Allometry and ecomorphology of Scandinavian raptors

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Licentiate thesis

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Sammanfattning

Ända sedan Charles Darwin observerade de berömda finkarna på Galapagosöarna har zoologer arbetat med att försöka förstå hur olika arters form och funktion (functional morphology) kan förstås i ljuset av deras livsstil och livsmiljö (ecology). Genom att använda den allometriska ekvationen kan det genomsnittliga sambandet mellan generell kroppsstorlek och storlek på en viss karaktär, t.ex. längden eller diametern på överarmsbenet humerus beräknas. Detta generella samband, som beskriver hur en viss karaktär förändras med ökad kroppsmassa hos ett antal arter, kan också säga en del om vilka krafter som verkar på just den kroppsdelen. Detta är ämnet för artikel I.

I andra artikeln används de allometriska sambanden för att studera skillnaderna mellan hanar och honor för ett antal skandinaviska rovfåglar. Resultatet visar att honan i så gott som samtliga fall har kortare skelettelement i både vinge och ben jämfört med vad som skulle förväntas med tanke på hennes vikt. Detta stärker hypotesen att behovet av en större bål är en viktig faktor bakom honans större storlek.

I tredje artikeln jämförs respektive art och kön med den generella linjen och avvikelser från denna linje ställs mot respektive arts specifika livsmiljö och livsstil. Det visas bland annat att fåglar som glidflyger mycket har längre överarmsben (humerus) och mindre yta på bröstbenskammen (carina sterni) än genomsnittet medan aktiva flygare har större yta på carina sterni och kortare vingben. Det konstateras också att fåglar som slår sitt byte har kortare och tjockare tarsometatarsus och tibiotarsus i benen medan de som griper efter sitt byte har längre och smalare. Den i detta samanhang lite udda bivråken, som gräver efter byte har, som förväntat, avsevärt kraftigare tarsometatarsus än genomsnittet.

Ingående artiklar

Denna licentiatavhandling är baserad på följande artiklar:

I. Florén P., Allometry of Scandinavian raptors.

II. Florén P., The Reversed Sexual Size Dimorphism of Scandinavian raptors.

III. Florén P., Ecomorphology of the locomotor apparatus of Scandinavian raptors.

Artikelns romerska siffra kommer att användas som referens i texten.

Innehåll

Introduktion

Få biologiska observationer har blivit så klassiska och allmänt kända som de finkar som Charles Darwin (1809-1882) studerade på Galapagosöarna under sin berömda världsomsegling med skeppet Beagle 1831-1836. Han kunde då konstatera att de olika arter av finkar som han fann på de olika öarna på många sätt hade stora likheter, och dessutom liknande en fink som levde på fastlandet, men också vissa signifikanta olikheter. Inte minst var det näbbarna som skilde sig åt. En rimlig slutsats var att ett par finkar från fastlandet hade råkat hamna på Galapagosöarna och där steg för steg anpassat sig till de olika livsmiljöer och födoalternativ som respektive ö erbjöd. Förutom att detta blev en viktig inspiration till arbetet med evolutionsteorin var detta också en av de första exemplen på hur en biolog kopplat samman form och funktion med ett djurs livsstil (nisch, vad djuret äter och hur det fångar sin mat etc.) och livsmiljö (habitat, där djuret normalt uppehåller sig). Det är just denna typ av samband som intresserar forskare inom området ekologisk zoomorfologi. Ekologisk syftar här på samband mellan den studerade arten och dess livsmiljö, zoo syftar på djur och morfologi slutligen betyder form. Den ekologiska morfologins grundläggande fråga sammanfattas i:

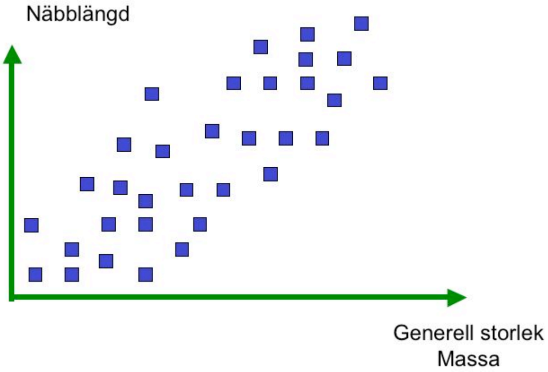
Hur kan ett djurs form förstås i relation till dess ”livsstil” och ”livsmiljö”?

I Darwins fall hade naturen lagt ganska mycket tillrätta för att underlätta möjligheterna att dra slutsatser. Det fanns en tydlig ”ursprungsfågel” att jämföra med, det fanns några tydliga skillnader i konstruktion (näbben) och de olika arterna hade tydligt åtskilda livsmiljöer på de olika öarna, var och en med sina egenskaper.

När dagens forskare skall försöka förstå motsvarande samband mellan ett antal arters form och ekologi så stöter han på en mängd komplikationer:

- Livsmiljön innehåller en stor mängd olika utmaningar som djuret behöver kunna hantera. Dessa utmaningar ställer ofta motstridiga krav på arten, ibland kan det t.ex. vara fördelaktigt att ha långa vingar, ibland korta.
- Det finns sällan någon enkel ”ursprungsfågel” att jämföra med.
- De arter man vill jämföra är sällan av samma storlek, vilket gör jämförelserna ännu mer komplexa.

Hur gör man då om man vill jämföra ett antal olika arter? Antag att man vill försöka studera ett antal olika arters näbblängd och om det eventuellt finns något samband med respektive arts födoval. Första steget blir då att mäta näbbarna och jämföra resultaten. Föga förvånande finner vi då att större fåglar i genomsnitt har större näbbar medan mindre fåglar har mindre näbbar. Nästa steg blir då att rita ett diagram där fågelns generella storlek, oftast fågelns massa, blir x-koordinat och näbblängden blir y-koordinat. Låt oss anta att diagrammet får ett utseende ungefär som i figur 1.



Figur 1. Principskiss över mätvärden för olika arters massa och näbblängd.

Vi kan då genast konstatera två saker:

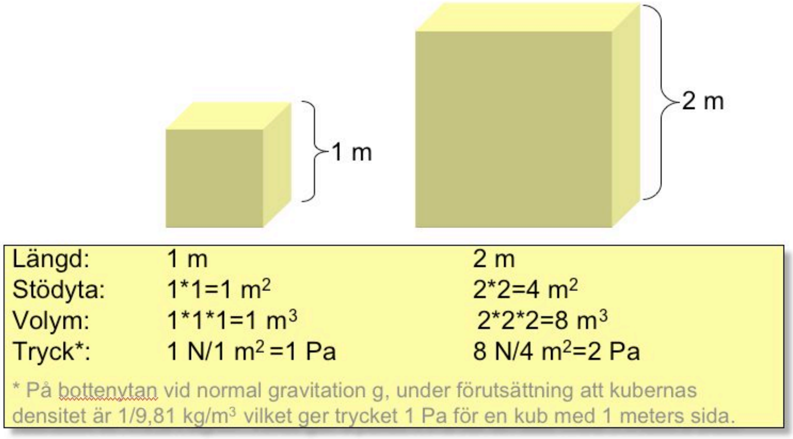
1. Sambandet mellan generell storlek och näbbens storlek framträder tydligt och skulle kunna sammanfattas i en regressionslinje som beskriver det generella sambandet mellan massa och näbblängd.
2. Det finns en spridning, större eller mindre, kring den generella linjen som mycket väl skulle kunna vara orsakad av olika arters anpassning till olika förutsättningar.

I de fall den studerade kroppsdelen eller organet har en viktig mekanisk funktion i kroppen, som t.ex. skelettet i vingar och ben har, är det rimligt att anta att detta avspeglar sig i det generella sambandet mellan fågelns massa och det studerade måttet. Om vi t.ex. studerar fotbenet tarsometatarsus så är det rimligt att anta att det kommer att öka i grovlek i lagom takt för att klara av att bära upp de större arternas större massor. Att göra det för tjockt för mindre arter innebär kostnader, både i form av onödig vikt och ökat behov av föda, medan ett för klent ben innebär risk för livshotande skador. Begreppet **allometri** syftar just på studier av dessa generella samband mellan olika kroppsdelars och organs mått och djurets generella storlek, ofta sammanfattad som fågelns massa. Artikel I behandlar just frågan om de skandinaviska rovfåglarnas allometri.

Om vi accepterar att det generella sambandet, åtminstone delvis, avspeglar grundläggande mekaniska krav är det, som redan sagts, rimligt att avvikelserna från denna linje har tillkommit av goda skäl. Avvikelserna från den generella linjen innebär sannolikt antingen ökade kostnader eller ökade risker, vilka måste uppvägas av andra fördelar. Man talar om att egenskapen ökar artens eller individens ”fitness”. Utmaningen är att identifiera dessa avvikelser och sedan försöka förstå vilka fördelar dessa kan innebära i fågelns livsmiljö. Det är denna typ av frågor som intresserar den som studerar **ekomorfologi**. Artikel II och III behandlar ämnet ekomorfologi, artikel II med fokus på skillnader mellan könen och artikel III med fokus på jaktmetod.

Artikel I. Allometri i ving- och benskelett

Redan de gamla grekerna, närmare bestämt Euklides (300 f.Kr.) och Arkimedes (287-212 f.Kr.) hade klart för sig att längd, yta och volym ändrade sig i olika takt när t.ex. en kubs generella storlek förändrades. Om vi har en kub med sidan 1 meter och en med sidan 2 meter kommer den större kuben att ha fyra gånger så stor bottenyta och åtta gånger så stor volym, se även figur 2.



Längd:	1 m	2 m
Stödyta:	1*1=1 m^2	2*2=4 m^2
Volym:	1*1*1=1 m^3	2*2*2=8 m^3
Tryck*:	1 N/1 m^2=1 Pa	8 N/4 m^2=2 Pa

* På bottenytan vid normal gravitation g, under förutsättning att kubernas densitet är 1/9,81 kg/m^3 vilket ger trycket 1 Pa för en kub med 1 meters sida.

Figur 2. Principiell jämförelse mellan två kuber, den ena dubbelt så stor som den andra.

Trycket på bottenytan orsakat av kubens egenvikt blir dubbelt stå stort för den större kuben, och är storleksskillnaderna större blir också skillnaden i tryck större. Vilket material man än tillverkar kuben i, så kommer den vid en viss storlek att krossas under sin egen vikt. Samma sak gäller för många biologiska ”konstruktioner”; ökar man storleken tillräckligt mycket så kommer den att kollapsa under sin egen vikt, så som t.ex. en stor val gör om den av misstag råkar komma upp på en strand. För ving- och benskelett handlar det sannolikt i huvudsak om att inte tryckas ihop eller böjas så mycket att skelettmaterialets hållfasthetsgräns överskrids. För senor är det framför allt dragpåkänningen den viktigaste faktorn. Detta resonemang är också den krassa bakgrunden till uttrycket att ”inga träd växer upp till himlen.”[1]. Samma typ av resonemang kan tillämpas på fåglar av olika storlekar, se figur 3.

Former eller kroppar som har samma proportioner, t.ex. kuber och kvadrater, kan kallas för isometriska (från grekiskans ”med samma mått”) eller geometriskt lika. Begreppet kan även användas om t.ex. två olika fågelarter som är olika stora men har samma proportioner.

Många forskare (se referenser i artikel I) har mätt och analyserat både däggdjur och fåglar i jakten på hur djuren möter den ökande belastningen på skelettet som större storlek innebär. Genom åren har fem olika huvudalternativ identifierats:

1. **Ökade dimensioner**. Genom att öka tvärsnittsytan på t.ex. benskelettet i snabbare takt än övriga mått (framför allt längdmått) kan den maximala belastningen hållas konstant. Detta alternativ föreslogs först av Galileo Galilei (1564–1642) i hans bok *Dialoger* från år 1636.
2. **Starkare material**. Genom att använda starkare material i skelettet skulle större djur kunna undvika skador. Även detta förslag nämndes först av Galilei. Senare tids forskning har dock gett litet eller inget vetenskapligt stöd detta alternativ.
3. **Bättre design**. Genom att förändra designen kan påkänningen i benet minskas. Större djur har t.ex. benens skelettdelar och skulderbladet staplade ovanpå varandra, vilket gör att benen utsätts framför allt för tryckkrafter, medan böj-

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[1] *Möjligen härstammar uttrycket från ett citat av Galilei år 1636: ”…nature cannot grow a tree not construct an animal beyond a certain size, while retaining the proportions which suffice in the case of a smaller structure”*

krafterna blir små. (Biewener 1982 och 1983, Schmidt-Nielsen 1975). Detta alternativ tas ej upp i detta arbete.

4. **Minskning av den dynamiska lasten**. Genom att röra sig mer försiktigt klarar större djur, t.ex. elefanten, att bära upp sin större kroppsmassa utan att skelettet skadas (Alexander et al. 1983, Biewener 1983, Maloiy 1979, Rubin 1984). Dessa djur har benens skelettdelar och skulderbladet staplade ovanpå varandra, vilket gör att benen utsätts framför allt för tryckkrafter, medan böjkrafterna blir små.
5. **Minskade säkerhetsmarginaler**. Det har föreslagits att större djur lever mycket närmare sina marginaler än mindre djur gör (Economos 1983, Biewener 1982). Detta alternativ tas ej upp i detta arbete.

I denna avhandling är det i första hand alternativ 1 och i viss mån alternativ 4 som behandlas.

