grabae</i>		0.035	0.390	0.279	0.016	0.762	0.940	0.646	0.848
<i>F. a. arctica</i>		<.001	1	0.040	0.076	0.172	0.618	0.365	1
<i>F. a. naumanni</i>		<.001	<.001	0.174	<.001	<.001	0.002	0.027	0.037
Dollsteinhola						<.001	0.518	0.884	0.126

E		Femur ANOVA results											
		Dollsteinhola						Måsøy					
		GL	Bp	Dp	SC	Bd	Dd	GL	Bp	Dp	SC	Bd	Dd
<i>F. a. grabae</i>		0.756	0.468	0.282	0.574	0.573	0.218	0.254	0.309	0.996	0.041	0.236	0.017
<i>F. a. arctica</i>		<.001	0.339	0.007	0.996	0.976	0.575	1	0.699	0.795	0.146	0.998	1
<i>F. a. naumanni</i>		<.001	<.001	<.001	0.086	0.008	<.001	0.005	<.001	<.001	0.827	0.079	0.030
Dollsteinhola								0.007	0.996	0.479	0.564	0.958	0.744

F		Tibiotarsus ANOVA results											
		Dollsteinhola						Måsøy					
		La	Dip	Bp	SC	Bd	Dd	La	Dip	Bp	SC	Bd	Dd
<i>F. a. grabae</i>		0.269	0.005	0.815	0.862	0.240	0.755	1	0.069	0.465	0.118	0.819	0.669
<i>F. a. arctica</i>		0.330	1	0.996	0.991	0.032	0.777	0.998	0.745	0.684	0.089	0.655	0.993
<i>F. a. naumanni</i>		<.001	<.001	<.001	0.038	0.265	0.017	0.014	0.006	0.002	0.933	0.145	0.253
Dollsteinhola								0.726	0.777	0.921	0.317	0.942	0.995

G		Tarsometatarsus ANOVA results							
		Dollsteinhola				Måsøy			
		GL	Bp	SC	Bd	GL	Bp	SC	Bd
<i>F. a. grabae</i>		0.054	1	0.993	0.995	0.810	0.782	0.970	0.767
<i>F. a. arctica</i>		0.431	0.084	1	0.059	0.880	0.914	0.990	0.707
<i>F. a. naumanni</i>		<.001	<.001	0.003	<.001	0.260	0.016	0.371	0.269
Dollsteinhola						0.282	0.141	0.986	0.014

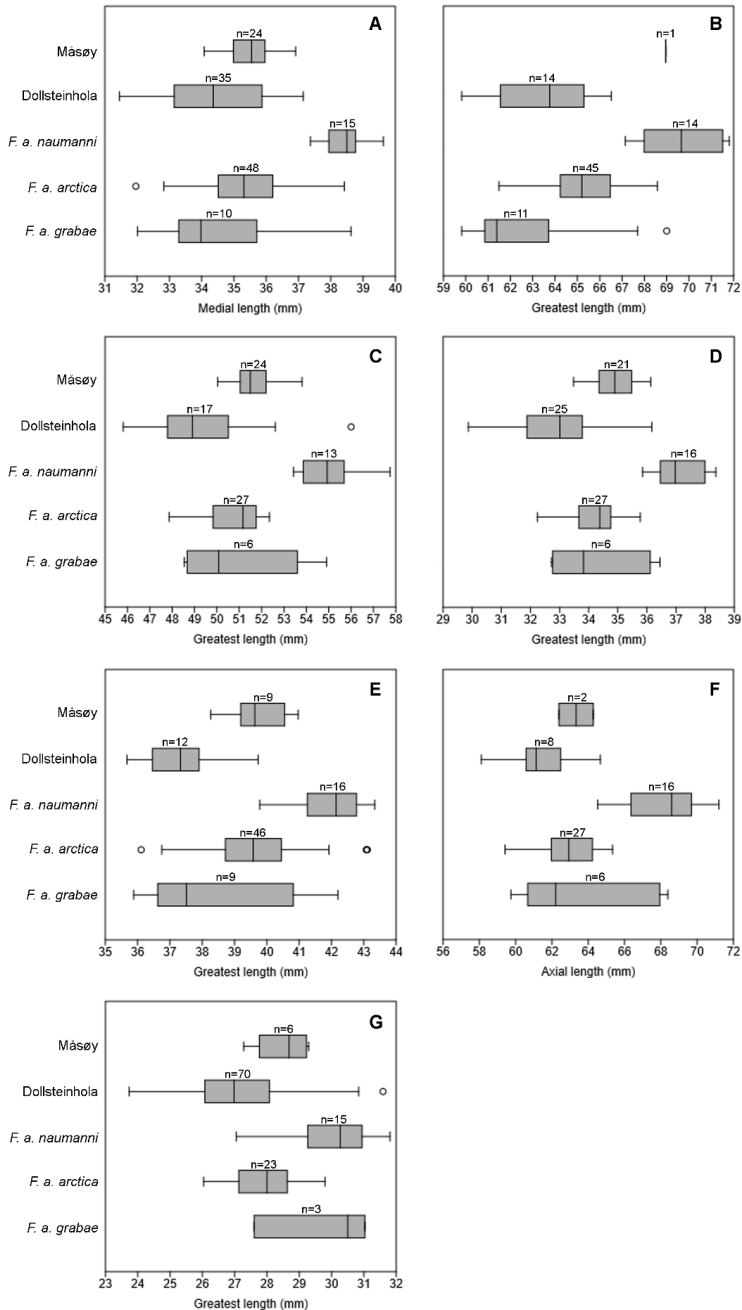


Fig 2. Boxplots of length measurements in modern and archaeological Atlantic Puffins. **A**, medial length of the coracoid. **B**, greatest length of the humerus. **C**, greatest length of the ulna. **D**, greatest length of the carpometacarpus. **E**, greatest length of the femur. **F**, axial

length of the tibiotarsus. **G**, greatest length of the tarsometatarsus. Number of specimens included are represented above each boxplot. Outliers are indicated by circles beyond the standard error.

4. Discussion

4.1 Subspecies

Our results have identified that there are osteological differences between the subspecies of Atlantic Puffin. It is evident that *F. a. naumanni* differs from *F. a. arctica* and *F. a. grabae* (Table 8; Fig. 2); *F. a. naumanni* is larger than all other subspecies. This difference is not just detected in the greatest length but also in the dimensions of the proximal and distal end, suggesting that *F. a. naumanni* on the whole is proportionally larger than the other two subspecies. Despite this, there is a degree of overlap between *F. a. naumanni* and the other subspecies. External measurements have already identified that *F. a. naumanni* are larger than the other two subspecies (Salomonsen, 1944; Gaston & Provencher, 2012). Our data show that the larger size of *F. a. naumanni* is also reflected in the osteological data and that for most bones it is possible to separate *F. a. naumanni* from the other subspecies. The results have shown that greatest length of long bones is the measurement showing the most variation between the subspecies. This appears most pronounced in the upper limb elements (coracoid, humerus, ulna and carpometacarpus) where we see less of an overlap. Our findings would suggest that measurements which exceed the mean of *F. a. naumanni* are highly likely to belong to this subspecies (See Tables 1-7).

According to external measurements of *F. a. grabae* and *F. a. naumanni* these two subspecies should be at opposite ends of the size spectrum. However, some of the proximal dimensions of the ulna, carpometacarpus and tibiotarsus are not significantly different from one another, in addition the greatest length of the tarsometatarsus also shows no difference (Table 8). In this case we believe this is down to a small sample size. The skeletal elements (coracoid, humerus and femur) for which a larger sample of *F. a. grabae* was available show a significant difference to *F. a. naumanni* (Table 8).

There are two specimens of *F. a. grabae* (NHMUK S/1973.66.92 and NHMD 223207) which do not fit with the expected smaller size of the subspecies. Both specimens are old (they were collected in 1946 and 1923 respectively), and it is not clear why they were assigned to subspecies *F. a. grabae*. It is possible they were wrongly assigned to *F. a. grabae*. However, both specimens come from known *F. a. grabae* breeding colonies during the breeding season; NHMUK S/1973.66.92 from Scotland taken in early June and NHMD 223207 from the Faroe Islands taken in August. It is possible that NHMD 223207 represents an early *F. a. arctica* winter migrant (Harris & Wanless, 2011). In addition, the wing length measurement associated with this specimen (173 mm), falls within the upper range for male *F. a. grabae* in Scotland 140 – 174mm (Harris, 1979), but also firmly within the range for *F. a. arctica* (Myrberget, 1963; Petersen, 1976). Alternatively, they may just be exceptionally large *F. a. grabae*, and can add important insight into the potentially high size variation within the subspecies *F. a. grabae*.

There is a high degree of overlap in the size of *F. a. arctica* and *F. a. grabae* (Fig. 2). Only a limited number of specimens of *F. a. grabae* were available to us, and a larger sample size could have revealed a greater difference between the two. However, as mentioned in the introduction, *F. a. grabae* is often not regarded as a valid subspecies (Moen, 1991; Harris & Wanless, 2011; Sangster et al., 2005; Lowther et al., 2020) and considered a part of *F. a. arctica* instead. When the mean values are looked at, the general trend does show a smaller size of *F. a. grabae* compared to *F. a. arctica*. However, there is a large amount of variation in the *F. a. grabae* bones, with some overlapping slightly with *F. a. naumanni*. This could indicate a large variation with a few particularly large individuals (see above). Alternatively, since one of the largest *F. a. grabae* specimens (NHMUK S/1973.66.92) was not measured by SJW, inter-observer variation may have resulted in a slight difference in measurements.

4.2 Archaeological Atlantic Puffin

The results show that the *F. arctica* specimens from Måsøy represent a homogenous population that fits best with *F. a. arctica* (Table 9). This is in line with the archaeological findings from nearby Varangerfjord and Grunnfjord (Olsen, 1967; Lahtiperä, 1979), and indicates that only *F. a. arctica* was present in northern Norway during the Little Ice Age, and there was no southward shift in the range of *F. a. naumanni*.

The results of *F. arctica* from Dollsteinhola indicate a large amount of variation in size, more so than seen in the Måsøy assemblage. Variation in Dollsteinhola ranges from quite large individuals (still within the *F. a. arctica* size range) to some very small individuals (smaller than both *F. a. grabae* and *F. a. arctica*). However, there is no evidence to suggest that *F. a. naumanni* was present at Dollsteinhola; the measurements show no similarity to the larger *F. a. naumanni* (Table 9) thus making it unlikely that they would have ventured, in any great numbers, as far south as Dollsteinhola during the Holocene.

The Dollsteinhola specimens overlap in size with both *F. a. grabae* and smaller *F. a. arctica* specimens, but there are differences in individual elements. The comparison between Dollsteinhola and *F. a. arctica* show significant differences in the coracoid, humerus, carpometacarpus and femur (Table 9). The mean length of the Dollsteinhola specimens (Fig. 2) is consistently smaller than current *F. a. arctica* populations, albeit not statistically significant (Table 9). The geographically closest modern population to Dollsteinhola is located just 20 Km to the north at Runde. Runde is home to the largest Norwegian *F. a. arctica* colony south of the Arctic Circle (Harris & Wanless, 2011) (estimated at 50 – 70,000 breeding pairs in 2014 (Hundeide, 2015)). A direct comparison to 10 specimens of *F. a. arctica* from Runde (Fig. 3) showed that in almost all elements the mean greatest length for the Runde population was larger than the Dollsteinhola population. However, the comparison also showed that in many of the other measurements Dollsteinhola was on average slightly larger than Runde *F. a. arctica*. In essence, the Dollsteinhola population displayed shorter, yet sturdier skeletal elements than modern populations of *F. a. arctica*.

The Dollsteinhola assemblage spans ca. 3000 years from 6600 to 3600 BP (Lie, 1989) and covers both a warmer and colder period. Sea-surface temperatures in the Norwegian Sea were at maximum warmth around 9700–6700 BP, approximately 3–5°C warmer than present day (Bircs & Koç, 2002). After this period of maximum sea-surface temperature came a period of gradual cooling at a rate of 1°C every 1000 years until 3500 years BP (Bircs & Koç, 2002). Such shifts in climatic conditions likely affected Atlantic Puffin prey resources. Successful breeding seasons for Atlantic Puffin require a steady supply of small shoaling fish within a few tens of kilometres of the colony (Harris & Wanless, 2011). The prey of Atlantic Puffin is heavily dependent upon the availability of zooplankton, and with just slight changes to sea-surface temperatures these communities are heavily influenced (Corten, 2001; Durant et al., 2006; Hundeide, 2015). The main prey of the more southern Norwegian Atlantic Puffin are the Lesser Sandeel (*Ammodytes marinus*), Atlantic Herring (*Clupea harengus*), Saithe (*Pollachius virens*) and Haddock (*Melanogrammus aeglefinus*) (Barrett et al., 1987; Lowther et al., 2020). Warmer sea temperatures have been linked with negative impacts on Sandeel recruitment (Arnott & Ruxton, 2002) and may have caused earlier blooms of phytoplankton, meaning important prey such as the Atlantic Herring spawn earlier. Through these indirect effects of temperature on Atlantic Puffin food resources, the fluctuating climate during the middle Holocene likely affected Atlantic Puffin breeding success, population size, and distributional range. Dollsteinhola is located close to the borders of the modern breeding ranges of both *F. a. arctica* and *F. a. grabae*. We consider it therefore likely that given the climatic oscillations and their concomitant effects on marine prey, breeding ranges of the two subspecies shifted north or south accordingly. The smaller specimens in Dollsteinhola are then likely to represent *F. a. grabae* specimens (or a smaller clinal population, if *F. a. grabae* is disregarded as a subspecies), while the larger ones would represent *F. a. arctica*. Puffins rarely come to land in the winter (Fayet et al., 2017; Anker-Nilssen, 2018), but winter wreck events could result in the blending of both subspecies across the seasons. We have recorded juvenile Atlantic Puffin specimens from Dollsteinhola, suggesting that a breeding colony was present. If *F. a. grabae* was indeed breeding at Dollsteinhola, this would

indicate a 145 Km shift north from the subspecies current breeding range (See Fig. 1), as the closest modern population of *F. a. grabae* is at Utvær.

However, shifting ranges of *F. a. arctica* and *F. a. grabae* do not account for the differences in proportions that we observed in the Dollsteinhola material. The Dollsteinhola population displayed slightly shorter, sturdier skeletal elements than modern populations of *F. a. arctica*. These differences are most pronounced in the carpometacarpus. For wing propelled divers such as the Atlantic Puffin shorter wing bones (and potentially smaller flight feathers) reduce drag when diving and moving through the water (Pennycuik, 1987; Livezy, 1988; 1989; Louw, 1992). This may have made the Dollsteinhola population better divers than their modern counterparts. Alternatively, shorter carpometacarpi may be linked to changes in flight; a number of studies have found the carpometacarpus to be particularly important as it is the attachment site for the primary flight feathers (Nudds, 2007; Simons, 2010; Wang et al., 2011). A shorter carpometacarpus might have led to a somewhat reduced flight efficiency. Whether this difference in proportions points towards functional difference in middle Holocene Atlantic Puffins or signal an influx of a smaller yet sturdier morphotype is unclear. Understanding the full scale of Atlantic Puffin morphometrics from a wider geographical and temporal scale would be helpful in exploring these specimens further.

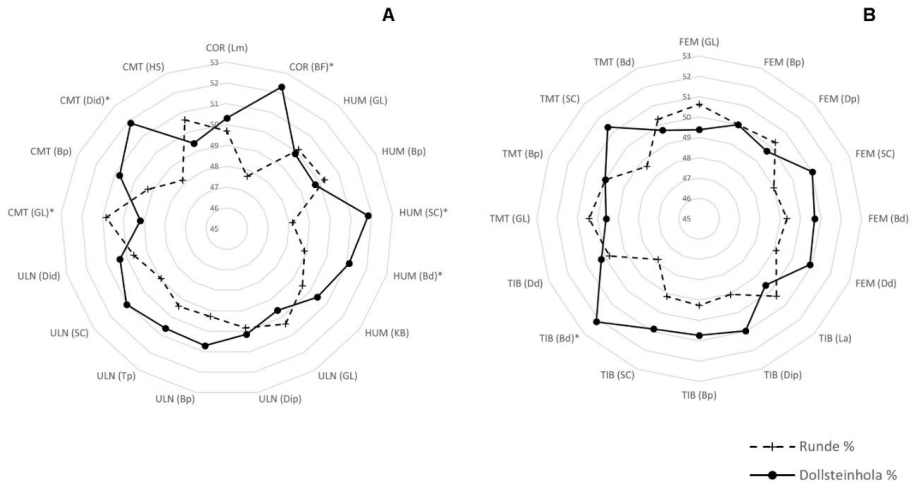


Fig 3. A comparison of the mean values for Modern *F. a. arctica* from Runde and the *F. arctica* specimens from Dollsteinhola, taken as percentages to highlight which measurements are larger for the two groups. **A** represents measurements of the upper limbs, **B** represents measurements of the lower limbs. Measurements with * are statistically significant. Abbreviations of the bone elements are as follows; COR = coracoid, HUM = humerus, ULN = ulna, CMT = carpometacarpus, FEM = femur, TIB = tibiotarsus, TMT = tarsometatarsus. The mean values can be found in the supplementary material (**S4 Table**).

5. Conclusion

Our research has provided the first osteological study of modern *Fratercula arctica*. Our results show that the modern subspecies *F. a. naumanni* is generally recognisable osteologically from the two other subspecies by its larger size and different proportions. This supports the general view that *Fratercula arctica* is a polytypic species, whereby *F. a. naumanni* and *F. a. arctica* are subspecies. However, the subspecies *F. a. grabae* is less distinguishable from *F. a. arctica* and it might not represent a separate subspecies, but rather a north-south clinal variation. These results reflect ornithological observations. The archaeological specimens from Måsøy showed they were one population likely to be *F. a. arctica*, displaying no recognisable difference in size to modern populations, and suggesting that for this subspecies during the Little Ice Age

there appeared to be no changes to the skeleton. The specimens from Dollsteinhola encompass the modern size range of both *F. a. arctica* and *F. a. grabae* but display slightly different proportions. It seems most likely that the Dollsteinhola assemblage represents a dynamic response to the climatic oscillations that occurred during the mid-Holocene whereby, *F. a. arctica* and *F. a. grabae* shifted north or south depending on the climatic conditions. This does not, however, explain the shorter and stockier proportions of the Dollsteinhola material. Understanding the full scale of Atlantic Puffin morphometrics from a wider geographical and temporal scale would be helpful in exploring these specimens further.

6. Competing interests

The authors have no competing interests to declare.

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Supporting information

S1 Text. Measurements. Description of all measurements featured within this paper.

S2 Appendix. Modern subspecies ANOVA results. Details of the one-way ANOVA and Tukey's pairwise results for the modern subspecies.

S3 Appendix. Modern subspecies and archaeological specimens ANOVA results. Details of the one-way ANOVA and Tukey's pairwise results for the modern subspecies in comparison to the archaeological specimens from Dollsteinhola and Måsøy.

S4 Table. Dollsteinhola and Runde mean values. Mean values of Dollsteinhola measurements and modern Runde *F. a. arctica* measurements.

Appendix

Appendix 1. List of modern specimens used for comparison. *Fratercula arctica arctica*; B 462, B 465, B 466, B 467, B 468, B 469, B 470, B 471, B 1851, B 1852, B 2763, BM 5210, BM 7114, BM 7115, BM 10577, BM 10578, NHMD 223202, NHMD 223209, NHMD 223210, NHMD 223215, NHMD 223216, NHMD 223217, NHMD 223219, NHMD 223220, NHMD 223222, NHMD 223223, NHMD 223224, NHMD 223225, NHMD 223226, NHMD 223227, NHMD 223228, NHMD 223229, NHMD 223230, NHMD 223231, NHMD 223232, NHMD 223233, NHMD 223236, NHMD 223237, NHMD 223238, NHMD 223239, NHMD 223244, NHMD 223245, NHMD 223253, NHMD 223256, NHMD 223257, NHMD 223260, NHMD 223262, NHMD 223264.

Fratercula arctica grabae from diagnostic external characteristics during preparation; CN 248, NHMD 223207, NHMUK S/1973.66.92, MHNG 856.011, MHNG 856.012. *Fratercula arctica grabae* from location during breeding season; B 3052, NHMD 223250, NHMD 223251, NHMD 223252, NHMD 223258, NHMD 223263 (All recorded as *F. a. arctica* on the museum labels. However, their location in

F. a. grabae breeding colonies during the breeding season is why we have reclassified them for this paper).

Fratercula arctica naumanni from diagnostic external characteristics during preparation; B 981, B 982, B 1829, BM 10334, BM 10335, BM 10336, BM 10339, BM 10342, BM 10343, BM 10344, BM 10345, BM 10346, BM 10347, BM 10348, NHMUK 1931.8.2.17. *Fratercula arctica naumanni* from location during breeding season; BM 10341 (recorded as *F. a. arctica* on the museum label. However, its location in *F. a. naumanni* breeding colonies during the breeding season is why we have reclassified it for this paper).