Om nu alternativ 1 är riktigt, och de större djuren ökar diametern på ving- och benskelett snabbare än geometrisk likhet, för att möta den ökande belastningen, kan man undra om det finns någon identifierbar princip som beskriver hur detta går till. Följande förslag har diskuterats:

1. **Isometri eller geometrisk likhet**, innebär, som redan sagts, att diametrar och längder ökar proportionellt lika mycket. Detta kommer att leda till att trycket kommer att öka med ökad storlek. Ändå har forskare kunnat visa att geometrisk likhet gäller i förvånansvärt många av de undersökta fallen.
2. **Elastisk likhet** är det vanligaste alternativet till geometrisk likhet. Den bygger på att den elastiska nedböjningen skall hållas konstant och har hämtats från en konstruktionsprincip, som tidigare använts av ingenjörer vid konstruktion av t.ex. broar. (Rashevsky 1960 och framför allt McMahon 1973, 1975a and 1975 b).
3. **Statisk-stress likhet** har en liknande bakgrund som elastisk likhet, men är mycket sällan använd i biologiska sammanhang (McMahon 1975a).
4. **Dynamisk likhet** innebär att djuret kompenserar ökad massa med att röra sig på ett sådant sätt att belastningen ändå blir nära nog konstant (Rubin och Lanyon 1984, Alexander 1977 och 1981 samt Biewener 1982 och 1983). Denna hypotes ansluter till punkt 4 ovan ”minskning av den dynamiska lasten”. En viktig förutsägelse är att en muskelbelastning är mer förutsägbar än en last orsakad av en massas plötsliga inbromsning, t.ex. när en fågel tar mark lite oförsiktigt. Detta leder till att ben belastade av massa måste vara grövre (som beredskap för höga laster vid t.ex. oförsiktiga landningar) än ben belastade enbart av muskler.

Trots att två av ovanstående modeller har sitt ursprung inom ingenjörsvetenskapen så är det ingen av dem som direkt bygger på grundläggande hållfasthetslära för att beskriva möjliga samband mellan generell kroppsstorlek och skelettets dimensioner. Utgångspunkten har varit det faktum att benvävnaden har konstant hållfasthet (mätt i kraft per ytenhet) och att fågeln behöver hålla den maximala belastningen under denna nivå för att inte drabbas av en fraktur. Därför har tre nya modeller tagits fram baserade på tre typiska så kallade belastningsfall:

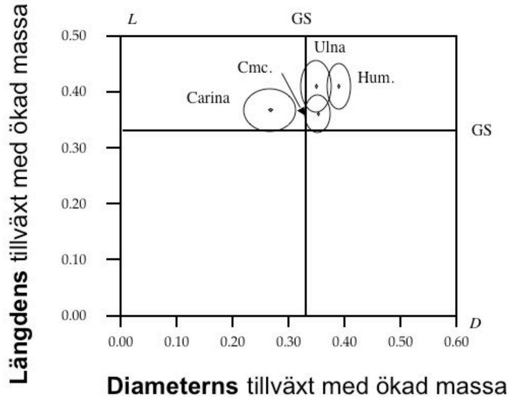
A. **Axial sammanpressning**, benet trycks samman i sin längdriktning.
B. **Knäckning**, benet trycks samman under sådana villkor att det böjs och sedan knäcks.
C. **Nedböjning**, benet dras åt ena hållet av en muskel och åt andra hållet av t.ex. vingens lyftkraft. Detta orsakar ett böjande moment inuti vingen.

Det finns självfallet flera andra belastningsfall, t.ex. vridning och skjuvning, men dessa gav antingen samma samband mellan bendimensioner och massa som något av fallen ovan, eller var svåra att tillämpa i ett biologiskt sammanhang. Eftersom de tre nya modellerna alla bygger på att hålla den maximala spänningen konstant har de alla fått det engelska namnet ”Static stress” men med tillägg ”Modell II-IV” för att skilja dem från ”Statisk stress” ovan. De tre nya modellerna är:

5. **Modell II – konstant maxspänning vid sammanpressning**
   Hur snabbt skall diametern öka för att trycket från kroppens massa eller muskler skall hållas konstant?
6. **Modell III – konstant maxspänning vid knäckning**
   Hur snabbt skall diametern öka för att risken för knäckning (orsakat av kroppsvikt eller muskler) skall hållas konstant? Egentligen är de aktuella benen troligen för korta för knäckning, men jag har ändå tagit med den i analysen.
7. **Modell IV – konstant maxspänning vid nedböjning**
   Hur snabbt skall diametern öka för att belastningen från en böjande kraft (orsakad av kroppsvikt eller muskler) skall hållas konstant?

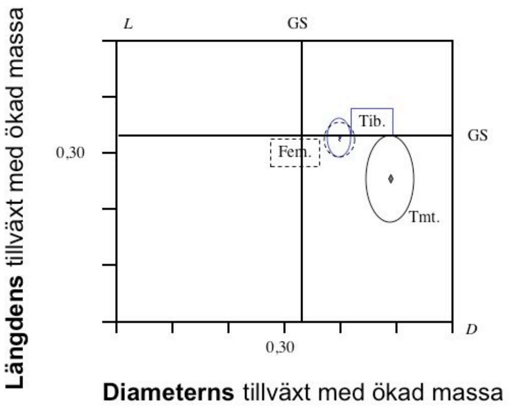
När modellerna skulle härledas visade det sig att alla tre modellerna hade två varianter; antingen orsakades belastningen av kroppsvikten eller av en muskelkraft. Eftersom kroppsvikten ökar i proportion till volymen, medan muskelkraften ökar i proportion till dess tvärsnittsyta, blev det två olika varianter på vardera modellen. Härledningar och vilka förutsägelser som de tre modellerna gav upphov till redovisas i artikel I.

Låt oss först titta på vingskelettets ben. Som framgår av figur 3 är samtliga vingben inklusive carina sterni (bröstbenskammen) längre än förväntat från geometrisk likhet, framför allt humerus (överarmsbenet) och ulna (det grövre underarmsbenet). Samtliga har även större diameter än förväntat, med undantag av bröstbenskammen.



Figur 3. Längdens och diameterns tillväxt med ökande massa för några ben i vingskelettet. GS anger geometrisk likhet, Cmc. carpometacarpus, Hum humerus, L benlängd och D diameter. D för carina sterni är höjden på kammen.

För benets skelett blir bilden delvis annorlunda, se figur 4. Lårbenet (femur) och underarmsbenet (tibiotarsus) följer geometrisk likhet väl, medan det sammanvuxna fotbenet (tarsometatarsus) är avsevärt kortare än förväntat utifrån geometrisk likhet.



Figur 4. Längdens och diameterns tillväxt med ökande massa för några ben i benskelettet. GS anger geometrisk likhet, Fem. avser femur, Tib. tibiotarsus, Tmt. tarsometatarsus, L benlängd och D diameter.

Vi skulle något förenklat kunna säga att vingbenen ökar mer i längd och grovlek med ökad massa än förväntat vid geometrisk likhet, allra mest humerus. Att längden ökar snabbare än förväntat kan hänga samman med att större fåglar måste öka vingytan för att behålla en rimlig vingbelastning. Att humerus ökar snabbare i grovlek stöder hypotesen att det är flygmuskeln som är dimensionerande för humerus.

Benskelettet ökar med ökande kroppsmassa som förväntat, eller mindre än förväntat, vid geometrisk likhet. Framför allt gäller detta fotbenet tarsometatarsus som proportionellt sett är avsevärt kortare och tjockare än förväntat hos de större fåglarna, och dessutom har den största variationen mellan arterna. Detta stöder hypotesen att ben som belastas av kroppsmassan, t.ex. vid en ovarsam landning, behöver vara grövre och gärna kortare än ben som enbart belastas av muskelkraft, inte minst det ben som alltid får ta första smällen, tarsometatarsus. Dessa resultat stöder hypotesen om dynamisk likhet.

Hypotes	**Totalt**		**Vinge**		**Ben**	
	Antal	%	**Antal**	%	**Antal**	%
1. Isometri eller geometrisk likhet	16	42 %	13	65 %	3	17 %
2. Elastisk likhet***	13	34 %	8	40 %	5	28 %
3. Modell I statisk stress likhet	5	13 %	1	5 %	4	22 %
5a. Modell II – sammanpressning (muskel)	2	33 %	2	67 %	–	
5b. Modell II – sammanpressning (kropp)	1	17 %	–		1	33 %
6a. Modell III – knäckning (muskel)	3	50 %	3	100 %	–	
6b. Modell III – knäckning (kropp)	1	17 %		–	1	33 %
7a. Modell IV – nedböjning (muskel)	2	33 %	2	67 %	–	
7b. Modell IV – nedböjning (kropp)	–		–		–	

Tabell 1. Sammanställning över vilka av de testade modellerna som fallit inom det 95%-iga konfidensintervallet, angett dels som antal, dels som andel av totalt antal möjliga fall.

Som framgår av tabellen ovan så stämmer de modeller som bygger på muskelkraft bättre med vingens skelett, medan de som bygger på kroppsmassa oftare stämmer in på benens skelett.

Artikel II. Skillnader mellan könen

I artikel II används kunskapen om hur de olika benen i ving- och benskelett förändras när fågelns generella storlek ökar för att tydliggöra skillnader mellan hane och hona inom samma art. Det är inte skillnaden i absoluta tal som av ses utan skillnaden mellan hona och hane om hanen hade förstorats isometriskt (alla längdmått ökar med samma proportioner) till samma massa som honan. På detta sätt kan skillnader som inte främst har sin grund i generella storleksskillnader sållas bort, och kvar finns de skillnader som skulle kunna ha sin grund i specifika anpassningar hos honan.

Det viktigaste resultatet är att hypotesen om att honan är större för att kunna hantera bristen på mat under tiden med ägg och ungar får starkt stöd. För så gott som samtliga arter har honan större andel bål och kortare ving- och benskelett än en hane med samma vikt skulle ha haft. Resultaten antyder också att det finns flera andra skillnader mellan hanar och honor som skulle kunna vara anpassningar till skillnader i t.ex. jaktbeteenden (se t.ex. Andersson och Norberg 1981). Här måste dock ytterligare fältstudier till för att kunna komma vidare. I inget av de ornitologiska verk som författaren har haft tillgång till görs någon skillnad på hanars och honors byten, jaktmetoder eller liknande.

Artikel III. Avvikelser från genomsnittet

I tredje artikeln används kunskapen om hela gruppens genomsnittliga samband mellan generell storlek och t.ex. en viss längd för att identifiera varje arts och köns speciella avvikelser. Skillnaden i vingskelett mellan glidflygare, ryttlare och aktiva flygare undersöks. En jämförelse mellan de fåglar som slår sitt byte med snabbhet och kraft (hitters) och de som framför allt griper tag i det (grabbers) görs. I tabell 2, nedan, har de viktigaste resultaten sammanställts. Som framgår av tabellen kunde sju av hypoteserna bekräftas medan tre av dem inte stöds av data.

Hypotes	**Resultat**
1. Glidflygare förväntas ha längre humerus, aktiva flygare kortare	**Stöds av data**!
2. Vindryttlande fåglar förväntas ha kortare vingben.	Stöds ej
3. Aktiva flygare förväntas ha större yta på bröstbenskammen där flygmuskeln fäster.	**Stöds av data!**
4. Snabba flygare förväntas ha mindre höjd på bröstbenskammen.	Stöds ej
4. ”Hitters” förväntas ha kortare och framför allt tjockare skelett i underben och fot.	**Stöds delvis av data**.
5. ”Hitters” förväntas ha längre lårben för att kunna ta upp energin från tillslaget.	Stöds ej
6. ”Grabbers” kan förväntas ha längre skelettelement i underben och fot.	**Stöds av data**.
7. Snabba ”grabbers” kan förväntas ha större diameter i underben och fot.	Stöds ej.
8. Långsamma ”grabbers” kan förväntas ha mer långsmala underben och fotben.	**Stöds av data.**
9. Grävare förväntas ha grövre skelett i underben och fot.	**Stöds av data.**
10. Fotbenet tarsometatarsus kan förväntas ha den största variationen av alla ben på grund av de varierande belastningarna.	**Stöds av data.**

Tabell 2. Översiktlig sammanställning över de olika hypoteser som prövats och resultaten av dessa prövningar.

Tack till personer och institutioner

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I

Allometry of Scandinavian raptors

By Per Florén

Abstract

Three traditional allometric hypotheses of allometry (geometric, elastic and static stress isometry) are tested, using measurements of bones of Scandinavian raptors. The hypothesis of dynamic similarity is discussed but the data available do not allow for testing it. Five new allometric relationships based on three types of loads (pressure, buckling and bending caused by forces proportional to body mass or muscle force) are introduced and tested.

The results show that all hypotheses, except one, fall within 95% confidence interval of at least one allometric relationship. Geometric and elastic similarities are most frequent but the other similarities do apply, too. The five new allometric hypotheses suggest the following: wing bones are adapted to resist muscle forces (both pressure, buckling and bending). Leg bones on the other hand are subjected to resist forces proportional to body mass, either to buckling (femur and tibiotarsus) or to pressure (carpometacarpus).

The results can also be interpreted in this way: Wing bones are longer but *not* significantly thicker (and therefore not stronger) than expected from isometry. Leg bones are significantly thicker (and therefore probably stronger) than expected from isometry, but isometric in length, except for tarsometatarsus, which is shorter than expected from isometry.