B and BM numbers relate to the University Museum of Bergen. NHMD and CN numbers relate to the Natural History Museum of Denmark. MHNG numbers are from the Natural History Museum of Geneva. NHMUK numbers are related to the Natural History Museum at Tring.

Supplementary Material: S1 Text, Measurements.

S1 Text. Measurements. Description of all measurements featured within the paper.

All measurements were taken following Von den Driesch (1976) or Kraft (1972). You will find the diagrams of the measurements on the pages indicated next to the description.

Coracoid

Medial length (**Lm**) – Similar to the greatest length measurement, however, measured from the processus acrocoracoideus to the angulus medialis. Diagram of the measurement can be found in Von den Driesch (1976, pp.113)

Basal breadth (**Bb**) – The distance from the processus lateralis to the angulus medialis. Diagram of the measurement can be found in Von den Driesch (1976, pp.113)

Breadth of the facies articularis sternalis (**BF**) – Measurement from the angulus medialis to the end of the facies articularis sternalis. Diagram of the measurement can be found in Von den Driesch (1976, pp.113)

Humerus

Greatest length (**GL**) – Measurement from the caput articulare humeri to the processus felxoriosus. Diagram of the measurement can be found in Von den Driesch (1976, pp.116)

Breadth of the proximal (**Bp**) – Breadth of the proximal end from the tuberculum laterale to the tuberculum mediale. Diagram of the measurement can be found in Von den Driesch (1976, pp.116)

Smallest breadth of the corpus (**SC**) – Measurement of the smallest breadth of the shaft, often around mid-shaft. Diagram of the measurement can be found in Von den Driesch (1976, pp.116)

Breadth of the distal end (**Bd**) – Measurement taken from the epicondylus medialis to the epicondylus lateralis. Diagram of the measurement can be found in Von den Driesch (1976, pp.116)

Smallest depth of the distal shaft (**KB**) – Measurement taken of the distal shaft above the condylus dorsalis. Diagram of the measurement can be found in Kraft (1972, pp.30)

Ulna

Greatest length (**GL**) – Measurement taken from the top of the olecranon to the conylus ventralis ulnae, giving the full length of the ulna. Diagram of the measurement can be found in Von den Driesch (1976, pp.118)

Diagonal of the proximal end (**Dip**) – Measurement of the greatest diagonal of the proximal end from the caudal border of the olecranon to the cranial border of the facies articularis. Diagram of the measurement can be found in Von den Driesch (1976, pp.118)

Breadth of the proximal end (**Bp**) – Measurement from the facies articularis medialis to the facies articularis lateralis. Diagram of the measurement can be found in Von den Driesch (1976, pp.118)

Depth of the proximal end (**Tp**) – Measurement from the top of the olecranon to the bottom of the cotyla dorsalis. Diagram of the measurement can be found in Kraft (1972, pp.32)

Smallest breadth of the corpus (**SC**) – Measurement of the smallest breadth of the shaft, often around mid-shaft. Diagram of the measurement can be found in Von den Driesch (1976, pp.118)

Diagonal of the distal end (**Did**) – Diagonal measurement from the tuberculum carpale to the condylus dorsalis ulnae. Diagram of the measurement can be found in Von den Driesch (1976, pp.118)

Carpometacarpus

Greatest length (**GL**) – Measurement taken from the trochlea carpalis to the most distal point, the facies articularis digitalis major. Diagram of the measurement can be found in Von den Driesch (1976, pp.120)

Breadth of the proximal end (**Bp**) – breadth of the proximal extremity, measurement taken from the tip of the processus extensorius to the edge of the facies articularis

ulnocarpalis. Diagram of the measurement can be found in Von den Driesch (1976, pp.120)

Diagonal of the distal end (**Did**) – This measurement is of the distal articular surface only. Diagram of the measurement can be found in Von den Driesch (1976, pp.120)

Height of the symphysis (**HS**) – Measurement taken from the bottom of the spatium intermetacarpale to the facies articularis digitalis III. Diagram of the measurement can be found in Kraft (1972, pp.32)

Femur

Greatest length (**GL**) – Measurement taken from the top of the trochanter femoris to the furthest distal point, the condylus lateralis. Diagram of the measurement can be found in Von den Driesch (1976, pp.125)

Breadth of the proximal end (**Bp**) – Measurement taken from the caput femoris to the most lateral point of the trochanter major. Diagram of the measurement can be found in Von den Driesch (1976, pp.125)

Depth of the proximal end (**Dp**) – Measurement is taken from the fixed location of the cranial points on the caput femoris and on the trochanter major. Diagram of the measurement can be found in Von den Driesch (1976, pp.125)

Smallest breadth of the corpus (**SC**) – Measurement of the smallest breadth of the shaft, often around mid-shaft. Diagram of the measurement can be found in Von den Driesch (1976, pp.125)

Breadth of the distal end (**Bd**) – Measurement taken of the lateral and medial aspect of the condylus medialis and the condylus lateralis. Diagram of the measurement can be found in Von den Driesch (1976, pp.125)

Depth of the distal end (**Dd**) – Measurement taken from the fixed location of the caudal points of the condyli medialis and lateralis. Diagram of the measurement can be found in Von den Driesch (1976, pp.125)

Tibiotarsus

Axial length (**La**) – Measurement taken from the tuberculum centrale to the distal border of the trochlea tibiotarsi. Diagram of the measurement can be found in Von den Driesch (1976, pp.126–127)

Diagonal of the proximal end (**Dip**) – Measurement taken from the condylus medialis femoralis to the crista lateralis. Diagram of the measurement can be found in Von den Driesch (1976, pp.126–127)

Breadth of the proximal end (**Bp**) – Measurement taken from the edge of the facies articularis lateralis (where the caput fibulae is found) to the facies articularis medialis. Diagram of the measurement can be found in Kraft (1972, pp.34)

Smallest breadth of the corpus (**SC**) – Measurement of the smallest breadth of the shaft, often around mid-shaft. Diagram of the measurement can be found in Von den Driesch (1976, pp.126–127)

Breadth of the distal end (**Bd**) – Measurement taken of the lateral and medial aspect of the condylus medialis and the condylus lateralis. Diagram of the measurement can be found in Von den Driesch (1976, pp.126–127)

Depth of the distal end (**Dd**) – Measurement taken from the fixed points on the distal condyles taken from the caudal aspect. Diagram of the measurement can be found in Von den Driesch (1976, pp.126–127)

Tarsometatarsus

Greatest length (**GL**) – Measurement taken from the condylus interarticularis to the trochlea metatarsi III. Diagram of the measurement can be found in Von den Driesch (1976, pp.129)

Breadth of the proximal (**Bp**) – Measurement of the maximum breadth of the proximal end, taken from the facies articularis medialis to the facies articularis lateralis. Diagram of the measurement can be found in Von den Driesch (1976, pp.129)

Smallest breadth of the corpus (**SC**) – Measurement of the smallest breadth of the shaft, often around mid-shaft. Diagram of the measurement can be found in Von den Driesch (1976, pp.129)

Breadth of the distal end (**Bd**) – Measurement of the maximum breadth of the distal end from the trochlea metatarsi II to the trochlea metatarsi IV. Diagram of the measurement can be found in Von den Driesch (1976, pp.129)

Supplementary Material: S2 Appendix, Modern subspecies ANOVA results.

S2 Appendix. Modern subspecies ANOVA results. Details of the one-way ANOVA and Tukey's pairwise results for the modern subspecies.

Coracoid

Coracoid Lm shows the groups are normally distributed (Shapiro-Wilk $p = 0.497$). The Levene's test for homogeneity of variance reports a p value of 0.02, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 1 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 4). The coracoid Bb groups are also normally distributed (Shapiro-Wilk $p = 0.9818$). Levene's test for homogeneity reports a p value of 0.09 for the equality of variances, so there is no significant difference. This means the assumptions of the ANOVA are safely met. Table 2 presents the results of the one-way ANOVA in standard form and Table 5 shows the Tukey's pairwise results. The coracoid BF measurement shows the groups are normally distributed (Shapiro-wilk $p = 0.198$). Levene's test for homogeneity reports a p value of 0.547 for the equality of variances, so there is no significant difference. The sample sizes do differ. However, the assumptions of the ANOVA are safely met. Table 3 presents the results of the one-way ANOVA in standard form and Table 6 shows the Tukey's pairwise results.

Table 1, One-way ANOVA results for the medial length (Lm) of the coracoid. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	126.461	2	63.2305	34.72	3.344E-11
Within groups	127.471	70	1.82102		
Welch F test		21.47		73.08	2.624E-10

Table 2, One-way ANOVA results for the basal breadth (Bb) of the coracoid. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	16.1684	2	8.08421	10.98	7.022E-05
Within groups	52.2935	71	0.736528		

Table 3, One-way ANOVA results for the basal articular surface (BF) of the coracoid. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	15.2398	2	7.61989	18.35	3.76E-07
Within groups	29.4782	71	0.415186		

Table 4, Coracoid Lm ANOVA – Tukey’s pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.185	<.001
<i>F. a. arctica</i>	2.51	-	<.001
<i>F. a. naumanni</i>	9.94	10.77	-

Table 5, Coracoid Bb ANOVA – Tukey’s pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.721	<.001
<i>F. a. arctica</i>	1.092	-	<.001
<i>F. a. naumanni</i>	5.358	6.166	-

Table 6, Coracoid BF ANOVA – Tukey’s pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.071	<.001
<i>F. a. arctica</i>	3.171	-	<.001
<i>F. a. naumanni</i>	7.839	7.128	-

Humerus

The humerus GL shows the groups are normally distributed (Shapiro-wilk p 0.172). The Levene’s test for homogeneity of variance reports a p value of 0.05, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch’s F test (in the case of unequal variances) was consulted and included in Table 7 along with the one-way ANOVA results, as the p value of the Welch’s test was significant ($p < .001$) it was possible to continue to Tukey’s pairwise (Table 12). The Humerus Bp is normally distributed (Shapiro-Wilk p value of 0.853). Levene’s test for homogeneity reports a p value of 0.330 for the equality of variances, so there is no significant difference. This means the assumptions of the ANOVA are safely met. Table 8 presents the results of the one-way ANOVA in standard form and Table 13 shows the Tukey’s pairwise results. The humerus SC normal distribution was distorted by an outlier (a single large SC measure on *F. a. grabae* specimen) giving a Shapiro-wilk p value of 0.002. Despite this the graphs show that the rest of the data has a normal distribution. The Levene’s test for homogeneity reports a p value of 0.415 for the equality of variances, so there is no significant difference. Despite the outlier all other

assumptions of the ANOVA are met, and we therefore continued to run the ANOVA, the results of which are presented in Table 9 and Tukey's pairwise results in Table 14. The Humerus Bd is normally distributed (Shapiro-Wilk p value of 0.926). Levene's test for homogeneity reports a p value of 0.07 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 10 presents the results of the one-way ANOVA in standard form and Table 15 shows the Tukey's pairwise results. The Humerus KB is normally distributed (Shapiro-Wilk p value of 0.272). Levene's test for homogeneity reports a p value of $<.001$, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 11 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p<.001$) it was possible to continue to Tukey's pairwise (Table 16).

Table 7, One-way ANOVA results for the greatest length (GL) of the humerus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i>(same)
Between groups	327.192	2	163.596	42.71	1.099E-12
Within groups	256.618	67	3.83011		
Welch <i>F</i> test		19.38		41.79	9.389E-08

Table 8, One-way ANOVA results for the breadth of the proximal end (Bp) of the humerus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i>(same)
Between groups	22.1475	2	11.0737	25.49	4.259E-09
Within groups	31.2762	72	0.434392		

Table 9, One-way ANOVA results for the smallest breadth of the corpus (SC) of the humerus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i>(same)
Between groups	0.921719	2	0.460859	12.38	2.5E-05
Within groups	2.60669	70	0.0372384		

Table 10, One-way ANOVA results for the breadth of the distal end (Bd) of the humerus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i>(same)
Between groups	2.88361	2	1.4418	16.2	1.769E-06
Within groups	6.05387	68	0.0890275		

Table 11, One-way ANOVA results for the smallest depth of the distal shaft (KB) of the humerus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	1.5607	2	0.780352	13.26	1.369E-05
Within groups	4.00086	68	0.0588362		
Welch F test		20.08		14.31	0.0001372

Table 12, Humerus GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	<.001	<.001
<i>F. a. arctica</i>	5.292	-	<.001
<i>F. a. naumanni</i>	12.41	10.53	-

Table 13, Humerus Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	<.001	<.001
<i>F. a. arctica</i>	5.672	-	<.001
<i>F. a. naumanni</i>	9.951	6.933	-

Table 14, Humerus SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.554	<.001
<i>F. a. arctica</i>	1.472	-	<.001
<i>F. a. naumanni</i>	5.987	6.378	-

Table 15, Humerus Bd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.133	<.001
<i>F. a. arctica</i>	2.755	-	<.001
<i>F. a. naumanni</i>	7.381	6.722	-

Table 16, Humerus KB ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.292	<.001
<i>F. a. arctica</i>	2.138	-	<.001
<i>F. a. naumanni</i>	6.522	6.281	-

Ulna

The ulna GL shows the groups are normally distributed (Shapiro-wilk p 0.759). The Levene's test for homogeneity of variance reports a p value of 0.008, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 17 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 23). The ulna Dip is normally distributed (Shapiro-Wilk p value of 0.991). Levene's test for

homogeneity reports a p value of 0.168 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 18 presents the results of the one-way ANOVA in standard form and Table 24 shows the Tukey's pairwise results. The ulna Bp is normally distributed (Shapiro-Wilk p value of 0.220). Levene's test for homogeneity reports a p value of 0.266 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 19 presents the results of the one-way ANOVA in standard form and Table 25 shows the Tukey's pairwise results. The ulna Tp measurement shows a relatively normal distribution when glancing at the residual graphs, however, Shapiro-wilks test for normality gives a p value of 0.05. As the graphs show the data has a fairly normal distribution we continue to use the one-way ANOVA and do not move to a non-parametric test. The Levene's test for homogeneity reports a p value of $<.001$ for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 20 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p=<.001$) it was possible to continue to Tukey's pairwise (Table 26). The ulna SC measurement shows a relatively normal distribution when glancing at the residual graphs, however, two large measurements for the subspecies *F. a. grabae* have led to a Shapiro-wilks p value of 0.003. As the graphs show the data has a fairly normal distribution we continue to use the one-way ANOVA and do not move to a non-parametric test. The Levene's test for homogeneity reports a p value of $<.001$ for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 21 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p=<.001$) it was possible to continue to Tukey's pairwise (Table 27). The ulna Did is normally distributed (Shapiro-Wilk p value of 0.986). Levene's test for homogeneity reports a p value of 0.04 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was

consulted and included in Table 22 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 28).

Table 17, One-way ANOVA results for the greatest length (GL) of the ulna. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	167.146	2	83.573	40.81	1.159E-10
Within groups	88.0552	43	2.0478		
Welch F test		11.44		50.44	2.112E-06

Table 18, One-way ANOVA results for the diagonal of the proximal end (Dip) of the ulna. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	4.59556	2	2.29778	10.67	0.0001786
Within groups	9.04174	42	0.215279		

Table 19, One-way ANOVA results for the breadth of the proximal end (Bp) of the ulna. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.27703	2	1.63851	19.13	1.243E-06
Within groups	3.59809	42	0.0856688		

Table 20, One-way ANOVA results for the depth of the proximal end (Tp) of the ulna. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.34374	2	1.67187	14.2	1.943E-05
Within groups	4.94386	42	0.117711		
Welch F test		11.5		22.01	0.0001172

Table 21, One-way ANOVA results for the smallest breadth of the corpus (SC) of the ulna. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	1.04119	2	0.520596	8.69	0.0006287
Within groups	2.75565	46	0.0599054		
Welch F test		11.26		15.38	0.0006029

Table 22, One-way ANOVA results for the diagonal of the distal end (Did) of the ulna. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	4.32572	2	2.16286	29.54	5.614E-09
Within groups	3.36853	46	0.0732289		
Welch F test		13.89		41.84	1.321E-06

Table 23, Ulna GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.969	<.001
<i>F. a. arctica</i>	0.338	-	<.001
<i>F. a. naumanni</i>	8.221	12.47	-

Table 24, Ulna Dip ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.014	0.970
<i>F. a. arctica</i>	4.156	-	<.001
<i>F. a. naumanni</i>	0.330	5.882	-

Table 25, Ulna Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.128	<.001
<i>F. a. arctica</i>	2.807	-	<.001
<i>F. a. naumanni</i>	7.658	7.385	-

Table 26, Ulna Tp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	<.001	0.904
<i>F. a. arctica</i>	5.512	-	<.001
<i>F. a. naumanni</i>	0.605	6.299	-

Table 27, Ulna SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.026	1
<i>F. a. arctica</i>	3.779	-	<.001
<i>F. a. naumanni</i>	0.035	5.353	-

Table 28, Ulna Did ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.991	<.001
<i>F. a. arctica</i>	0.182	-	<.001
<i>F. a. naumanni</i>	6.775	10.54	-

Carpometacarpus

The carpometacarpus GL shows the groups are normally distributed (Shapiro-wilk p 0.844). The Levene's test for homogeneity of variance reports a p value of 0.04, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 29 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 33). The carpometacarpus Bp is normally distributed (Shapiro-Wilk p value of 0.681). Levene's test for homogeneity reports a p value of 0.592 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 30 presents the results of the one-way ANOVA in standard form and Table 34 shows the Tukey's pairwise results. The carpometacarpus Did is normally distributed (Shapiro-Wilk p value of 0.973). Levene's test for homogeneity reports a p value of 0.194 for the equality of variances, so there is no

significant difference. This means all the assumptions of the ANOVA are safely met. Table 31 presents the results of the one-way ANOVA in standard form and Table 35 shows the Tukey's pairwise results. The carpometacarpus HS is normally distributed (Shapiro-wilk p value of 0.712). The Levene's test for homogeneity of variance reports a p value of $<.001$, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 32 along with the one-way ANOVA results, as the p value of the Welch's test was significant (0.009) it was possible to continue to Tukey's pairwise (Table 36).

Table 29, One-way ANOVA results for the greatest length (GL) of the carpometacarpus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i>(same)
Between groups	94.0161	2	47.008	49.39	3.53E-12
Within groups	43.7856	46	0.951861		
Welch <i>F</i> test		12.35		60.31	4.239E-07

Table 30, One-way ANOVA results for the breadth of the proximal end (Bp) of the carpometacarpus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i>(same)
Between groups	3.89637	2	1.94818	12.54	4.5E-05
Within groups	7.14644	46	0.155357		

Table 31, One-way ANOVA results for the diagonal of the distal end (Did) of the carpometacarpus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i>(same)
Between groups	2.78986	2	1.39493	16.01	5.275E-06
Within groups	4.00744	46	0.0871182		

Table 32, One-way ANOVA results for the height of the symphysis (HS) of the carpometacarpus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i>(same)
Between groups	0.899687	2	0.449844	5.269	0.008704
Within groups	3.9275	46	0.0853804		
Welch <i>F</i> test		11.85		7.105	0.009374

Table 33, Carpometacarpus GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.963	<.001
<i>F. a. arctica</i>	0.370	-	<.001
<i>F. a. naumanni</i>	8.656	13.66	-

Table 34, Carpometacarpus Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.258	0.184
<i>F. a. arctica</i>	2.257	-	<.001
<i>F. a. naumanni</i>	2.531	7.069	-

Table 35, Carpometacarpus Did ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.961	<.001
<i>F. a. arctica</i>	0.379	-	<.001
<i>F. a. naumanni</i>	5.38	7.62	-

Table 36, Carpometacarpus HS ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.218	0.893
<i>F. a. arctica</i>	2.399	-	0.009
<i>F. a. naumanni</i>	0.640	4.403	-

Femur

The femur GL shows the groups are normally distributed (Shapiro-wilk p 0.160). The Levene's test for homogeneity of variance reports a p value of 0.08 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 37 presents the results of the one-way ANOVA in standard form and Table 43 shows the Tukey's pairwise results. The femur Bp shows the groups are normally distributed (Shapiro-wilk p 0.315). The Levene's test for homogeneity of variance reports a p value of 0.629 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 38 presents the results of the one-way ANOVA in standard form and Table 44 shows the Tukey's pairwise results. The femur Dp shows the groups are normally distributed (Shapiro-wilk p value of 0.330). The Levene's test for homogeneity of variance reports a p value of 0.508 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 39 presents the results of the one-way ANOVA in standard form and Table 45 shows the Tukey's pairwise results. The femur SC shows the groups are normally distributed (Shapiro-wilk p value of 0.321). The Levene's test for homogeneity of variance reports a p value of 0.507 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 40 presents the results of the one-way ANOVA in standard form and Table 46 shows the Tukey's pairwise

results. The femur Bd shows the groups are normally distributed (Shapiro-wilk p value of 0.799). The Levene's test for homogeneity of variance reports a p value of 0.578 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 41 presents the results of the one-way ANOVA in standard form and Table 47 shows the Tukey's pairwise results. The femur Dd is normally distributed (Shapiro-Wilk p value of 0.649). Levene's test for homogeneity reports a p value of 0.005 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 42 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 48).