Introduction

The scope of ecological morphology is to identify how different morphological characteristics of animals are related to their ecological habitat and the animals' actions in this habitat or niche (see, for example, Norberg 1979, 1981, Zeffer et al. 2003). Classical examples among birds are the relationship between the form and size of the bill and how it is used for feeding (the most well known example is probably Darwin's finches), or the shape of the bird's foot and how it is used (Norberg 1979, Greenwalt 1975). One important aspect of morphology, and the subject of this article, is the role of size and how this influences the shape, construction and the behaviour of the animal.

History

One of the first scientists doing observations in this area was Galileo Galilei (1564–1642). Among other things he discussed how large a land animal could grow before it collapsed under its own weight (Galilei 1636). He concluded that neither terrestrial animals nor trees could grow beyond a certain size. These results were built on Euclid's (300 B.C.) and Archimedes (287-212 B.C.) rules of geometric similarity, stating that for "similar" geometrical bodies the corresponding surfaces increase as the square and volumes increase as the cube of linear dimensions.

Galilei also identified two strategies an animal or tree could use to meet the increasing demands when becoming larger:
1. Dimensions. Changing the proportions of the animal, for example thicker leg bones.
2. Materials. Using stronger material in the skeleton.

Science has since then been able to verify the first assumption and falsify the second and finally add a third, fourth and fifth strategy:

3. Design. Changing the geometry of the skeleton and bones (for example decreasing the curvature of a leg bone).
4. Dynamics. Changing the way the animals move (for example, do elephants neither run fast or jump).
5. Reduced safety margins. Larger animals could be living much closer to its margins than small animals do.

Another early and important contribution in this area was made by Borelli (1608-1679) who found that the force of a muscle was proportional to its cross-sectional area, whereas the "energy" that the muscle is able to deliver apparently varies in proportion to its volume (Günter 1975). He also calculated that two animals of similar build, but of different size, can jump the same actual height and that the maximal velocity they can reach is constant.

D'Arcy Thompson introduced dimensional analysis and similarity criteria into general biology. He studied the locomotion of terrestrial animals and the flight of birds from a physical point of view in his classic book "On Growth and Form" (1917).

The first scientists using the (allometric) power equation ($y \propto x^b$) was Snell in 1891 (Schmidt-Nielsen 1984, p. 25) and DuBois in 1898 (Stahl et al. 1967). This equation was later used in Julian Huxley's famous work "Problems of relative growth" (1932). Pennycuick (1967) did one of the first attempts to measure moments and factors of safety in the wing skeleton of a bird.

In the middle of the 1970:s McMahon (1973, 1975a, 1975b, McMahon et al. 1975c, 1983) and Alexander (1977, 1981, 1983, Alexander et al. 1975, 1977, 1979), brought the knowledge to a new and deeper level. Analysis was made not only of the static forces, but also on dynamic stress on, for example, the leg bones. An alternative to the traditional isometry (all lengths changing with the same proportion, also called geometric similarity) was presented by McMahon (1973, 1975a, 1975b) and McMahon et al. (1975c) and evaluated by him. Some more popular introduction to this subject is found in McMahon and Bonner (1983), Alexander (2003), and Schmidt-Nielsen (1970, 1984).

Some important concepts

Scale-effects. This concept does usually focus on the *qualitative changes* that occur with increase in size. For example, surface tension tends to be a dominating force in the lives of small organisms, whereas gravity plays a negligible role. The reverse is true for large organisms. A less obvious, but still very important, scale effect is the change of surface to volume ratio that already Galilei pointed out as the reason behind the statement: "No trees can grow to the sky".

Scale-model. When we use the word scale in the sense of "scale -model" we mean that some model is *qualitatively similar* to a prototype, with respect to one or more specific features. Scale-models are frequently used in wind-tunnel experiments. A model of an aeroplane or car, much smaller than the original, is tested to find out the best aerodynamic form.

Allometry. Allometry means "with the different measure". Huxley & Teissier (1936, quoted in Prothero 1986) defined allometry to "… denote growth of a part at a different rate from that of the body as a whole". Gould (1966, quoted in Prothero 1986) has used the term allometry much more broadly, to encompass "the study of size and its consequences".

> *"Real organisms usually are not isometric, even when organized on similar patterns. Instead, certain proportions change in a regular fashion … In biology, such nonisometric scaling is often referred to as allometric."*
> Schmidt-Nielsen 1984, p. 15

Scaling. Scaling may be regarded as a subfield of allometry, wherein the *structures are qualitatively similar* (for example: the wing of *Falco columbarius* and of *Aquila chrysaeto*s are both used for flight) in some well-defined sense. Granted qualitative similarity, our concern immediately shifts to quantitative considerations (for example: are there differences in dimensions of the skeleton?).

> *"…scaling deals with the structural and functional consequences of changes in size or scale among otherwise similar organisms."*
> Schmidt-Nielsen 1984, p. 7

Isometry or geometric similarity. Isometry means "with the same measure". Two forms are isometric only if the proportions are constant. The side of squares and cubes of different sizes are always isometric. An easy way to picture this is to think of a photographic enlargement. The proportions remain the same whether it is a small picture or a huge enlargement. This could also be described as:

> *"Any corresponding linear dimensions on two geometrically similar bodies, whether cubes, pyramids, cones, or more complex shapes, will be in the same constant proportion."*
> Schmidt-Nielsen 1984, p. 11

The central question of this article

The central question of this article is:

> How are the skeletons of Scandinavian birds of prey designed and dimensioned
> to meet the demands of the physical stress they meet in their natural life?

This means that the focus of this article is on the mechanical strength of the skeleton of the bird's wings and bones. Birds of prey are heavily dependent of their design to survive. Falcons need to be faster, more manoeuvrable than their prey. Hawks need to surprise their prey by flying just above the ground making quick turns around corners. Birds of prey are of different sizes from the smallest Falcons to the biggest Eagles. This makes them ideal for this type of research.

To do this the author used the allometric equation and the science of the strength of materials to analyse different suggestions of what forces acts on the skeleton, and what stresses this results in. Based on these alternative analyses three new allometric equations are identified (that is, equations describing relationships between different measurements, such as length and diameter of a bone and body mass). The three new allometric equations are tested together with the four traditional allometric equations, for example, geometric and elastic similarity.

Material and methods

Skeletons from Scandinavian birds of prey were measured and the data were used to test the different allometric equations. One problem is that birds of prey both differ much in size between the sexes and between different geographic areas. Males and females of the same species are treated as different groups, and data were used only from specimens found in Scandinavia. Skeletons came from the Natural History museums in Oslo, Copenhagen, Gothenburg and Stockholm. The species included in this work are presented in Table 1.

Table 1. Species used, their body masses m and number n of skeleton measured.

Species (Scientific and English names)		**Female**		**Male**	
		m kg	**n**	**m kg**	**n**
Pernis apivorus (Linné 1758)	Honey Buzzard	0.832	5	0.746	5
Haliaeetus albicilla (Linné 1758)	White-tailed Eagel	5.346	6	4.182	5
Milvus milvus (Linné 1758)	Red Kite	1.050	2	0.954	4
Circus aeruginosus (Linné 1758)	Marsh Harrier	0.716	5	0.550	5
Circus cyaneus (Linné 1766)	Hen Harrier	0.489	5	0.353	5
Circus pygargus (Linné 1758)	Montagu's Harrier	0.355	3	0.268	4
Accipiter gentilis (Linné 1758)	Goshawk	1.168	6	0.795	5
Accipiter nisus (Linné 1758)	Sparrow Hawk	0.258	8	0.154	5
Aquila chrysaetos (Linné 1758)	Golden Eagel	4.691	7	3.600	5
Buteo buteo (Linné 1758)	Common Buzzard	0.987	5	0.735	6
Buteo lagopus (Pontoppidan 1763)	Rough-legged Buzzard	1.035	5	0.850	5
Pandion haliaetus (Linné 1758)	Osprey	1.700	5	1.386	5
Falco columbarius (Linné 1758)	Merlin	0.195	5	0.165	5
Falco peregrinus (Tunstall 1771)	Peregrine	1.050	6	0.635	6
Falco rusticolus (Linné 1758)	Gerfalcon	1.693	5	1.090	5
Falco subbuteo (Linné 1758)	Hobby	0.260	6	0.170	5
Falco tinnunculus (Linné 1758)	Kestrel	0.215	6	0.173	6
Falco vespertinus (Linné 1766)	Red-footed Falcon	0.167	3	0.155	5

Measurements were made by slide calliper with an accuracy of ±0.1 mm. Bones longer than 130 mm were measured with a ruler with the accuracy of ±0.5 mm.

Body mass and external measurement

This work focuses on the bones of legs and wings including the carina sterni. The number of skeleton of each species and sex measured are presented in Table 1.

For each bone (except carina sterni) three measurements were taken, the maximum length, the maximum diameter on the narrowest part of the bone and the second diameter perpendicular to the first one. As Alexander et al. (1984) have shown the legs on left and right side do not differ significantly from each other. Therefore, only one wing and one leg were measured on each individual; see further Figs 2 – 4. The different symbols, constants and variables used are defined in Tables 2, 3 and 4.

Table 2. The symbols, constants and variables used in this article. The SI system is used, but note that measurements of lengths sometimes, for practical reasons, are presented in mm.

Symbol	Unit	Name	Definition
A	m^2	Area	
A_{muscle}	m^2	The perpendicular area of the muscle	
b	–	Allometric exponent	
D	m	Diameter of bone	See Figs 1, 2 and 3.
d	m	Diameter of bone	See Figs 1, 2 and 3.
E	N/m^2	Modulus of elasticity	A material constant
F	N	Force	
F_{muscle}	N	Muscle force	
F_{lift}	N	Lift force of a birds wing	
g	m/s^2	Gravitation	
I	m^4	Momentum of inertia	
K		Any constant	
l	m	Length	Dimension of length
L	mm	Measured lengths	Se Figs 1, 2, and 3 and Table 3 for definitions
m	kg	Mass, mostly body mass	
m_{muscle}	kg	Muscle mass	
$m_{skeleton}$	kg	Skeleton mass	
m	kg	Mass, mostly body mass	
mg	N	Weight	
M	Nm	Bending momentum	
S	m^2	Wing area	The area of both wings spread as in soaring flight, including the body area in between the wings.
V	m^3	Volume	
V_{body}	m^3	Volume of the body	
V_{muscle}	m^3	Volume of the muscle	
W	m^3	Resistance to bending	Depending of geometric form.
ρ	kg/m^3	Density	m/V
ρ_{body}	kg/m^3	Density of the body	m/V
σ	N/m^2	Stress from push or pull.	F/A
σ_{bone}	N/m^2	The strength of bone.	F/A
τ	N/m^2	Stress from shearing.	F/A

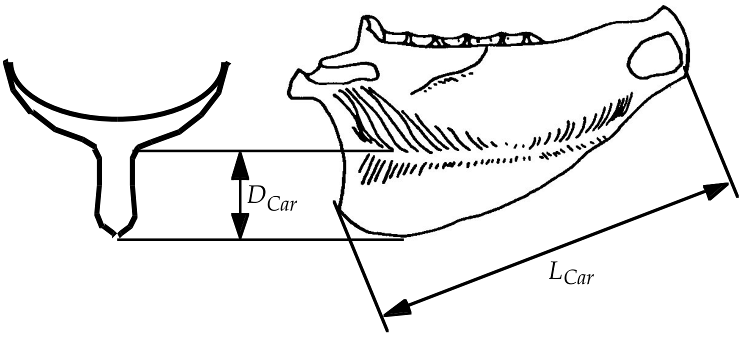

Figure 1. Measurements of carina sterni, as defined in Table 3.

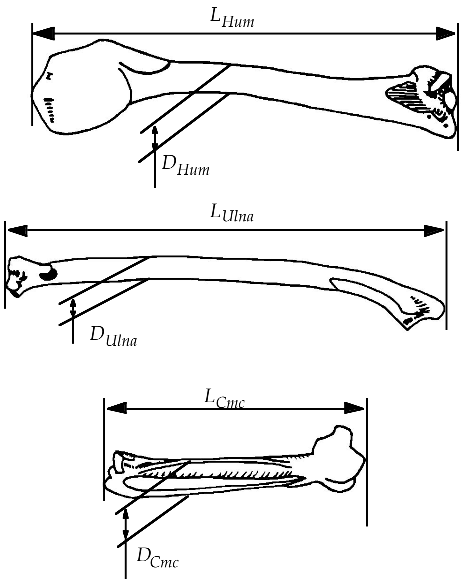

Figure 2. Measurements of the wing bones humerus, ulna and carpometacarpus, as defined in Table 3.

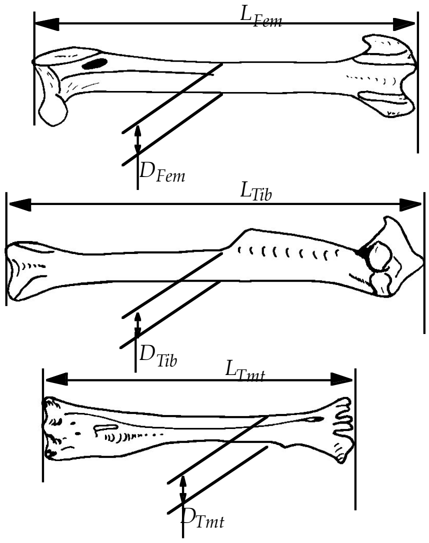

Figure 3. Measurements of the leg bones femur, tibiotarsus and tarsometatarsus, as defined in Table 3.

Table 3. The skeleton measurements measured and their symbols.