Table 37, One-way ANOVA results for the greatest length (GL) of the femur. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	91.3539	2	45.677	18.11	4.966E-07
Within groups	171.545	68	2.52273		

Table 38, One-way ANOVA results for the breadth of the proximal end (Bp) of the femur. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	6.1971	2	3.09855	18.3	4.385E-07
Within groups	11.5153	68	0.169343		

Table 39, One-way ANOVA results for the depth of the proximal end (Dp) of the femur. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	2.04558	2	1.02279	12.21	2.952E-05
Within groups	5.69728	68	0.0837835		

Table 40, One-way ANOVA results for the smallest breadth of the corpus (SC) of the femur. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	0.552391	2	0.276196	9.367	0.0002588
Within groups	1.97564	67	0.0294872		

Table 41, One-way ANOVA results for the breadth of the distal end (Bd) of the femur. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.25207	2	1.62604	11.72	4.232E-05
Within groups	9.43412	68	0.138737		

Table 42, One-way ANOVA results for the depth of the distal end (Dd) of the femur. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	5.05622	2	2.52811	17.11	9.907E-07
Within groups	9.89736	67	0.147722		
Welch F test		16.93		19.29	4.307E-05

Table 43, Femur GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.064	<.001
<i>F. a. arctica</i>	3.239	-	<.001
<i>F. a. naumanni</i>	7.607	7.101	-

Table 44, Femur Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.002	<.001
<i>F. a. arctica</i>	5.02	-	<.001
<i>F. a. naumanni</i>	8.333	5.833	-

Table 45, Femur Dp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.832	<.001
<i>F. a. arctica</i>	0.817	-	<.001
<i>F. a. naumanni</i>	5.169	6.653	-

Table 46, Femur SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.329	<.001
<i>F. a. arctica</i>	2.03	-	<.001
<i>F. a. naumanni</i>	5.325	5.266	-

Table 47, Femur Bd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.073	<.001
<i>F. a. arctica</i>	3.156	-	<.001
<i>F. a. naumanni</i>	6.368	5.356	-

Table 48, Femur Dd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.002	<.001
<i>F. a. arctica</i>	5.034	-	<.001
<i>F. a. naumanni</i>	8.11	5.455	-

Tibiotarsus

The tibiotarsus La shows the groups are normally distributed (Shapiro-wilk p 0.876). The Levene's test for homogeneity of variance reports a p value of 0.002 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 49 along with the one-way ANOVA

results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 55). The tibiotarsus Dip shows the groups are normally distributed (Shapiro-wilk p 0.665). The Levene's test for homogeneity of variance reports a p value of 0.188 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 50 presents the results of the one-way ANOVA in standard form and Table 56 shows the Tukey's pairwise results. The tibiotarsus Bp shows the groups are normally distributed (Shapiro-wilk p value of 0.207). The Levene's test for homogeneity of variance reports a p value of 0.319 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 51 presents the results of the one-way ANOVA in standard form and Table 57 shows the Tukey's pairwise results. The tibiotarsus SC shows the groups are normally distributed (Shapiro-wilk p value of 0.658). The Levene's test for homogeneity of variance reports a p value of 0.406 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 52 presents the results of the one-way ANOVA in standard form and Table 58 shows the Tukey's pairwise results. The tibiotarsus Bd shows the groups are normally distributed (Shapiro-wilk p value of 0.594). The Levene's test for homogeneity of variance reports a p value of 0.986 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 53 presents the results of the one-way ANOVA in standard form and Table 59 shows the Tukey's pairwise results. The tibiotarsus Dd measurement shows a relatively normal distribution when glancing at the residual graphs, however, Shapiro-wilk test for normality gives a p value of $< .001$. As the graphs show the data has a fairly normal distribution we continue to use the one-way ANOVA and do not move to a non-parametric test. One measurement of *F. a. grabae* is especially small and is likely to have caused the abnormality in the data. The Levene's test for homogeneity reports a p value of $< .001$ for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 54 along with the one-way ANOVA results, as the p value of the

Welch's test was significant ($p=0.003$) it was possible to continue to Tukey's pairwise (Table 60).

Table 49, One-way ANOVA results for the axial length (La) of the tibiotarsus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	301.08	2	150.54	36.56	3.133E-10
Within groups	189.417	46	4.11776		
Welch F test		11.68		40.96	5.256E-06

Table 50, One-way ANOVA results for the diagonal of the proximal end (Dip) of the tibiotarsus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	5.11902	2	2.55951	17.96	1.848E-06
Within groups	6.41388	45	0.142531		

Table 51, One-way ANOVA results for the breadth of the proximal end (Bp) of the tibiotarsus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	4.25193	2	2.12597	20.69	5.563E-07
Within groups	4.31503	42	0.102739		

Table 52, One-way ANOVA results for the smallest breadth of the corpus (SC) of the tibiotarsus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	0.852747	2	0.426374	8.222	0.0008852
Within groups	2.38536	46	0.0518557		

Table 53, One-way ANOVA results for the breadth of the distal end (Bd) of the tibiotarsus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.16184	2	1.58092	21.97	2.009E-07
Within groups	3.31033	46	0.0719636		

Table 54, One-way ANOVA results for the depth of the distal end (Dd) of the tibiotarsus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	2.83447	2	1.41724	6.932	0.002337
Within groups	9.40488	46	0.204454		
Welch F test		11.85		10.23	0.002622

Table 55, Tibiotarsus La ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.756	<.001
<i>F. a. arctica</i>	1.011	-	<.001
<i>F. a. naumanni</i>	6.888	11.9	-

Table 56, Tibiotarsus Dip ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.002	0.997
<i>F. a. arctica</i>	5.143	-	<.001
<i>F. a. naumanni</i>	0.097	7.778	-

Table 57, Tibiotarsus Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.644	<.001
<i>F. a. arctica</i>	1.272	-	<.001
<i>F. a. naumanni</i>	6.114	8.505	-

Table 58, Tibiotarsus SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.759	0.009
<i>F. a. arctica</i>	1.004	-	0.002
<i>F. a. naumanni</i>	4.368	5.191	-

Table 59, Tibiotarsus Bd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	1	<.001
<i>F. a. arctica</i>	0.039	-	<.001
<i>F. a. naumanni</i>	5.935	9.061	-

Table 60, Tibiotarsus Dd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.108	0.002
<i>F. a. arctica</i>	2.922	-	0.046
<i>F. a. naumanni</i>	5.042	3.47	-

Tarsometatarsus

The tarsometatarsus GL shows the groups are normally distributed (Shapiro-wilk p 0.277). The Levene's test for homogeneity of variance reports a p value of 0.253 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 61 presents the results of the one-way ANOVA in standard form and Table 65 shows the Tukey's pairwise results. The tarsometatarsus Bp shows the groups are normally distributed (Shapiro-wilk p 0.962). The Levene's test for homogeneity of variance reports a p value of 0.741 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 62 presents the results of the one-way ANOVA in standard form and Table 66 shows the Tukey's pairwise results. The tarsometatarsus SC shows the groups are normally distributed (Shapiro-wilk p value of 0.256). The Levene's test for homogeneity of variance reports a p value of 0.05 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 63 along with the one-way ANOVA results, as the p

value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 67). The tarsometatarsus Bd shows the groups are normally distributed (Shapiro-wilk p value of 0.653). The Levene's test for homogeneity of variance reports a p value of 0.896 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 64 presents the results of the one-way ANOVA in standard form and Table 68 shows the Tukey's pairwise results.

Table 61, One-way ANOVA results for the greatest length (GL) of the tarsometatarsus. Taking into account only modern material

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i> (same)
Between groups	46.1549	2	23.0774	18.06	3.075E-06
Within groups	48.5663	38	1.27806		

Table 62, One-way ANOVA results for the breadth of the proximal end (Bp) of the tarsometatarsus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i> (same)
Between groups	4.41039	2	2.20519	22.17	4.168E-07
Within groups	3.78029	38	0.0994813		

Table 63, One-way ANOVA results for the smallest breadth of the corpus (SC) of the tarsometatarsus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i> (same)
Between groups	0.83093	2	0.415465	6.123	0.005045
Within groups	2.51051	37	0.0678515		
Welch <i>F</i> test		23.55		26.64	8.982E-07

Table 64, One-way ANOVA results for the breadth of the distal end (Bd) of the tarsometatarsus. Taking into account only modern material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i> (same)
Between groups	2.14758	2	1.07379	14.55	2.519E-05
Within groups	2.58299	35	0.0737997		

Table 65, Tarsometatarsus GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.028	0.897
<i>F. a. arctica</i>	3.804	-	<.001
<i>F. a. naumanni</i>	0.630	8.237	-

Table 66, Tarsometatarsus Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.700	0.003
<i>F. a. arctica</i>	1.145	-	<.001
<i>F. a. naumanni</i>	5.059	9.01	-

Table 67, Tarsometatarsus SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.898	0.152
<i>F. a. arctica</i>	0.624	-	0.005
<i>F. a. naumanni</i>	2.693	4.72	-

Table 68, Tarsometatarsus Bd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>
<i>F. a. grabae</i>	-	0.788	0.015
<i>F. a. arctica</i>	0.935	-	<.001
<i>F. a. naumanni</i>	4.177	7.255	-

Supplementary Material: S3 Appendix, Modern subspecies and archaeological specimens ANOVA results.

S3 Appendix. Modern subspecies and Archaeological specimens ANOVA results. Details of the one-way ANOVA and Tukey's pairwise results for the modern subspecies in comparison to the archaeological specimens from Dollsteinhola and Måsøy.

Coracoid

Coracoid Lm shows the groups are normally distributed (Shapiro-wilk $p = 0.409$). The Levene's test for homogeneity of variance reports a p value of $<.001$, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 1 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 4). The coracoid Bb groups are normally distributed (Shapiro-Wilk $p = 0.983$). Levene's test for homogeneity reports a p value of 0.06 for the equality of variances, so there is no significant difference. This means the assumptions of the ANOVA are safely met. Table 2 presents the results of the one-way ANOVA in standard form and Table 5 shows the Tukey's pairwise results. The coracoid BF measurement shows the groups are not normally distributed (Shapiro-wilk $p = <.001$), this is due to a number of outliers, two large measurements in the archaeological material from Dollsteinhola and three outliers in the *F. a. arctica* measurements. Despite this the residual graphs do show a relatively normal distribution and as a result a one-way ANOVA remains appropriate. Levene's test for homogeneity reports a p value of 0.223 for the equality of variances, so there is no significant difference. The sample sizes do differ. However, the assumptions of the ANOVA are met. Table 3 presents the results of the one-way ANOVA in standard form and Table 6 shows the Tukey's pairwise results.