Bone	**Length**	**First diameter**	**Second diameter**
Humerus	L_{Hum}	D_{Hum}	d_{Hum}
Ulna	L_{Ulna}	D_{Ulna}	d_{Ulna}
Carpometacarpus	L_{Cmc}	D_{Cmc}	d_{Cmc}
Carina sterni	L_{Car}	D_{Car}	
Femur	L_{Fem}	D_{Fem}	d_{Fem}
Tibiotarsus	L_{Tib}	D_{Tib}	d_{Tib}
Tarsometatarsus	L_{Tmt}	D_{Tmt}	d_{Tmt}

To be able to evaluate as many allometric equations as possible it is necessary to obtain data of the body masses for the different species and sexes. Unfortunately, it was not possible to retrieve the masses of the individuals that later become the skeletons measured. Instead it became necessary to collect body mass data from other sources, mainly from ornithological literature (Bruun et al. 1978, Brown et al. 1968, Cerny 1984, Cramp et al. 1985, Forsman 1984, Glutz et al1966-82, Hagen 1942, 1952, Haftorn 1971, Rendahl 1935). Data was also collected from Nidingen's bird watch station and the Natural History Museum in Stockholm. As mentioned above birds of prey can differ relatively much between different geographical regions. Therefore, when possible, body mass used was from the same geographic region as the skeletons.

Data from different sources do not always coincide. When they did not, the different measurements had to be prioritised. The used criteria were:

1. Data from Scandinavia or close was prioritised over data from other geographical regions.
2. Data from wild living birds was prioritised over data from birds hold captive (Alexander et al. 1984).
3. Measurements that separated males and females were preferred to those who did not.
4. Measurements built on a larger number of individuals were preferred to measurements with fewer.
5. Original observations over quoted observations.

If different sources had the same priority related to these five aspects, and differed in numbers, the mean between them was used.

Theory and hypothesis

In this work three new and four old allometric equations will be presented and evaluated, but before this can be done we have to make some basic assumptions:

1. **The density of an animal body** is almost **constant** (≈ 940 kg/m^3 without feathers) for different animals of different sizes (Alexander 1983); the only exception is for large animals, much heavier than any bird.

$$\rho_{body} = constant \tag{1}$$

This means that volume and mass of a bird (or any animal) are proportional:

$$V_{body} \propto m_{body} \tag{2}$$

$$V_{muscle} \propto m_{muscle} \tag{3}$$

2. The **fraction of skeletal mass and muscle mass** to body mass is almost constant (skeletal mass ≈ 4-7% and muscle mass ≈ 55% of body mass) (Alexander 1983, Anderson et al. 1979, Brodkorb 1955, Prange et al. 1979 and Schmidt-Nielsen 1970), giving

$$m_{muscle} \propto m_{body} \tag{4}$$

$$m_{skeleton} \propto m_{body} \tag{5}$$

3. **The mechanical strength of bones** is close to constant (maximum stress from tension ≈ 150 * MN/m^2, maximum stress from pressure ≈ 240 * MN/m^2.) for birds and mammals of different sizes and species (excluded here are bones weakened by any physiological or medical

dysfunction) (Alexander 1981, Biewener 1982, Economos 1983, Maloiy 1979, Rubin et al. 1984 and Schmidt-Nielsen 1975). This means that Galileo's second suggestion, the one where he suggested that larger animals should have stronger bones, is not sufficient. This in turn means that the strength of a bone is limited by its size, and only by that.

$$\sigma_{bone} = constant \qquad (6)$$

4. The general form, length and geometry of a bone are probably genetically predestinated, but the thickness and therefore the **strength of the bone** can, if time is given, **adjust to the load** (Alexander et al. 1984, Mattheck 1984).

5. **The force a muscle can produce** can be take to be about proportional to its cross sectional area ($\approx 0.3 * \mathrm{MN/m^2}$). This means that the forces an animal can produce with its muscles are proportional to its size, when muscle fibre size, and density and physiology are taken to be similar (Alexander 1981, Hill 1950 and McMahon 1975b),

$$F_{muscle} \propto A_{muscle}. \qquad (7)$$

The allometric equation

The allometric equation is a powerful tool to describe and analyse different forms of allometric relationships (see for example Schmidt-Nielsen 1984, p. 14-17). The power equation has the form

$$y = a * x^b, \qquad (8)$$

where y is the measurement that one wants to compare between animals of different sizes, for example the length of humerus, "a" is a constant and x is a reference measurement, usually the mass of the animal. This equation can also be written in the form

$$y \propto x^b \qquad (9)$$

or in logarithmic form as

$$\log y = \log a + b * \log x. \qquad (10)$$

The latter is the equation of a straight line with the intercept log a and the slope b. This means that any method for linear regression, for example least square regression (LSR) method, can be used to determine the values of b and log a for a given set of x and y. (The theoretical background for the allometric equation can be found in Günter 1975 page 673-675)

There have been some critics of the frequent, and sometimes uncritical, use of linear regression on log-transformed data in allometric scaling (see, for example, Smith 1980, 1984a). The critique often focuses on the use of relative size of data (for example brain mass or metabolic power relative to body mass) and questions if power functions really emerge from simple models of biological system. It points out that plotted log-transformed data tend look very convincing and that a strait line in a log-log-plot does not guarantee that we have found some new biological "law". It also questions if organs, for example brains, of the same size always are equal in functionality, and if comparisons of size therefore is relevant. Finally the reviewer wants to se more use of "a priori equations conceived on theoretical grounds" not just "post hoc interpretations" (Smith 1984). One typical example is this quotation:

> *"The point is not that there is anything inappropriate about logarithmic transformations… The argument presented here is that the exclusive and uncritical use of log-log transformations has lead to misinterpretations in the analysis of relative size data."* (Smith 1980 p. 99)

The critique has been shown not to be fully relevant (Harvey 1982). Prothero (1986) has shown that:

> *"…if a power function gives a reasonable fit to bivariate data extending over three or more orders of magnitude in the x-direction and two or more orders in the y-direction, and if the exponent is removed from either zero or one, then a linear equation will always give a poorer fit, and usually a much poorer fit to the data."*

The critique is really not relevant to the use of allometric scaling of size and strength of bones in legs and wings. Based on the predictions of geometric and elastic similarity, for example, we have reasons to believe we have a power function explaining the data, and therefore it is reasonable to do the log-log-transformation, and to expect a strait line with a certain slope. We also know that the mechanical properties of bones and muscles are nearly constant between species.

Calculation of values of the allometric equations

The allometric exponent *b* was obtained in the following way:

1. All variables (lengths and diameters of bones and body masses) were logarithmised.
2. The equations for the regression line were calculated with help of the least squares method of regression (LSR) using Stat View 4.0 for Mac OS. For each regression standard error, R2, maximum and minimum values for 95% confidence interval were calculated.

Some authors (Kermack et al. 1950, Pagel et al. 1988 and Rayner 1985) have argued that other methods of regression may give more reliable values, for example Major Axis (MA) or Reduced Major Axis (RMA) (Smith 1984b gives a number of examples of articles where the different regression methods are used), especially when the variation in the data set is large.

Other authors are more sceptical. Alexander (1983), for example, compared the two regression methods (LSR and MA) described by Sokal and Rohlf (1981) and found that the two models only differed in the third significant figure. And Seim et al. (1983) p.161 commented on the use of the three methods for regression (LSR, MA & RMA):

> *"None of the methods have universal application. The three methods give rise to the same conclusions only in data-sets with very high correlation coefficients."*

Prothero (1986) discussed which regression method to use. He concluded that:

> *"In practice, when the correlation coefficient is high (r > 0.95), it will make very little difference which method is used."*

Considering the uncertainties with the data used and the small differences between the results of the alternative methods I have used the least squares regression method, for which computer programs are available, and thus is easier to use.

Prediction 1. Isometry or geometric similarity

When two animals are isometric (geometrically similar) the two animals, although different in size, are identical in form and proportions. This means that all lengths of the two animals differ with the same factor (if the leg is twice as long, then the wing should be twice as long and wide, too). Examples of isometric organism are sea mammals of different sizes (Economos 1983).

In geometrically similar animals a typical area A (for example the perpendicular area of the humerus at its waist) is proportional to a typical length l squared (for example the length of the humerus). And the body volume V is proportional to a typical length l raised to the exponent 3. And as the body density is (almost) constant (eq. 1) body volume and body mass are proportional too. We then (using eq. 2) get the following relationships between length, area and volume/mass:

$$l \propto V_{body}{}^{1/3} \propto m_{body}{}^{1/3} \tag{11}$$

$$A \propto l^2 \propto V_{body}{}^{2/3} \propto m_{body}{}^{2/3} \tag{12}$$

$$V \propto l^3 \propto V_{body}{}^{3/3} \propto m_{body}{}^{3/3} = m_{body} \tag{13}$$

Based on the above assumptions and relations a number of allometric exponents "*b*" can be predicted for relations between length, diameter, area, and volume/mass see Table 4. These exponents will be found if animals are geometrically similar.

Problems with geometric similarity and gravity

Many writers have pointed out that isometric animals of different sizes will have problems when confronted to gravity, or as already Galilei (1636) pointed out:

> *"…nature cannot grow a tree not construct an animal beyond a certain size, while retaining the proportions which suffice in the case of a smaller structure"*

The reason for this is that the perpendicular surface of a bone increases with a factor four (the square of two, eq. 11) if all lengths increase with a factor two, and the volume, and therefore the body mass, will increase with a factor eight (the cube of two, eq. 12). The result of this is that the load of the bone, due to body weight, will double, when size doubles, but the strength of the skeleton is constant.

How do animals solve the problem of increased loads from mass and gravity? The consequences of increased loads would be that animals large enough would collapse under their own weight. But problems will occur much earlier since the safety margins will decrease, when the animal gets bigger. Less will be needed to break a bone and injuries will become more frequent.

The same kind of problem will arise from the increase of wing loading (force/wing area) due to isometric growth. When wing loading increases the bird will have to increase the speed needed for take off and its flight capabilities will decrease substantially, for example, the abilities to make turns, to fly slowly, to soar etc. There are, as we already has seen, five possible answers to this challenge:

1. Dimensions. Animals of larger sizes could develop relatively **thicker**, and therefore **stronger, bones**. This has been shown for example for mammals (Anderson et al. 1979, Biewener 1982, Prange et al. 1979, Schmidt-Nielsen 1975). But it is not enough to say that the bones become thicker for heavier animals, we also want to know the "principles" behind the increased bone diameters. One suggested principle is elastic similarity (prediction 2); four other suggestions are presented below and have been tested (predictions 3, 5.6 and 7).

2. Materials. Animals of larger sizes could use **stronger materials** in their bones. Birds or mammals have **not used this alternative**; they all have skeletons of roughly the same strength (Alexander 1981, Biewener 1982, Economos 1983, Maloiy et al. 1979, Rubin et al. 1984, Schmidt-Nielsen 1975). This alternative was therefore not tested in this study.

3. Design. Animals of larger sizes could change **the geometry of the bones and the skeleton** to decrease the stress from the animals weight and movements. This has been shown, for example, in the decreased curvature of humerus and tibia for a number of mammals (Biewener 1982 and 1983, Schmidt-Nielsen 1975). Another example is the change from compression to tension elements in skeletons (Schmidt-Nielsen 1975). This was not tested in this article.

4. Dynamics. Animals of larger sizes could **move in a way that decreases the maximum loading** of the bones (Alexander et al. 1983, Biewener 1983, Maloiy et al. 1979, Rubin et al. 1984).. Elephants do not run fast or jump, which limits the maximum loading of the bones substantially. To understand this aspect we have to take the birds' behaviour into account. How do they move, fly and hunt? The dynamic forces of a bone can arise from two sources:
1. muscle force, or from
2. the combination of body mass, velocity and gravity.
It is suggested that loads from muscle force is more predictable and that bones loaded from muscle force therefore do not need as large safety margins as bones loaded with mass/velocity loads. This aspect will be cowered in prediction 3 below.

5. Reduced safety margins. Animals of smaller sizes have much **larger safety margins** than needed. This is against the general principles that nature do not use more material or energy than necessary, but there are a number of examples of this. It has been shown (Economos 1983, Biewener 1982) that a mouse can coop with gravitation seven times stronger than normal. Perhaps it is not the larger animals that have low safety margins; perhaps it is the small animals that have extremely high safety margins? This suggestion will not be tested in this article.

Comments about physical similarity:

Günter (1975) defined four different kinds of physical similarity:
1. Dynamic similarity. Two systems are said to be dynamically similar if homologous parts of the systems experience similar net forces.
2. Kinematic similarity exists when the motions of two systems are similar
3. Hydrodynamic similarity. In similar flow the ratio of inertial to viscous forces must be the same at corresponding points.
4. Thermic similarity exists between prototype and model when temperature distribution and heat flow at homologous areas are both similar.

Prediction 2. Elastic similarity

If an organism, be a bird, mammal or tree, does not follow geometric similarity (for example bone length and bone diameter do not change proportionally) then what law does it follow? The most frequent alternative suggestion is called elastic similarity and predicts that lengths and diameters (defined at right angle to the length) scale differently but in a predicable way.

The idea of elastic similarity has its origin in the science of engineering, where it was used as a rule of thumb in constructing, for example, bridges. Rashevsky (1960) and most of all McMahon (1973, 1975a and 1975 b) introduced it in the biological science. Other examples of important works in the area are Alexander (1977), Maloiy et al. (1979) and McMahon et al. (1976). Elastic similarity can be derived in at least three different ways.