Table 1. One-way ANOVA results for the medial length (Lm) of the coracoid. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	$p(\text{same})$
Between groups	180.716	4	45.1789	25.48	1.647E-15
Within groups	225.159	127	1.77291		
Welch F test		40.56		61.76	1.033E-16

Table 2, One-way ANOVA results for the basal breadth (Bb) of the coracoid. Taking into account modern and archaeological material (Måsøy site only) material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	16.6209	3	5.54031	7.718	0.000151
Within groups	52.4	73	0.717808		

Table 3, One-way ANOVA results for the basal articular surface (BF) of the coracoid. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	17.873	4	4.46826	7.379	2.163E-05
Within groups	79.3231	131	0.60552		

Table 4, Coracoid Lm ANOVA results – Tukey’s Pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.378	<.001	0.997	0.374
<i>F. a. arctica</i>	2.545	-	<.001	0.008	1
<i>F. a. naumanni</i>	10.07	10.91	-	<.001	<.001
<i>Dollsteinhola</i>	0.504	4.794	13.91	-	0.023
<i>Måsøy</i>	2.557	0.311	9.571	4.314	-

Table 5, Coracoid Bb ANOVA results – Tukey’s Pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.862	<.001	-	1
<i>F. a. arctica</i>	1.106	-	<.001	-	0.981
<i>F. a. naumanni</i>	5.427	6.246	-	-	0.088
<i>Dollsteinhola</i>	-	-	-	-	-
<i>Måsøy</i>	0.093	0.543	3.38	-	-

Table 6, Coracoid BF ANOVA results – Tukey’s Pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.346	<.001	0.092	0.820
<i>F. a. arctica</i>	2.626	-	<.001	0.774	0.851
<i>F. a. naumanni</i>	6.491	5.902	-	0.017	<.001
<i>Dollsteinhola</i>	3.565	1.641	4.467	-	0.297
<i>Måsøy</i>	1.519	1.427	6.456	2.756	-

Humerus

The humerus GL shows the groups are normally distributed (Shapiro-wilk p 0.172). The Levene’s test for homogeneity of variance reports a p value of 0.07 for the equality of variances, so there is no significant difference. This means the assumptions of the

ANOVA are safely met. Table 7 presents the results of the one-way ANOVA in standard form and Table 12 shows the Tukey's pairwise results. The Humerus Bp is normally distributed (Shapiro-Wilk p value of 0.852). Levene's test for homogeneity reports a p value of 0.124 for the equality of variances, so there is no significant difference. This means the assumptions of the ANOVA are safely met. Table 8 presents the results of the one-way ANOVA in standard form and Table 13 shows the Tukey's pairwise results. The humerus SC normal distribution was distorted by two outliers, a single large SC measure on *F. a. grabae* specimen and a larger measurement on a specimen from Dollsteinhola, giving a Shapiro-wilk p value of <.001. despite this the graphs show that the rest of the data has a normal distribution. The Levene's test for homogeneity reports a p value of 0.515 for the equality of variances, so there is no significant difference. Despite the outliers all other assumptions of the ANOVA are met and we therefore continued to run the ANOVA, the results of which are presented in Table 9 and Tukey's pairwise results in Table 14. The Humerus Bd is normally distributed (Shapiro-Wilk p value of 0.991). Levene's test for homogeneity reports a p value of 0.281 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 10 presents the results of the one-way ANOVA in standard form and Table 15 shows the Tukey's pairwise results. The Humerus KB is normally distributed (Shapiro-Wilk p value of 0.194). Levene's test for homogeneity reports a p value of <.001, this means that the variances are unequal, which compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 11 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 16).

Table 7, One-way ANOVA results for the greatest length (GL) of the humerus. Taking into account modern and archaeological (Dollsteinhola site only) material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	390.793	3	130.264	33.14	5.029E-14
Within groups	314.433	80	3.93041		

Table 8, One-way ANOVA results for the breadth of the proximal end (Bp) of the humerus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	29.0788	4	7.26969	18.11	2.089E-11
Within groups	43.3594	108	0.401476		

Table 9, One-way ANOVA results for the smallest breadth of the corpus (SC) of the humerus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	0.963491	4	0.240873	5.582	0.0004359
Within groups	4.1854	97	0.0431484		

Table 10, One-way ANOVA results for the breadth of the distal end (Bd) of the humerus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.02765	4	0.756913	8.438	5.644E-06
Within groups	9.86789	110	0.0897081		

Table 11, One-way ANOVA results for the smallest depth of the distal shaft (KB) of the humerus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	1.69422	4	0.423555	8.078	9.392E-06
Within groups	5.82034	111	0.0524355		
Welch F test		37.54		7.805	0.000111

Table 12, Humerus GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.002	<.001	0.858	-
<i>F. a. arctica</i>	5.224	-	<.001	0.018	-
<i>F. a. naumanni</i>	12.25	10.39	-	<.001	-
<i>Dollsteinhola</i>	1.121	4.266	11.87	-	-
<i>Måsøy</i>	-	-	-	-	-

Table 13, Humerus Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	<.001	<.001	0.522	0.003
<i>F. a. arctica</i>	5.9	-	<.001	0.009	0.992
<i>F. a. naumanni</i>	10.35	7.211	-	<.001	0.005
<i>Dollsteinhola</i>	2.216	4.746	10.16	-	0.043
<i>Måsøy</i>	5.29	0.623	5.053	3.994	-

Table 14, Humerus SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.869	<.001	0.413	0.329
<i>F. a. arctica</i>	1.367	-	<.001	0.734	0.594
<i>F. a. naumanni</i>	5.562	5.925	-	0.058	0.641
<i>Dollsteinhola</i>	2.464	1.74	3.862	-	0.971
<i>Måsøy</i>	2.675	2.058	1.953	0.884	-

Table 15, Humerus Bd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.303	<.001	0.612	0.233
<i>F. a. arctica</i>	2.744	-	<.001	0.994	0.994
<i>F. a. naumanni</i>	7.353	6.696	-	<.001	<.001
<i>Dollsteinhola</i>	2.017	0.586	6.236	-	0.955
<i>Måsøy</i>	2.952	0.571	5.659	0.999	-

Table 16, Humerus KB ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.5	<.001	0.788	0.111
<i>F. a. arctica</i>	2.265	-	<.001	0.993	0.642
<i>F. a. naumanni</i>	6.908	6.653	-	<.001	0.015
<i>Dollsteinhola</i>	1.604	0.599	6.272	-	0.544
<i>Måsøy</i>	3.462	1.952	4.54	2.168	-

Ulna

The ulna GL measurement shows the groups are not normally distributed (Shapiro-wilk $p = 0.002$), this is due to a single outlier, a slightly larger GL measurement in the archaeological material from Dollsteinhola. Despite this the residual graphs do show a relatively normal distribution and as a result a one-way ANOVA remains appropriate. The Levene's test for homogeneity of variance reports a p value of 0.002, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 17 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 23). The ulna Dip is normally distributed (Shapiro-Wilk p value of 0.677). Levene's test for homogeneity reports a p value of 0.164 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are

safely met. Table 18 presents the results of the one-way ANOVA in standard form and Table 24 shows the Tukey's pairwise results. The ulna Bp normal distribution was distorted by two outliers, a single large Bp measure on *F. a. arctica* specimen and a larger measurement on a specimen from Dollsteinhola, giving a Shapiro-wilk p value of 0.009. Despite this the graphs show that the rest of the data has a normal distribution and therefore a one-way ANOVA was still appropriate. Levene's test for homogeneity reports a p value of 0.309 for the equality of variances, so there is no significant difference. This means the assumptions of the ANOVA are met. Table 19 presents the results of the one-way ANOVA in standard form and Table 25 shows the Tukey's pairwise results. The ulna Tp measurement shows a relatively normal distribution when glancing at the residual graphs, however, Shapiro-wilks test for normality gives a p value of 0.02. As the graphs show the data has a fairly normal distribution we continue to use the one-way ANOVA and do not move to a non-parametric test. The Levene's test for homogeneity reports a p value of <.001 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 20 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 26). The ulna SC measurement shows a relatively normal distribution when glancing at the residual graphs, however, two large measurements for the subspecies *F. a. grabae* along with an outlier for the Måsøy assemblage have led to a Shapiro-wilks p value of 0.003. As the graphs show the data has a fairly normal distribution we continue to use the one-way ANOVA and do not move to a non-parametric test. The Levene's test for homogeneity reports a p value of <.001 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 21 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 27). The ulna Did is normally distributed (Shapiro-Wilk p value of 0.785). Levene's test for homogeneity reports a p value of 0.126 for the equality of variances, so there is no

significant difference. This means the assumptions of the ANOVA are met. Table 22 presents the results of the one-way ANOVA in standard form and Table 28 shows the Tukey's pairwise results.

Table 17, One-way ANOVA results for the greatest length (GL) of the ulna. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	248.332	4	62.0831	24.78	1.819E-13
Within groups	205.444	82	2.50542		
Welch F test		23.49		28.55	1.028E-08

Table 18, One-way ANOVA results for the diagonal of the proximal end (Dip) of the ulna. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	7.0956	4	1.7739	8.61	7.142E-06
Within groups	17.3064	84	0.206029		

Table 19, One-way ANOVA results for the breadth of the proximal end (Bp) of the ulna. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.69022	4	0.922555	9.042	4.011E-06
Within groups	8.57014	84	0.102025		

Table 20, One-way ANOVA results for the depth of the proximal end (Tp) of the ulna. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	4.27955	4	1.06989	10.59	5.575E-07
Within groups	8.38723	83	0.101051		
Welch F test		23.98		13.04	8.851E-06

Table 21, One-way ANOVA results for the smallest breadth of the corpus (SC) of the ulna. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	1.24878	4	0.312195	5.951	0.0002823
Within groups	4.51183	86	0.0524632		
Welch F test		23.87		7.928	0.0003247

Table 22, One-way ANOVA results for the diagonal of the distal end (Did) of the ulna. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	5.72293	4	1.43073	19.17	2.453E-11
Within groups	6.49272	87	0.074629		

Table 23, Ulna GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	1	<.001	0.307	0.849
<i>F. a. arctica</i>	0.306	-	<.001	0.070	0.278
<i>F. a. naumanni</i>	7.432	11.28	-	<.001	<.001
<i>Dollsteinhola</i>	2.739	3.754	13.49	-	<.001
<i>Måsøy</i>	1.431	2.819	8.756	6.162	-

Table 24, Ulna Dip ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.028	0.999	0.004	0.055
<i>F. a. arctica</i>	4.248	-	<.001	0.744	0.995
<i>F. a. naumanni</i>	0.338	6.013	-	<.001	0.002
<i>Dollsteinhola</i>	5.174	1.714	6.997	-	0.528
<i>Måsøy</i>	3.892	0.562	5.535	2.205	-

Table 25, Ulna Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.370	<.001	0.706	0.130
<i>F. a. arctica</i>	2.572	-	<.001	0.951	0.880
<i>F. a. naumanni</i>	7.018	6.767	-	<.001	<.001
<i>Dollsteinhola</i>	1.805	1.019	7.131	-	0.529
<i>Måsøy</i>	3.37	1.33	5.681	2.202	-

Table 26, Ulna Tp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	<.001	0.991	<.001	0.012
<i>F. a. arctica</i>	5.949	-	<.001	0.988	0.609
<i>F. a. naumanni</i>	0.653	6.798	-	<.001	0.005
<i>Dollsteinhola</i>	6.14	0.688	6.891	-	0.401
<i>Måsøy</i>	4.669	2.026	5.115	2.496	-

Table 27, Ulna SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.042	1	0.064	0.335
<i>F. a. arctica</i>	4.038	-	<.001	1	0.508
<i>F. a. naumanni</i>	0.038	5.72	-	0.005	0.072
<i>Dollsteinhola</i>	3.802	0.008	5.097	-	0.649
<i>Måsøy</i>	2.66	2.248	3.735	1.937	-

Table 28, Ulna Did ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	1	<.001	0.838	0.984
<i>F. a. arctica</i>	0.181	-	<.001	0.627	0.816
<i>F. a. naumanni</i>	6.711	10.44	-	<.001	<.001
<i>Dollsteinhola</i>	1.465	1.984	11.22	-	0.141
<i>Måsøy</i>	0.747	1.528	9.046	3.316	-

Carpometacarpus

The carpometacarpus GL shows the groups are normally distributed (Shapiro-wilk p 0.829). The Levene's test for homogeneity of variance reports a p value of 0.02, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 29 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 33). The carpometacarpus Bp is normally distributed (Shapiro-Wilk p value of 0.201). Levene's test for homogeneity reports a p value of 0.575 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 30 presents the results of the one-way ANOVA in standard form and Table 34 shows the Tukey's pairwise results. The carpometacarpus Did is normally distributed (Shapiro-Wilk p value of 0.514). Levene's test for homogeneity reports a p value of 0.380 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 31 presents the results of the one-way ANOVA in standard form and Table 35 shows the Tukey's pairwise results. The carpometacarpus HS is normally distributed (Shapiro-wilk p value of 0.08). The Levene's test for homogeneity of variance reports a p value of <.001, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 32 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 36).

Table 29, One-way ANOVA results for the greatest length (GL) of the carpometacarpus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	185.034	4	46.2585	40.09	3.031E-19
Within groups	103.86	90	1.15401		
Welch F test		26.24		44.74	2.38E-11

Table 30, One-way ANOVA results for the breadth of the proximal end (Bp) of the carpometacarpus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	5.02339	4	1.25585	8.993	3.481E-06
Within groups	12.9873	93	0.139648		

Table 31, One-way ANOVA results for the diagonal of the distal end (Did) of the carpometacarpus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	2.97844	4	0.744611	6.789	7.923E-05
Within groups	9.9812	91	0.109684		

Table 32, One-way ANOVA results for the height of the symphysis (HS) of the carpometacarpus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	2.8524	4	0.7131	7.461	3.09E-05
Within groups	8.60241	90	0.0955823		
Welch F test		25.8		6.969	0.0006059

Table 33, Carpometacarpus GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.999	<.001	0.035	0.762
<i>F. a. arctica</i>	0.336	-	<.001	<.001	0.172
<i>F. a. naumanni</i>	7.861	12.41	-	<.001	<.001
<i>Dollsteinhola</i>	4.122	6.205	17.61	-	<.001
<i>Måsøy</i>	1.67	3.178	9.011	8.942	-

Table 34, Carpometacarpus Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.449	0.331	0.390	0.940
<i>F. a. arctica</i>	2.38	-	<.001	1	0.618
<i>F. a. naumanni</i>	2.67	7.456	-	<.001	0.002
<i>Dollsteinhola</i>	2.52	0.232	7.656	-	0.518
<i>Måsøy</i>	1.082	2.006	5.406	2.225	-

Table 35, Carpometacarpus Did ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.999	0.009	0.279	0.646
<i>F. a. arctica</i>	0.338	-	<.001	0.040	0.365
<i>F. a. naumanni</i>	4.795	6.791	-	0.174	0.027
<i>Dollsteinhola</i>	2.816	4.063	3.17	-	0.884
<i>Måsøy</i>	1.943	2.584	4.262	1.318	-

Table 36, Carpometacarpus HS ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.499	0.993	0.016	0.484
<i>F. a. arctica</i>	2.267	-	0.033	0.076	1
<i>F. a. naumanni</i>	0.605	4.162	-	<.001	0.037
<i>Dollsteinhola</i>	4.514	3.697	7.281	-	0.126
<i>Måsøy</i>	2.301	0.127	4.107	3.39	-

Femur

The femur GL shows the groups are normally distributed (Shapiro-wilk p 0.108). The Levene's test for homogeneity of variance reports a p value of 0.06 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 37 presents the results of the one-way ANOVA in standard form and Table 43 shows the Tukey's pairwise results. The femur Bp shows the groups are normally distributed (Shapiro-wilk p 0.517). The Levene's test for homogeneity of variance reports a p value of 0.888 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 38 presents the results of the one-way ANOVA in standard form and Table 44 shows the Tukey's pairwise results. The femur Dp shows the groups are normally distributed (Shapiro-wilk p value of 0.567). The Levene's test for homogeneity of variance reports a p value of 0.791 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 39 presents the results of the one-way ANOVA in standard form and Table 45 shows the Tukey's pairwise results. The femur SC shows the groups are normally distributed (Shapiro-wilk p value of 0.498). The Levene's test for homogeneity of variance reports a p value of 0.822 for the equality of variances, so there is no significant difference. This

means all the assumptions of the ANOVA are safely met. Table 40 presents the results of the one-way ANOVA in standard form and Table 46 shows the Tukey's pairwise results. The femur Bd shows the groups are normally distributed (Shapiro-wilk p value of 0.743). The Levene's test for homogeneity of variance reports a p value of 0.486 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 41 presents the results of the one-way ANOVA in standard form and Table 47 shows the Tukey's pairwise results. The femur Dd is normally distributed (Shapiro-Wilk p value of 0.656). Levene's test for homogeneity reports a p value of 0.002 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 42 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 48).

Table 37, One-way ANOVA results for the greatest length (GL) of the femur. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	159.101	4	39.7754	17.8	1.042E-10
Within groups	194.432	87	2.23485		

Table 38, One-way ANOVA results for the breadth of the proximal end (Bp) of the femur. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	7.42157	4	1.85539	11.06	2.603E-07
Within groups	14.7669	88	0.167805		

Table 39, One-way ANOVA results for the depth of the proximal end (Dp) of the femur. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.88964	4	0.972409	11.85	9.885E-08
Within groups	7.13695	87	0.0820339		

Table 40, One-way ANOVA results for the smallest breadth of the corpus (SC) of the femur. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	0.650823	4	0.162706	5.698	0.0003874
Within groups	2.59843	91	0.0285541		

Table 41, One-way ANOVA results for the breadth of the distal end (Bd) of the femur. Taking into account only modern material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.41453	4	0.853632	6.389	0.0001445
Within groups	11.8905	89	0.133601		

Table 42, One-way ANOVA results for the depth of the distal end (Dd) of the femur. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	5.51716	4	1.37929	10.59	4.734E-07
Within groups	11.461	88	0.130239		
Welch F test		26.18		12.91	6.222E-06

Table 43, Femur GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.116	<.001	0.756	0.254
<i>F. a. arctica</i>	3.441	-	<.001	<.001	1
<i>F. a. naumanni</i>	8.082	7.544	-	<.001	0.005
<i>Dollsteinhola</i>	1.685	6.446	11.18	-	0.007
<i>Måsøy</i>	2.89	0.242	5.029	4.928	-

Table 44, Femur Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.005	<.001	0.468	0.309
<i>F. a. arctica</i>	5.043	-	<.001	0.339	0.699
<i>F. a. naumanni</i>	8.371	5.86	-	<.001	<.001
<i>Dollsteinhola</i>	2.338	2.664	6.697	-	0.996
<i>Måsøy</i>	2.729	1.821	5.781	0.531	-

Table 45, Femur Dp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.997	0.003	0.282	0.996
<i>F. a. arctica</i>	0.826	-	<.001	0.007	0.795
<i>F. a. naumanni</i>	5.224	6.724	-	<.001	<.001
<i>Dollsteinhola</i>	2.808	4.939	9.28	-	0.479
<i>Måsøy</i>	0.538	1.586	6.056	2.314	-

Table 46, Femur SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.592	0.002	0.574	0.041
<i>F. a. arctica</i>	2.062	-	0.003	0.996	0.146
<i>F. a. naumanni</i>	5.412	5.352	-	0.086	0.827
<i>Dollsteinhola</i>	2.101	0.521	3.625	-	0.564
<i>Måsøy</i>	4.05	3.292	1.499	2.125	-

Table 47, Femur Bd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.163	<.001	0.573	0.236
<i>F. a. arctica</i>	3.216	-	0.002	0.976	0.998
<i>F. a. naumanni</i>	6.489	5.458	-	0.008	0.079
<i>Dollsteinhola</i>	2.105	0.833	4.842	-	0.958
<i>Måsøy</i>	2.947	0.415	3.679	0.978	-

Table 48, Femur Dd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.002	<.001	0.218	0.017
<i>F. a. arctica</i>	5.361	-	<.001	0.575	1
<i>F. a. naumanni</i>	8.637	5.81	-	<.001	0.030
<i>Dollsteinhola</i>	3.009	2.099	6.198	-	0.744
<i>Måsøy</i>	4.496	0.105	4.215	1.715	-

Tibiotarsus

The tibiotarsus La shows the groups are normally distributed (Shapiro-wilk p 0.808). The Levene's test for homogeneity of variance reports a p value of 0.011 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result, Welch's F test (in the case of unequal variances) was consulted and included in Table 49 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 55). The tibiotarsus Dip shows the groups are normally distributed (Shapiro-wilk p 0.392). The Levene's test for homogeneity of variance reports a p value of 0.333 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 50 presents the results of the one-way ANOVA in standard form and Table 56 shows the Tukey's pairwise results. The tibiotarsus Bp shows the groups are normally distributed (Shapiro-wilk p value of 0.127). The Levene's test for homogeneity of variance reports a p value of 0.329 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 51 presents the results of the one-way ANOVA in standard form and Table 57 shows the Tukey's pairwise results. The tibiotarsus SC shows the groups are normally distributed (Shapiro-wilk p

value of 0.906). The Levene's test for homogeneity of variance reports a p value of 0.608 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 52 presents the results of the one-way ANOVA in standard form and Table 58 shows the Tukey's pairwise results. The tibiotarsus Bd shows the groups are normally distributed (Shapiro-wilk p value of 0.400). The Levene's test for homogeneity of variance reports a p value of 0.243 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 53 presents the results of the one-way ANOVA in standard form and Table 59 shows the Tukey's pairwise results. The tibiotarsus Dd measurement shows a relatively normal distribution when glancing at the residual graphs, however, Shapiro-wilks test for normality gives a p value of <.001. As the graphs show the data has a fairly normal distribution we continue to use the one-way ANOVA and do not move to a non-parametric test. One measurement of *F. a. grabae* is especially small and is likely to have caused the abnormality in the data. The Levene's test for homogeneity reports a p value of <.001 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 54 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < 0.001$) it was possible to continue to Tukey's pairwise (Table 60).