Alternative 1. Imagine a beam or, if you want to be more zoological, the trunk of a horse with cylindrical shape (with length l and diameter d) resting on one support in each end (see Fig 5). The rod will now, because of its own weight, bend down in the middle, more or less depending on material (strength, density, elasticity), diameter and length of the beam.

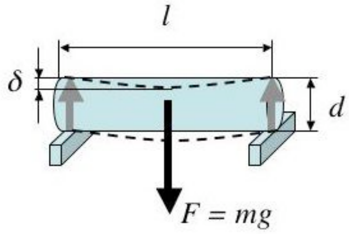

Figure 4. The figure illustrates the force, F acting on a beam of length l and width d due to mass m and gravity g. See the text for details.

If the thickness of the beam is adjusted so that the quotient δ/l (where δ is the maximum distance the beam bends down and l is the length of the beam) is held constant, for different lengths, the construction will not fail (McMahon 1975, McMahon and Bonner 1983, p. 128). This criterion will be fulfilled if length and diameter follow the relation $l^3 = constant * d^2$.

Alternative 2. Consider a tall, slender cylindrical column of length *l* and diameter *d* loaded by the force *F*, representing the total weight of the column, acting at the center of mass. Such a column will fail in compression if the applied stress, from its own weight, exceeds the maximum compressive stress. It may also fail in what is known as elastic buckling, whereby a small lateral displacement allows the weight to apply a toppling moment, which the elastic forces of the bent column below are not sufficient to resist. This may happen if the column is lender enough, which is if *l*/*d* is greater then 25. This can of course be the case in for example trees but seldom in animals including birds.

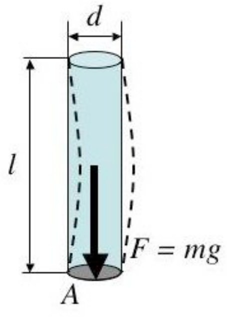

Figure 5. The figure illustrates the force F acting on a beam of length l and width d when loaded by its own mass m and gravity g. See the text for details.

The critical length for such a column (or cone) to buckle under its own weight is:
$l = constant * d^{2/3}$ where the constant includes the elastic modulus E and the density ρ of the column or cone (McMahon 1973).

Alternative 3. The third, and perhaps most interesting, way to derive the relation of elastic similarity starts with considering the forces acting on hind limb of a walking or running quadrupedal animal (McMahon and Bonner 1983 pp. 133-135). Although not mentioned in the example the situation of a bird's leg is very much the same.

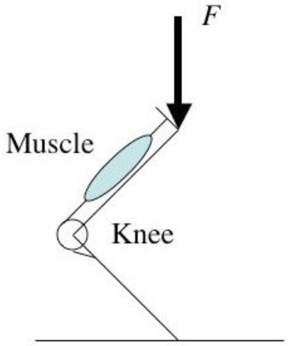

Figure 6. The figure illustrates the force F acting on a leg and a knee due to mass and gravity. See the text for details.

The boundary between stable and unstable conditions is reached when the increase in extending torque generated by the small movement of the femur is equal to the increase in buckling torque contributed by the same movement. Therefore, the condition of neutral stability is found by setting the change of "extending torque" equal to the change of "buckling torque". This will result in an equation $l = constant * d^{2/3}$, where the constant includes the elastic modulus E. This is the same equation that we found in alternative 1 and 2 and as equation 14.

There are a number of ways to end up with the same elastic criterion for a stable construction

$$l^3 \propto d^2, \qquad (14)$$

which could be rewritten to

$$d \propto l^{3/2}, \qquad (15)$$

or to

$$l \propto d^{2/3}. \qquad (16)$$

The mass of the rod, column etc. can be written as

$$m \propto d^2\, l \qquad (17)$$

and inserting equation (15) we get

$$l \propto m^{1/4} \qquad (18)$$

and inserting equation (16) we get

$$d \propto m^{3/8}. \qquad (19)$$

The coefficients expected for elastic similarity are presented in Table 4.

Comments about elastic similarity:

Economos (1983) argued (based on measurements of body mass, head and body length) that small mammals (≤ 20 kg) follow geometric similarity and larger animals (> 20 kg) follow elastic similarity. In his paper from 1984 he puts the line between small and big animals at 100 kg (based on measurements of body mass and height at the shoulders), but the idea is the same: Elastic similarity is not valid for smaller mammals. Economos said nothing about birds but if we generalise his arguments to birds they would not be expected to follow elastic similarity.

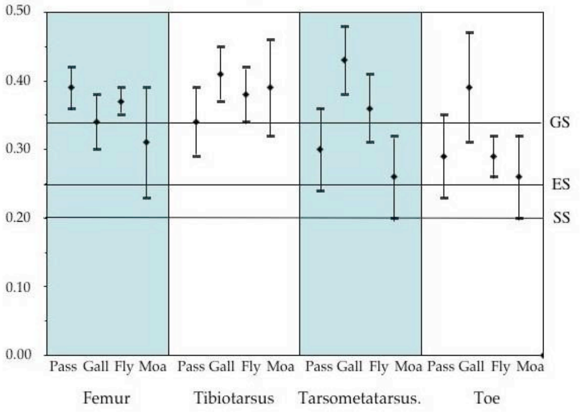

Figure 7. The result of Alexander's analysis of the length of femur, tibiotarsus, tarsometatarsus and the toe of three groups of birds where Pass is Passeriformes, Gall is Galliformes, Mos is Anomalopterygidae, and Fly is the result of all flying birds in the examination. The mean value, upper and lower 95% confidence intervals for each group are inserted. The horizontal lines mark the values of b predicted by the different hypotheses, GS for Geometric similarity, ES for Elastic similarity, SS stands for Static stress similarity.

Alexander et al. (1979b) showed that the length and diameter dimensions of limb bones in 37 species, ranging in size from 0.03 - 2 300 kg, scale geometrically with the animal's body size. The same type of arguments is used by Peters (1983, p217).

Alexander (1983) tested if geometric or elastic similarity offered the best fit for the leg bones and toes of a number of species from the groups Passeriformes, Galliformes and Anomalopterygidae (the extinct Moas). The resulting exponents in Fig 7 for bone lengths of flying birds are all significantly larger than the expected exponent predicted by elastic similarity ($b = 0.25$). But, on the other hand, for the Moas elastic similarity was the better hypothesis for femur, tarsometatarsus and toe.

One could describe the world of elastic similarity as a four-dimensional world, where length and diameter are separate dimensions that cannot be substituted, as did Günter and Morgado (1982).

Prediction 3. Static stress similarity (model I)

The idea of static stress is closely related to the derivation of elastic similarity, alternative 1. Imagine a number of beams, made of the same material and with the same cross-sectional shape bending under their own weight.

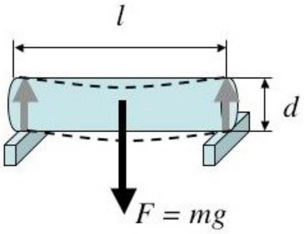

Figure 8. The figure illustrates the force F acting on a beam of length l and width d due to its own mass m and gravity g. See the text for details.

This time the relationship between length and diameter should be adjusted so that the average, compressive stress σ in the top half of the beams will be constant (McMahon 1975a). It can be shown that if diameter d and length l of the beam has the following relationship the criteria of constant average stress is fulfilled:

$$l \propto d^{1/2} \qquad (20)$$

It can be shown that the relation between l and d will be the same if maximum stress is considered instead of average stress. Based on the constant density of mammal and bird bodies a number of predictions can be made. These are presented in Table 4.

This prediction has, as far as the author knows, only been used in (McMahon 1975a) where it was concluded that:

> *"Elastic similarity provides the best comparison with data on gross morphometry, body surface area, metabolic power, and the kinematics of locomotion."*

Although not popular, it seems reasonable to test this prediction together with the other predictions.

Prediction 4. Dynamic stress similarity

The predictions of elastic and static stress similarity have their focus on the static loads of body mass and how the limbs have to be redesign to meet the increased load when animals get bigger. In some cases this has turned out to be true, in some cases not, as has been shown above (Fig 7).

Based on the findings of Alexander et al. (1979b) of geometrically similar limb bones of 37 species Biewener (1982) calculated that a seven-fold increase in peak compressive stress and a 6.5-fold increase in the peak bending stress would occur in the limb bones with every 1000-fold increase in animal mass. One way to meet this increased stress is of cause to use stronger materials, but as we know, this is not a solution used among birds and mammals. So, if the material strength of bones is constant, this implies that large animals have a smaller safety margins than small animals, or that small animals are "wasteful" with bone tissue and are built to have unreasonably high safety margins. Thus, either the skeletons of small animals are drastically over-designed, or large animals are in constant danger of structural collapse (Biewener 1982). Both alternatives are evolutionary uncomfortable. Is there any other explanation?

Rubin and Lanyon (1984) have shown that the peak functional strains measured from bone-bonded strain gauges in a range of animals during their customary activity, “are remarkably similar”. Rubin and Lanyon have also shown that the safety factor to failure for five terrestrial vertebrates during fast running is almost the same ranging from 3.0 (for Turkey) to 2.2 (for Buffalo). They suggested that the axial forces produced in the bone are not proportional to the mass of the animal but to the cross sectional areas of the musculature. This might be the explanation behind the constant safety factors as both musculature and bone cross sectional area scale to mass with the exponent $b = 2/3$ (eq. 12). Rubin and Lanyon comment on the difference between elastic and dynamic strain similarity:

> *“It appears from the data presented here that large animals avoid dangerous levels of limb bone stress through another form of elastic similarity, which entails allometrically scaling the locomotory forces imposed on them.”*

Another author that emphasis the focus of dynamic stress similarity in favour of elastic stress similarity is Günter (1975, p672) who wrote:

> *“As a general rule, we may state that dynamic similarity is the main factor when we are analyzing mechanical problems, where gravitational forces predominate – movements of the head, legs, and of the body in general, related to skeleton, joints, and tendons and caused by the contraction of striated musculature.*

A method larger animals can use to reduce peak force (and ensure a reasonable factor of safety) in their limb bones, is to increase the fraction of the stride period that a given limb is in contact with the ground (Alexander 1977, Biewener 1982, 1983). Alexander (1981) performed an extensive analysis on how the optimization of factors of safety could be understood in the light of the probability and cost of failure, the cost of growing the component, and the associated use of the component. He concluded:

> *“Low factors of safety are feasible for structures such as tendons and apodemes subject to closely predictable loads, but higher factors of safety must be expected were loads are highly unpredictable.”*

One result of this is that bones that normally are loaded only with forces that are predictable, that is, forces produced only by the animal’s own muscles, would be expected to have substantially lower safety margins than bones with unpredictable loads. Such loads can be produced by, for example, falling, jumping, landing or from being hit by something. Unfortunately, the hypothesis of dynamic stress similarity cannot provide predictions about the relationships between length, diameter and mass without having knowledge of the dynamic forces acting on the limbs and body of the animal during its natural movements. But Alexander’s analysis of the optimization of factors of safety predicts that the birds wings, with mostly predictable loads, can have significantly lower safety factors compared to the factors that the legs can have. This is supported by the findings of Prange et al. (1979):

> *“…the avian skeleton is not proportionately lighter than that of mammals. Pneumatization may make some birds bones lighter, but the leg bones of birds are more robust than those of mammals. This results in an internal redistribution rather than a reduction of skeletal mass.”*

A few conclusions can be made based on what is said above about dynamic similarity:

1. Bird wings, which normally are loaded with predictable forces, will be loaded with unpredictable forces if they collide with, for example, wires or tree branches. If colliding during flight is a common problem in the bird's habitat, then we would expect the safety margins of the wing bones to be larger than average.
2. If the mechanical construction of the bird's leg can meet the forces of impact during landing and restrict the forces acting on the leg bones so they never exceed the muscle forces, then the bones of the legs can have reduced safety margins. (A human example is that of the parachutist who does not land with straight legs.)

Alexander et al. (1983) described the **dynamic similarity** which basic idea is that:

> *"The dynamic similarity hypothesis predicts that various gait parameters* x *will have equal values for quadrupedal mammals of all sizes and taxa, whenever they walk or run with equal Froude numbers* u^2/gh*."*

This hypothesis is not relevant for this work.

Prediction 5. Static stress similarity (model II breaking) – new approach

In the theory of static stress, the main principle is to assume that the maximum stress in a beam needs to be held constant, as the strength of the skeleton is constant. But it does not seem reasonable to compare a bird with a beam resting on its both ends. An alternative is to analyse the situation in a column, where a force F acts on the top of the beam with a cross sectional area A and maximum stress of σ_{max}. (This could, for example, be a simplified model of the situation for the tarsometatarsus.) The maximum stress σ at the cross sectional area A (see Fig 9) has to be smaller than the maximum stress σ_{max} of the material of the column,

$$\sigma_{max} \geq \sigma = F/A. \qquad (21)$$

If we consider the situation where $\sigma_{max} = \sigma$ and the bone cannot stand any more stress without breaking we get

$$\sigma_{max} = constant = F/A \qquad (22)$$

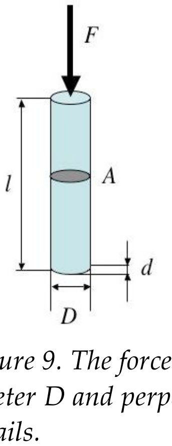

Figure 9. The force F acting on a beam of length l and with elliptic cross section area A (maximum diameter D and perpendicular to this the diameter d) in static stress similarity (model II). See the text for details.