Table 49, One-way ANOVA results for the axial length (La) of the tibiotarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	380.855	4	95.2138	23.77	2.25E-11
Within groups	216.282	54	4.00522		
Welch F test		6.48		19.89	0.0009183

Table 50, One-way ANOVA results for the diagonal of the proximal end (Dip) of the tibiotarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	6.06214	4	1.51553	11.93	2.362E-07
Within groups	8.38325	66	0.127019		

Table 51, One-way ANOVA results for the breadth of the proximal end (Bp) of the tibiotarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	4.4823	4	1.12058	11.6	4.066E-07
Within groups	6.08789	63	0.0966331		

Table 52, One-way ANOVA results for the smallest breadth of the corpus (SC) of the tibiotarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	1.04754	4	0.261884	5.333	0.0008196
Within groups	3.4866	71	0.0491071		

Table 53, One-way ANOVA results for the breadth of the distal end (Bd) of the tibiotarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.3229	4	0.830724	9.82	3.536E-06
Within groups	5.07592	60	0.0845987		

Table 54, One-way ANOVA results for the depth of the distal end (Dd) of the tibiotarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	3.37622	4	0.844055	4.921	0.001691
Within groups	10.2911	60	0.171518		
Welch F test		15.32		8.788	0.0006846

Table 55, Tibiotarsus La ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.950	<.001	0.269	1
<i>F. a. arctica</i>	1.025	-	<.001	0.330	0.998
<i>F. a. naumanni</i>	6.985	12.06	-	<.001	0.014
<i>Dollsteinhola</i>	2.86	2.688	11.29	-	0.726
<i>Måsøy</i>	0.189	0.421	4.664	1.759	-

Table 56, Tibiotarsus Dip ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.002	1	0.005	0.069
<i>F. a. arctica</i>		-	<.001	1	0.745
<i>F. a. naumanni</i>	0.104	8.239	-	<.001	0.006
<i>Dollsteinhola</i>	5.111	0.197	6.986	-	0.777
<i>Måsøy</i>	3.782	1.713	5.072	1.632	-

Table 57, Tibiotarsus Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.885	<.001	0.815	0.465
<i>F. a. arctica</i>	1.311	-	<.001	0.996	0.684
<i>F. a. naumanni</i>	6.305	8.77	-	<.001	0.002
<i>Dollsteinhola</i>	1.53	0.513	6.879	-	0.921
<i>Måsøy</i>	2.35	1.857	5.481	1.171	-

Table 58, Tibiotarsus SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.949	0.018	0.862	0.118
<i>F. a. arctica</i>	1.032	-	0.003	0.991	0.089
<i>F. a. naumanni</i>	4.488	5.334	-	0.038	0.933
<i>Dollsteinhola</i>	1.392	0.642	4.108	-	0.317
<i>Måsøy</i>	3.446	3.624	1.114	2.713	-

Table 59, Tibiotarsus Bd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	1	0.002	0.240	0.819
<i>F. a. arctica</i>	0.036	-	<.001	0.032	0.655
<i>F. a. naumanni</i>	5.474	8.357	-	0.265	0.145
<i>Dollsteinhola</i>	2.95	4.23	2.869	-	0.942
<i>Måsøy</i>	1.52	1.924	3.318	1.069	-

Table 60, Tibiotarsus Dd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.174	0.002	0.755	0.669
<i>F. a. arctica</i>	3.19	-	0.069	0.777	0.993
<i>F. a. naumanni</i>	5.504	3.788	-	0.017	0.253
<i>Dollsteinhola</i>	1.687	1.632	4.541	-	0.995
<i>Måsøy</i>	1.893	0.603	2.906	0.538	-

Tarsometatarsus

The tarsometatarsus GL shows the groups are normally distributed (Shapiro-wilk p 0.07). The Levene's test for homogeneity of variance reports a p value of 0.043 for the equality of variances, this means that the variances are unequal, this compromises the assumptions of a one-way ANOVA. As a result Welch's F test (in the case of unequal variances) was consulted and included in Table 61 along with the one-way ANOVA results, as the p value of the Welch's test was significant ($p < .001$) it was possible to continue to Tukey's pairwise (Table 65). The tarsometatarsus Bp shows the groups are

normally distributed (Shapiro-wilk p 0.646). The Levene's test for homogeneity of variance reports a p value of 0.676 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 62 presents the results of the one-way ANOVA in standard form and Table 66 shows the Tukey's pairwise results. The tarsometatarsus SC shows the groups are normally distributed (Shapiro-wilk p value of 0.448). The Levene's test for homogeneity of variance reports a p value of 0.09 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 63 presents the results of the one-way ANOVA in standard form and Table 67 shows the Tukey's pairwise results. The tarsometatarsus Bd shows the groups are normally distributed (Shapiro-wilk p value of 0.496). The Levene's test for homogeneity of variance reports a p value of 0.328 for the equality of variances, so there is no significant difference. This means all the assumptions of the ANOVA are safely met. Table 64 presents the results of the one-way ANOVA in standard form and Table 68 shows the Tukey's pairwise results.

Table 61, One-way ANOVA results for the greatest length (GL) of the tarsometatarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i> (same)
Between groups	113.16	4	28.29	11.78	5.063E-08
Within groups	268.961	112	2.40143		
Welch <i>F</i> test		11.26		12.8	0.0003643

Table 62, One-way ANOVA results for the breadth of the proximal end (Bp) of the tarsometatarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i> (same)
Between groups	9.66289	4	2.41572	20.43	1.033E-12
Within groups	13.4789	114	0.118236		

Table 63, One-way ANOVA results for the smallest breadth of the corpus (SC) of the tarsometatarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	<i>F</i>	<i>p</i> (same)
Between groups	1.12663	4	0.281658	3.603	0.008146
Within groups	9.77186	125	0.0781749		

Table 64, One-way ANOVA results for the breadth of the distal end (Bd) of the tarsometatarsus. Taking into account modern and archaeological material.

	Sum of sqrs	df	Mean square	F	p(same)
Between groups	6.66498	4	1.66625	14.89	9.367E-10
Within groups	12.3092	110	0.111902		

Table 65, Tarsometatarsus GL ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.291	0.998	0.054	0.810
<i>F. a. arctica</i>	2.775	-	<.001	0.431	0.880
<i>F. a. naumanni</i>	0.460	6.009	-	<.001	0.260
<i>Dollsteinhola</i>	3.876	2.421	9.054	-	0.282
<i>Måsøy</i>	1.547	1.33	2.866	2.801	-

Table 66, Tarsometatarsus Bp ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.946	0.012	1	0.782
<i>F. a. arctica</i>	1.05	-	<.001	0.084	0.914
<i>F. a. naumanni</i>	4.64	8.265	-	<.001	0.016
<i>Dollsteinhola</i>	0.112	3.621	12.59	-	0.141
<i>Måsøy</i>	1.62	1.205	4.493	3.303	-

Table 67, Tarsometatarsus SC ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.994	0.394	0.993	0.970
<i>F. a. arctica</i>	0.582	-	0.019	1	0.990
<i>F. a. naumanni</i>	2.509	4.398	-	0.003	0.371
<i>Dollsteinhola</i>	0.599	0.002	5.204	-	0.986
<i>Måsøy</i>	0.892	0.664	2.563	0.729	-

Table 68, Tarsometatarsus Bd ANOVA - Tukey's pairwise

	<i>F. a. grabae</i>	<i>F. a. arctica</i>	<i>F. a. naumanni</i>	<i>Dollsteinhola</i>	<i>Måsøy</i>
<i>F. a. grabae</i>	-	0.983	0.123	0.995	0.767
<i>F. a. arctica</i>	0.759	-	<.001	0.059	0.707
<i>F. a. naumanni</i>	3.392	5.892	-	<.001	0.269
<i>Dollsteinhola</i>	0.548	3.832	10.34	-	0.014
<i>Måsøy</i>	1.658	1.802	2.839	4.562	-

Supplementary Material: S4 Table, Dollsteinhola and Runde mean values.

S4 Table. Comparison of mean values for modern *F. a. arctica* from Runde and the *F. arctica* specimens from Dollsteinhola. Highlighted values (light grey) represent the higher mean, * are the significantly different means.

	Runde (mean values)			Dollsteinhola (mean values)				
	Length	Proximal	Shaft	Distal	Length	Proximal	Shaft	Distal
Coracoid	Lm 33.98			Bb 11.99	Lm 34.40			Bb 10.21*
Humerus	GL 63.71	Bp 14.69	SC 3.04*	Bd 6.62*	GL 63.38	Bp 14.54	SC 3.27*	Bd 6.92*
	UL 50.23	Dip 7.93	SC 2.84	Dd 7.23	GL 49.46	Dip 7.98	SC 2.96	Dd 7.33
Carpometacarpus	GL 33.94*	Bp 7.76		Dd 4.92*	GL 32.84*	Bp 8.00		Dd 5.30*
	GL 38.40	Bp 4.98	SC 2.86	Bd 6.86	GL 37.46	Bp 7.63	SC 2.98	Bd 7.05
Tibiotarsus	La 62.31	Dip 8.11	SC 3.14	Dd 5.80	La 61.37	Dip 8.43	SC 3.25	Dd 6.04*
	GL 27.67	Bp 6.22	SC 3.38	Bd 6.82	GL 27.21	Bp 6.22	SC 3.57	Bd 6.74



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