This could be rewritten in the form:

$$F = constant * A \qquad (23)$$

or even simpler

$$F \propto A, \qquad (24)$$

where A is proportional to D and d

$$A \propto D * d. \qquad (25)$$

In the measurements of this article D is the maximum diameter at the waist of the bone, and d is the diameter perpendicular to D. When the cross sectional area is circular $D = d$, but more common is that the area is elliptical and therefore $D \neq d$.

We now have two alternatives for the force F acting on the column:
Alternative 1. The force F is due to the mass m of the bird, which gives us $F \propto m$
Alternative 2. The force F is due to some typical muscle force in the bird, which is proportional to the cross sectional area of the muscle. If we assume that the mass of the muscles is (almost) a constant fraction of the body mass (eq. 4) and that the cross sectional area of the muscle is proportional to $m^{2/3}$ (eq. 12) we get $F \propto m^{2/3}$.

Alternative 1. Using $F \propto m$ in equations (24) and (25) we get

$$m \propto D\, d. \qquad (26)$$

Alternative 2. Using $F \propto m^{2/3}$ in equation (24) and (25) we get

$$m^{2/3} \propto D\, d. \qquad (27)$$

But this alternative suggest the same relation between body mass and bone diameter as we would get from geometric similarity, so in fact it is only alternative 1 that is a new approach. The prediction for Static stress similarity (model II) is presented in Table 4.

Prediction 6. Static stress similarity (model III buckling) – new approach

Let us consider the situation described as alternative 2 under elastic similarity but assume that the force does not come from the weight of the column itself, but from some other force, as we did in prediction 5. We then have a column loaded with a force F and with a cross sectional area A proportional to the diameters D and d, see Fig 10. If we now study the alternative that the force F forces the column not to break (see prediction 5) but to buckle under the stress, what kind of relation between D, d and body mass m do we then get?

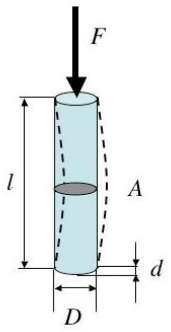

Figure 10. The figure illustrates the force acting on a column due to body mass and gravity or some muscle force. The same abbreviations are used as in Fig 9. See the text for details.

The maximum force that can be applied before the column buckles is (Bodelind et al. 1972)

$$F_{max}= \pi^2 E\ I/l^2, \tag{28}$$

where E is a material constant and I is a form dependent factor. For rods with elliptical cross sectional area I is

$$I=\pi\ dD^3/64, \tag{29}$$

and when I in equation (28) is substituted with equation (29) we get

$$F_{max} \propto dD^3/l^2. \tag{30}$$

We now have two alternatives for the force F acting on the column:
Alternative 1. The force F is due to the mass m of the bird, which gives us $F \propto m$
Alternative 2. The force F is due to some typical muscle force in the bird, which is proportional to the cross sectional area of the muscle. If we assume that the mass of the muscles are (almost) a constant fraction of the body mass equation (4) and that the cross sectional area of the muscle is proportional to $m^{2/3}$ (using equation 12) we get $F \propto A \propto m^{2/3}$

Alternative 1. Using $F \propto m$ in equation (30) we get

$$m \propto dD^3/l^2. \tag{31}$$

Alternative 2. Using $F \propto m^{2/3}$ in equation (30) we get

$$m^{2/3} \propto dD^3/l^2. \tag{32}$$

The prediction for Static stress similarity (model III buckling) is presented in Table 4.

Prediction 7. Static stress similarity (model IV bending) – new approach

A third way to load a beam, or a bone, is shown in Fig 11. This situation seems to be very similar to the situation of, for example, the humerus, but a more detailed analysis of the mechanics of the bird wing is needed to show if this is true. Assuming that this loading situation occurs, what should then the allometric consequences be?

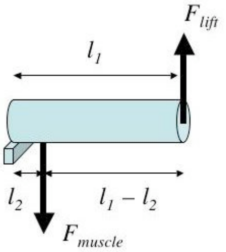

Figure 11. The figure illustrates muscle and lift forces acting in bending a beam. See the text for details.

The maximum stress σ at the cross sectional area A of the beam has to be smaller than the maximum stress σ_{max} of the material of the beam,

$$\sigma_{max} \geq \sigma = M_{max} / W, \qquad (33)$$

where M_{max} is the maximum moment in the beam, which is located at the point of F_{muscle} (se Fig 11), and W is a form dependent factor describing the beams resistance to bending, and

$$M_{max} \propto W. \qquad (34)$$

For a beam with elliptic cross section W is

$$W \propto d\, D^2, \qquad (35)$$

and M_{max} is

$$M_{max} = F_{lift}\,(l_1 - l_2), \qquad (36)$$

where the lengths l_1 is the length from the joint to the point where the lift force is applied to the beam and l_2 is the length from the joint to the point where the muscle attaches. If we assume that the proportions between l_1 and $l_1 - l_2$ is constant (that is to say $l_1 \propto l_1 - l_2$), we could rewrite the equation (36) as

$$M_{max} \propto F_{lift}\, l_1. \qquad (37)$$

If we substitute M_{max} and W in equation (34) with equation (37) and (35) we get

$$F_{lift}\, l_1 \propto d\, D^2, \qquad (38)$$

which is equal to

$$F_{lift} \propto d\, D^2 / l. \qquad (39)$$

We now have two alternatives for the force F acting on the beam like in prediction 5 and 6:
Alternative 1. The force F is proportional to the mass m of the bird, which gives $F \propto m$.
Alternative 2. The force F is proportional to some typical muscle force in the bird, which gives $F \propto m^{2/3}$.

Alternative 1. Using $F \propto m$ in equation (39) we get

$$m \propto dD^2/l. \qquad (40)$$

Alternative 2. Using $F \propto m^{2/3}$ in equation (39) we get

$$m^{2/3} = dD^2/l. \qquad (41)$$

The prediction for Static stress similarity (model IV) is presented in Table 4. These predictions can be tested; number 1-10 and 13-18 have been tested in this study. The results of these tests are presented below.

Table 4. Summary of the allometric predictions. GS Geometric similarity, ES Elastic similarity, SS Static stress similarity, SS (II) Static stress similarity (model II breaking, force from body mass or muscle force), SS (III) Static stress similarity (model III buckling, force from body mass or muscle force), SS (IV) Static stress similarity (model IV bending, force from body mass or muscle force).

No.-	Y-variable	X-variable	Similarity	Exponent *b*	Numerical value
1	Length (l)	Mass (m)	GS	1/3	0.333
2	Length (l)	Mass (m)	ES	1/4	0.25
3	Length (l)	Mass (m)	SS (I)	1/5	0.2
4	Diameter (D or d)	Mass (m)	GS	1/3	0.333
5	Diameter (D or d)	Mass (m)	ES	3/8	0.375
6	Diameter (D or d)	Mass (m)	SS (I)	2/5	0.4
7	Area ($D * d$)	Mass (m)	GS	2/3	0.667
8	Area ($D * d$)	Mass (m)	ES	6/8	0.75
9	Area ($D * d$)	Mass (m)	SS (II) (muscle)	2/3	0.667
10	Area ($D * d$)	Mass (m)	SS (II) (body)	1	1
11	Volume ($l * D * d$)	Mass (m)	GS	1	1
12	Volume ($l * D * d$)	Mass (m)	ES	1	1
13	(dD^3/l^2)	Mass (m)	GS	2/3	0.667
14	(dD^3/l^2)	Mass (m)	SS (III) (muscle)	2/3	0.667
15	(dD^3/l^2)	Mass (m)	SS (III) (body)	1	1
16	(dD^2/l)	Mass (m)	GS	2/3	0.667
17	(dD^2/l)	Mass (m)	SS (IV) (muscle)	2/3	0.667
18	(dD^2/l)	Mass (m)	SS (IV) (body)	1	1
19	Length (l)	Length (l)	GS	1	1
20	Length (l)	Length (l)	ES	1	1
21	Diameter (D or d)	Length (l)	GS	1	1
22	Diameter (D or d)	Length (l)	ES	3/2	1.5
23	Diameter (D or d)	Length (l)	SS (I)	2	2

Results

As mentioned in the introduction, the central question of this article is:

> How are the skeletons of Scandinavian birds of prey designed and dimensioned to meet the demands of the physical stress they meet in their natural life?

How do the bones' length and diameter increase with body mass?

Fig 12 shows how the length *L* (y-axis) and the diameter *D* (x-axis) of humerus, ulna, carpometacarpus, carina sterni, femur, tibiotarsus and tarsometatarsus increase with body mass. The ellipses indicate the 95% confidence interval.

The two lines marked GS indicate the level of isometric growth. If the value of a bone length is over this line the bone increase more in length than expected from isometry. If the value of a diameter is to the right of the line the diameter increase more than expected from isometry.

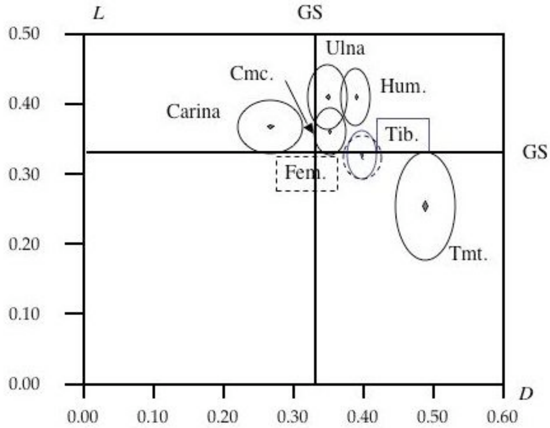

Figure 12. The results of the analysis of length L *and diameter* D *in relation to body mass. Further details can be found in the text. Hum. is humerus, Cmc. is carpometacarpus, Fem. is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. GS is the level of geometric similarity (0.33).*

The wing bones, humerus, ulna and carpometacarpus, all increase more with body mass than expected from isometry, both in length and in diameter. Humerus increases more in diameter than the other two wing bones, and carpometacarpus less in length.

Carina sterni increases more than expected from isometry in length but less in diameter, or height (se Fig 1 for definitions of the measurements of carina sterni).

Femur and tibiotarsus increase isometrically with body mass and more than expected for isometry in diameter. Tarsometatarsus increases much less in length with body mass than expected from isometry, but much more than expected in diameter. Tarsometatarsus is the bone with the largest confidence interval of all bones.

All bone measurements are listed in Appendix 1 and the results of the regressions are given in Tables 5 and 6.

Do the size of the bones follow geometric, elastic or static stress similarity?

Now we have seen how bones relate to isometry or geometric similarity. How do the bones relate to elastic and static stress similarity?

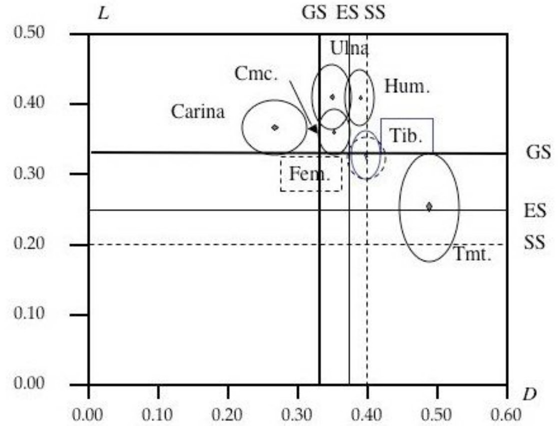

Figure 13. The results of the analysis of length L *and diameter* D *in relation to body mass. Further details can be found in the text. Hum. is humerus, Cmc. is carpometacarpus, Fem. is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus.*
GS is the level of geometric similarity, ES of elastic similarity and SS static stress similarity model I.

Humerus, ulna and tarsometatarsus are all well above both elastic and static stress similarity regarding length. Regarding diameter we can se that humerus has both elastic and static stress inside its 95% confidence interval while ulna and carpometacarpus has geometric and elastic similarity in theirs.

Carina sterni is found on the opposite side of the line for geometric similarity, compared to elastic and static stress similarity, in both length and diameter.

Femur and tibiotarsus are well above both elastic and static stress similarity for length and almost exactly on static stress regarding diameter, although elastic similarity is just inside the 95% confidence interval.

Tarsometatarsus is close to elastic similarity for length, although both geometric and static stress are both within 95% confidence interval. Regarding diameter tarsometatarsus is well above all three similarities.

Only three bones, the carpometacarpus, femur and tarsometatarsus, follow at least one of the allometric hypotheses (GS, ES and SS I) inside their 95% confidence interval for both length and diameter.

Table 5. Results from tests of allometric hypotheses for bone length, diameter etc. of the bones in the wings and carina sterni (Y-variable) versus body mass (X-variable). ***b*** *is the allometric exponent and the slope of the line log (Y) = b log (X) + log (a).* ***SE*** *is the standard error for b.* b_{max} *and* b_{min} *show maximum and minimum values for 95% confidence interval for b.* ***log (a)*** *is the value of intercept of the line log (Y) = b log (X) + log (a).* R^2 *is the correlation coefficient.* ***GS*** *means Geometric similarity,* ***ES*** *stands for Elastic similarity,* ***SS I*** *stands for Static stress similarity (model I)* ***SS II*** *stands for Static stress similarity (model II breaking)* ***SS III*** *stands for Static stress similarity (model III buckling) and* ***SS IV*** *stands for Static stress similarity (model IV bending). (m) stands for muscle load and (b) for body mass load,* **<->** *means a b-value between* ***SS IV*** *(b) and* ***GS***. **+** *means that the experimental value of the exponent b was higher than expected from all hypothesis.*

Y- variable	***b***	**SE**	b_{max}	b_{min}	***log (a)***	R^2	**Fitted hypotheses**
Humerus							
L_{Hum}	0.411	0.020	0.451	0.371	0.812	0.925	+
D_{Hum}	0.387	0.012	0.411	0.363	-0.244	0.970	ES, SS I
d_{Hum}	0.366	0.015	0.396	0.336	-0.238	0.947	ES
A_{Hum}	0.753	0.023	0.799	0.707	-0.481	0.970	ES
dD^3/l^2_{Hum}	0.705	0.037	0.779	0.631	-2.593	0.916	GS, SS III (m)
dD^2/l_{Hum}	0.729	0.026	0.781	0.677	-1.537	0.958	<->
Ulna							
L_{Ulna}	0.411	0.024	0.459	0.363	0.871	0.901	+
D_{Ulna}	0.346	0.015	0.376	0.316	-0.252	0.945	GS, ES
d_{Ulna}	0.344	0.015	0.374	0.314	-0.241	0.941	GS
A_{Ulna}	0.690	0.028	0.746	0.634	-0.493	0.947	GS, SS II (m)
dD^3/l^2_{Ulna}	0.560	0.060	0.680	0.440	-2.741	0.724	GS, SS III (m)
dD^2/l_{Ulna}	0.625	0.041	0.707	0.543	-1.617	0.874	GS, SS IV (m)
Carpometacarpus							
L_{Cmc}	0.362	0.016	0.394	0.330	0.739	0.939	GS
D_{Cmc}	0.349	0.013	0.375	0.323	-0.056	0.956	GS, ES
d_{Cmc}	0.357	0.020	0.397	0.317	-0.359	0.912	GS, ES
A_{Cmc}	0.706	0.027	0.760	0.652	-0.415	0.956	GS, ES, SS II
dD^3/l^2_{Cmc}	0.679	0.039	0.757	0.601	-2.003	0.903	GS, SS III (m)
dD^2/l_{Cmc}	0.693	0.030	0.753	0.633	-1.209	0.943	GS, SS IV (m)
Carina							
L_{Car}	0.367	0.019	0.405	0.329	0.752	0.916	GS
D_{Car}	0.266	0.022	0.310	0.222	0.539	0.805	ES

Table 6. Results from tests of allometric hypotheses for bone length, diameter etc. of the bones in the legs (Y-variable) versus body mass (X-variable). ***b*** *is the allometric exponent and the slope of the line log (Y) = b log (X) + log (a).* ***SE*** *is the standard error for b.* **b_{max}** *and* **b_{min}** *show maximum and minimum values for 95% confidence interval for b.* ***log (a)*** *is the value of intercept of the line log (Y) = b log (X) + log (a).* **R^2** *is the correlation coefficient.* ***GS*** *means Geometric similarity,* ***ES*** *stands for Elastic similarity,* ***SS I*** *stands for Static stress similarity (model I)* ***SS II*** *stands for Static stress similarity (model II breaking)* ***SS III*** *stands for Static stress similarity (model III buckling) and* ***SS IV*** *stands for Static stress similarity (model IV bending). (m) stands for muscle load and (b) for body mass load*
<-> *means a b-value between* ***SS IV*** *(b) and GS.* **+** *means that the experimental value of the exponent b was higher than expected from all hypothesis.*

Y- variable	***b***	**SE**	b_{max}	b_{min}	*log (a)*	R^2	**Fitted hypotheses**
Femur							
L_{Fem}	0.323	0.016	0.355	0.291	0.911	0.925	GS
D_{Fem}	0.397	0.015	0.427	0.367	-0.346	0.953	ES, SS I
d_{Fem}	0.416	0.012	0.440	0.392	-0.426	0.970	SS I
A_{Fem}	0.813	0.022	0.857	0.769	-0.772	0.976	<->
dD^3/l^2_{Fem}	0.961	0.045	1.051	0.871	-3.287	0.929	SS III (b)
dD^2/l_{Fem}	0.887	0.031	0.949	0.825	-2.029	0.960	<->
Tibiotarsus							
L_{Tib}	0.328	0.018	0.364	0.292	1.027	0.906	GS
D_{Tib}	0.395	0.012	0.419	0.371	-0.395	0.970	ES, SS I
d_{Tib}	0.358	0.012	0.382	0.334	-0.336	0.962	ES
A_{Tib}	0.753	0.016	0.785	0.721	-0.731	0.986	ES
dD^3/l^2_{Tib}	0.886	0.044	0.974	0.798	-3.575	0.924	<->
dD^2/l_{Tib}	0.819	0.027	0.873	0.765	-2.153	0.964	<->
Tarsometatarsus							
L_{Tmt}	0.255	0.039	0.333	0.177	1.058	0.572	GS, ES, SS I
D_{Tmt}	0.490	0.023	0.536	0.444	-0.702	0.931	+
d_{Tmt}	0.466	0.025	0.516	0.416	-0.755	0.914	+
A_{Tmt}	0.956	0.026	1.008	0.904	-1.458	0.976	SS II (b)
dD^3/l^2_{Tmt}	1.426	0.117	1.660	1.192	-4.979	0.823	+
dD^2/l_{Tmt}	1.191	0.065	1.321	1.061	-3.218	0.912	+

How does the bone's cross-section area increase with body mass?

The predictions of the relationship between cross-sectional area of the bones (Y-variable) and body mass (X-variable) are presented in prediction 5 in Table 4 (no. 7-10), and the results of the evaluation are presented in Fig 14 and Tables 5 and 6.

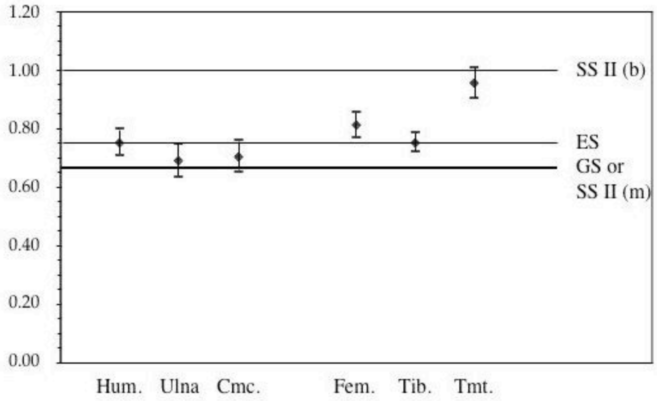

Figure 14. Graphic illustration of the values of the regression exponent b, with b_{max} *and* b_{min} *for the allometric relationship between the bone cross-section area A and body mass m. The horizontal lines mark the values of b predicted by the different hypotheses. Hum. is humerus, Cmc. is carpometacarpus, Fem. is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. GS stands for Geometric similarity, ES for Elastic similarity, SS II for Static stress similarity (model II breaking), (m) for muscle load and (b) for body mass load*

The results for the cross-sectional areas of the bones can be summarized as follows (see Fig 14) are:

1. The cross sectional area of the humerus increases with body mass as expected from elastic similarity, which is faster than expected from isometry.
2. Ulna is close to geometric similarity (including static stress model II, load from body mass). Elastic similarity is just outside the 95% confidence interval.
3. For carpometacarpus, both geometric and elastic similarity fall within the 95% confidence interval.
4. Femur falls in between elastic and static stress model II (load proportional to body mass).
5. Tibiotarsus follows elastic similarity.
6. Tarsometatarsus follows static stress model II (load from body mass).

In general this can be interpreted as follows. The cross sectional area of ulna and carpometacarpus increases with body mass as expected from isometry, or slightly more. The cross sectional area of the leg bones increases with body mass more than expected from isometry. Humerus and tibiotarsus increase as expected from elastic similarity. Femur and especially tarsometatarsus increase much more with body mass than expected from isometry. This supports the hypothesis about dynamic stress similarity and safety factors in prediction 4.

How does the bone's resistance to buckling change with body mass?

The predictions of the relationship between resistance to buckling (Y-variable) and body mass (X-variable) are presented in prediction 6 and Table 4 (no. 13-15), and the results of the evaluation are presented in Tables 5 and 6.

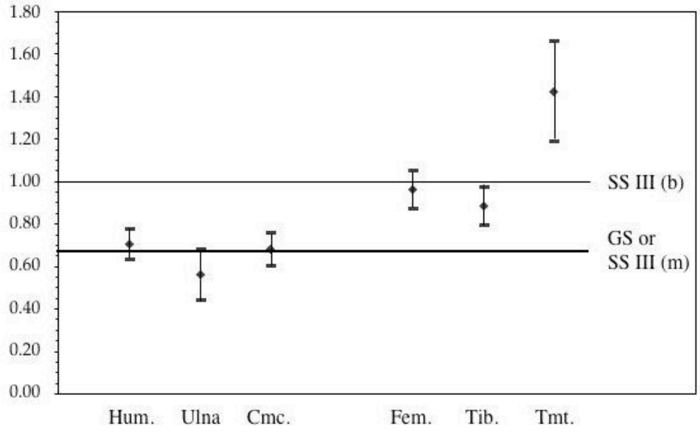

Figure 15. Graphic illustration of the values of slope b, with b_{max} *and* b_{min} *for the allometric relationship between the resistance to buckling* (dD^3/l^2) *related to body mass* (m)*. Hum. is humerus, Cmc. is carpometacarpus, Fem. is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. The horizontal lines mark the values of b predicted by the different hypotheses, GS for Geometric similarity, ES for Elastic similarity, SS III stands for Static stress similarity (model III breaking), (m) stands for muscle load and (b) for body mass load*

The results of the bone's resistance to buckling can be summarized as follows (see Fig 15):
1. The wing bones, humerus, ulna and carpometacarpus follow geometric similarity, which is similar to static stress similarity model III (buckling and load proportional to muscle forces).
2. The leg bones are closer to static stress similarity model III, with the load proportional to body mass, than to geometric similarity, although the 95% confidence interval for tarsometatarsus is slightly below and that for tarsometatarsus is significantly higher.

In general this shows the same trend as before: the wing bones relates to muscle force and the leg bones, especially tarsometatarsus, to body mass.

How does the bone's resistance to bending change with body mass?

The predictions of the relationship between resistance to bending (Y-variable) and body mass (X-variable) are presented in prediction 7 and in Table 4 (no. 16-18), and the results of the evaluation are presented in Tables 5 and 6.

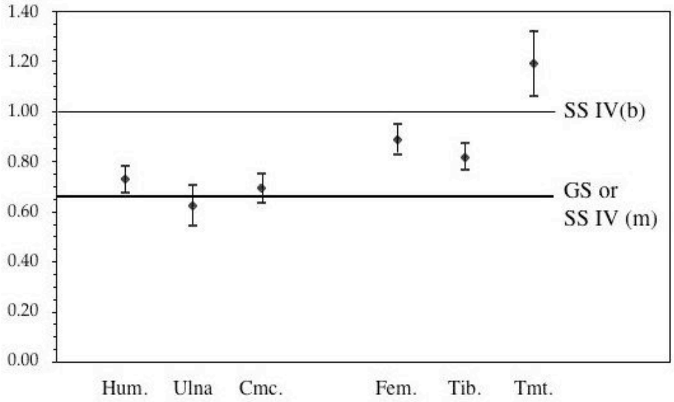

*Figure 16. Graphic illustration of the values of slope b, with b_{max} and b_{min} for the allometric relationship between constant resistance to bending related to body mass (*m*). Hum. is humerus, Cmc. is carpometacarpus, Fem. is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. The horizontal lines mark the values of b predicted by the different hypotheses, GS for Geometric similarity, ES for Elastic similarity, SS IV stands for Static stress similarity (model III breaking), (m) stands for muscle load and (b) for body mass load.*

The results (see Fig 16) are:
1. The two wing-bones *ulna* and *carpometacarpus* follow geometric similarity, which is similarity to static stress similarity model IV (bending and load proportional to muscle forces).
2. The humerus increase slightly more with body mass than expected from geometric similarity.
3. Femur and tibiotarsus have values between geometric similarity and static stress similarity model IV (bending and load proportional to body mass).
4. Tarsometatarsus is significantly higher than static stress similarity model IV (bending and load proportional to body mass).

In general, this, once again, show us the same trend: the wing bones relates to muscle force and the leg bones, especially tarsometatarsus, to body mass.

Discussion

The results show that there is a significant difference between wing bones and leg bones. Wing bones increase more in length with increasing body mass than expected from isometry, especially the humerus and ulna. The diameters follow a trend between geometric and elastic similarity, except for humerus, which increases more with body mass than expected from isometry.

The length of femur and tibiotarsus increases almost isometrically with increasing body mass. The diameter of the two bones increases significantly more than for geometric similarity. (The two bones are very close to static stress similarity model I, but elastic similarity is in the 95% confidence interval, too). Tarsometatarsus increases much less in length than expected from isometry (or any other similarity hypothesis) but much more in diameter.

Using the knowledge of the constant strength (resistance to breaking, bending and buckling) of bones the wing bones can be described in the following way, too (all related to isometry):

When the body mass increases the humerus increases more in length and strength than expected. Ulna increases more in length and slightly more in strength than expected. Carpometacarpus increases slightly more in both length and strength than expected.

The length of femur and ulna increases as expected with body mass, and their strength increases more than expected from isometry. Tarsometatarsus increases much less than expected in length and much more in strength.

As already mentioned, this pattern supports the discussion under prediction 4, dynamic stress similarity and safety factors, very well. The bone that meets the ground first in an unsuccessful landing is the bone that increases slowest in length and fastest in diameter (strength) with body mass of all bones.

The focus on length of wing bones can be interpreted as a response to the problem of increased wing loading for birds growing isometrically, because for geometrically similar birds the wing loading increases with body mass raised to 1/3. If the wings increase with body mass in length (and thus in area) more than expected for isometry, this could help keeping the wing loading down for larger birds.

The allometric hypotheses

All hypotheses except one (static stress similarity model IV bending with load proportional to body mass) were within the 95% confidence interval for at least one allometric relation (Table 7). If we count the number of times each hypothesis is within the confidence interval we will find that geometric and elastic similarity are most frequent (geometric similarity mainly for wings, elastic similarity mainly for legs). Static stress similarity model I is less frequent and found in five occasions. Static stress similarity model II (b) is the only hypothesis that lies inside the 95% confidence interval of tarsometatarsus diameters.

Table 7. The number of times the different allometric predictions are within the 95% confidence interval. The SS model II, III and IV (m) are equal to geometric similarity.

Allometric hypotheses	**Number of occurrences**		
	Total	**Wing**	**Leg**
Geometric similarity	16	13	3
Elastic similarity	13	8	5
Static stress similarity I	5	1	4
SS similarity II (m)	2	2	–
SS similarity II (b)	1	–	1
SS similarity III (m)	3	3	–
SS similarity III (b)	1	–	1
SS similarity IV (m)	2	2	–
SS similarity IV (b)	–	–	–

Finally we can note that the prediction given by Economos (1983), stating that small mammals (≤ 20 kg) would follow geometric similarity and large (> 20 kg) would follow elastic similarity is not true for birds.

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Appendix: Results of bone measurements

In this appendix the bone measurements of birds used in the allometric analyses are presented, together with data for specimens, which could not be sexed and/or which had too few measurements to be included in the allometric analyses. For each species and sex the dimensions (length *L*, diameter *D* and diameter *d*) for each bone is presented with mean-, maximum and minimum values, as well as number of observations and standard deviation. **All** includes male, female specimens as well as those that had no identified sex. **Mean** is the mean value of the measurements**.** **n** is the number of specimens. **S.D**. is the standard deviation of the measurements. **Max** and **Min** are the maximum and minimum values, respectively. The full Latin, English and Swedish names are given in Appendix 21.

Appendix 1. Length of humerus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	110.5	5	3.21	113.4	105.6	107.9	5	3.27	110.6	103.3	109.0	14	2.96	113.4	103.3
Ha. albicilla	231.1	6	10.29	248.0	219.0	220.2	5	17.96	245.0	200.0	226.1	11	14.64	248.0	200.0
Hi. pennatus											105.7	4	5.88	111.2	97.4
M. milvus	117.4	2	15.80	128.6	106.2	122.6	2	0.76	123.2	122.1	120.0	4	9.63	128.6	106.2
M. migrans						112.2	1		112.2	112.2	112.2	1		112.2	112.2
C. aeruginosus	111.9	5	2.24	113.9	108.1	102.1	5	1.45	103.6	100.2	106.7	12	5.16	113.9	100.2
C. cyaneus	90.7	5	3.15	92.9	85.2	87.5	5	9.62	104.6	82.3	89.6	13	6.21	104.6	82.3
C. pygargus	85.2	3	2.16	86.7	82.7	82.2	4	2.87	85.0	78.7	83.5	7	2.86	86.7	78.7
A. gentilis	105.2	6	3.83	111.3	102.2	93.6	5	3.75	97.6	89.7	99.9	11	7.07	111.3	89.7
A. nisus	61.3	8	1.38	63.6	59.6	51.6	5	1.07	53.3	50.8	57.1	14	5.12	63.6	50.8
Aq. chrysaetos	194.8	5	6.83	200.0	183.0	181.5	4	1.68	183.0	179.1	188.9	9	8.57	200.0	179.1
B. buteo	106.7	5	6.16	117.0	100.5	99.7	6	3.09	101.9	93.5	103.2	14	5.36	117.0	93.5
B. lagopus	117.4	5	1.95	119.8	115.2	107.9	5	3.54	111.8	103.2	113.7	12	5.80	121.4	103.2
P. haliaetus	145.1	5	4.53	149.8	139.0	141.8	6	5.11	149.5	136.0	142.6	12	5.27	149.8	135.0
F. columbarius	50.3	5	1.16	52.1	48.9	45.8	5	1.06	47.1	44.2	48.9	16	3.75	59.6	44.2
F. peregrinus	88.3	5	2.35	90.7	85.2	76.0	6	1.99	78.5	72.8	81.1	14	6.23	90.7	72.8
F. rusticolus	109.4	5	6.13	119.8	104.5	98.1	5	5.28	107.2	93.5	103.7	10	8.04	119.8	93.5
F. subbuteo	57.6	6	2.08	60.6	54.3	54.3	3	0.53	54.9	53.8	56.3	10	2.30	60.6	53.8
F. tinnunculus	54.9	5	1.87	58.0	53.1	53.3	6	1.19	54.9	52.2	54.2	13	1.72	58.0	52.2
F. vespertinus	50.5	3	1.71	52.5	49.2	50.3	5	1.50	52.6	49.1	50.4	8	1.46	52.6	49.1
G. glandarius	42.5	1		42.5	42.5	43.0	2	1.34	43.9	42.0	42.7	4	0.82	43.9	42.0
Pe. infaustus	29.9	1		29.9	29.9	32.4	1		32.4	32.4	31.2	2	1.75	32.4	29.9
Pica pica	46.3	2	2.43	48.0	44.6	44.4	1		44.4	44.4	46.4	5	1.73	48.0	44.4
Nu. caryocatactes						42.0	1		42.0	42.0	42.0	1		42.0	42.0
Co. monedula						45.9	3	1.98	48.0	44.1	46.0	4	1.64	48.0	44.1
Co. frugilegus															
Co. corone cx	66.6	5	2.89	69.5	63.4	69.9	5	1.55	71.7	67.5	67.8	15	2.46	71.7	63.4
Co. corone ce	66.6	1		66.6	66.6						66.3	2	0.36	66.6	66.1
Co. corax	93.7	1		93.7	93.7	98.5	3	0.25	98.8	98.3	95.3	6	4.10	98.8	88.3
Cy. olor						291.0	1		291.0	291.0	291.0	1		291.0	291.0
R. regulus						9.8	1		9.8	9.8	9.8	1		9.8	9.8

Appendix 2. Diameter D of humerus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	8.4	5	0.249	8.8	8.2	7.7	5	0.370	8.3	7.3	8.0	14	0.482	8.8	7.1
Ha. albicilla	15.5	6	1.072	17.4	14.5	14.9	5	0.948	16.3	13.8	15.3	11	1.015	17.4	13.8
Hi. pennatus											7.0	5	0.517	7.5	6.3
M. milvus	8.5	2	0.198	8.7	8.4	8.0	2	0.601	8.5	7.6	8.3	4	0.460	8.7	7.6
M. migrans						7.6	1		7.6	7.6	7.6	1		7.6	7.6
C. aeruginosus	7.5	5	0.168	7.7	7.2	6.9	5	0.091	7.0	6.8	7.2	12	0.313	7.7	6.8
C. cyaneus	6.6	5	0.655	7.1	5.5	6.3	5	0.807	7.6	5.3	6.5	13	0.626	7.6	5.3
C. pygargus	5.8	3	0.350	6.1	5.4	5.6	4	0.147	5.8	5.4	5.7	7	0.264	6.1	5.4
A. gentilis	8.6	6	0.310	9.1	8.2	7.5	5	0.616	8.5	7.0	8.1	11	0.725	9.1	7.0
A. nisus	5.1	8	0.162	5.4	4.9	4.4	5	0.160	4.5	4.1	4.8	14	0.416	5.4	4.1
Aq. chrysaetos	14.4	5	0.512	15.1	13.9	13.5	4	0.671	14.4	12.7	14.0	9	0.705	15.1	12.7
B. buteo	7.5	5	0.184	7.8	7.4	6.8	6	0.163	7.0	6.7	7.2	14	0.361	7.8	6.7
B. lagopus	8.0	5	0.397	8.4	7.4	7.2	5	0.371	7.7	6.7	7.7	13	0.561	8.6	6.7
P. haliaetus	10.2	5	0.455	10.6	9.5	10.4	6	0.517	11.1	9.9	10.3	12	0.458	11.1	9.5
F. columbarius	4.4	5	0.170	4.6	4.2	4.1	5	0.204	4.3	3.8	4.3	16	0.189	4.6	3.8
F. peregrinus	7.7	5	0.327	8.3	7.5	7.0	6	0.313	7.5	6.7	7.4	14	0.427	8.3	6.7
F. rusticolus	9.1	5	0.398	9.6	8.6	8.4	5	0.547	9.3	7.8	8.8	10	0.586	9.6	7.8
F. subbuteo	4.7	6	0.175	4.9	4.5	4.4	3	0.104	4.6	4.4	4.6	10	0.201	4.9	4.4
F. tinnunculus	4.4	5	0.254	4.6	4.0	4.4	6	0.192	4.7	4.2	4.4	13	0.223	4.7	4.0
F. vespertinus	3.8	3	0.202	4.0	3.6	3.6	5	0.104	3.7	3.5	3.7	8	0.170	4.0	3.5
G. glandarius	4.0	1		4.0	4.0	3.9	2	0.191	4.1	3.8	4.0	4	0.112	4.1	3.8
Pe. infaustus	2.8	1		2.8	2.8	2.8	1		2.8	2.8	2.8	2	0.028	2.8	2.8
Pica pica	4.2	2	0.283	4.4	4.0	4.2	1		4.2	4.2	4.3	5	0.199	4.5	4.0
Nu. caryocatactes						3.8	1		3.8	3.8	3.8	1		3.8	3.8
Co. monedula	4.6	3	0.365	5.0	4.3						4.6	4	0.300	5.0	4.3
Co. frugilegus															
Co. corone cx	6.2	5	0.181	6.4	5.9	6.5	5	0.091	6.6	6.4	6.3	15	0.319	6.7	5.5
Co. corone ce	6.1	1		6.1	6.1						6.2	2	0.233	6.4	6.1
Co. corax	8.6	1		8.6	8.6	9.3	3	0.199	9.5	9.1	8.8	6	0.722	9.5	7.5
Cy. olor						16.7	1		16.7	16.7	16.7	1		16.7	16.7
R. regulus						1.1	1		1.1	1.1	1.1	1		1.1	1.1

Appendix 3. Diameter d of humerus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	6.8	5	0.372	7.2	6.3	6.3	5	0.378	6.7	5.7	6.5	14	0.405	7.2	5.7
Ha. albicilla	13.5	6	0.989	15.1	12.2	13.2	5	0.673	14.1	12.5	13.4	11	0.83	15.1	12.2
Hi. pennatus											6.4	5	0.37	6.8	6.0
M. milvus	7.6	2	0.113	7.7	7.5	7.2	2	0.361	7.5	6.9	7.4	4	0.311	7.7	6.9
M. migrans						6.7	1		6.7	6.7	6.7	1		6.7	6.7
C. aeruginosus	6.7	5	0.097	6.8	6.5	6.0	5	0.227	6.3	5.7	6.3	12	0.381	6.8	5.7
C. cyaneus	5.7	5	0.493	6.2	4.9	5.5	5	0.579	6.4	4.8	5.7	13	0.482	6.4	4.8
C. pygargus	5.2	3	0.144	5.3	5.0	5.1	4	0.183	5.3	4.9	5.1	7	0.166	5.3	4.9
A. gentilis	7.8	6	0.172	8.0	7.6	6.7	5	0.516	7.6	6.3	7.3	11	0.663	8.0	6.3
A. nisus	4.7	8	0.188	5.0	4.5	3.9	4	0.211	4.1	3.6	4.4	13	0.448	5.0	3.6
Aq. chrysaetos	11.8	5	0.366	12.3	11.3	11.6	4	0.417	12.1	11.2	11.7	9	0.372	12.3	11.2
B. buteo	6.6	5	0.239	6.9	6.3	6.0	6	0.363	6.7	5.6	6.3	14	0.396	6.9	5.6
B. lagopus	7.2	5	0.421	7.8	6.7	6.4	5	0.284	6.9	6.2	6.9	13	0.53	7.8	6.2
P. haliaetus	8.6	5	0.338	8.9	8.1	8.2	6	0.443	8.8	7.6	8.3	12	0.423	8.9	7.6
F. columbarius	3.9	5	0.158	4.0	3.6	3.5	5	0.164	3.7	3.3	3.7	16	0.21	4.0	3.3
F. peregrinus	6.7	5	0.157	7.0	6.7	6.2	6	0.229	6.5	5.9	6.4	14	0.299	7.0	5.9
F. rusticolus	7.8	5	0.305	8.1	7.4	7.3	5	0.299	7.7	7.0	7.5	10	0.385	8.1	7.0
F. subbuteo	4.1	6	0.104	4.3	4.0	4.0	3	0.076	4.1	3.9	4.1	10	0.111	4.3	3.9
F. tinnunculus	3.9	5	0.297	4.2	3.5	4.0	6	0.103	4.1	3.9	3.9	13	0.215	4.2	3.5
F. vespertinus	3.3	3	0.1	3.4	3.2	3.2	5	0.124	3.3	3.0	3.2	8	0.13	3.4	3.0
G. glandarius	3.1	1		3.1	3.1	3.1	2	0.113	3.2	3.1	3.2	4	0.09	3.2	3.1
Pe. infaustus	2.2	1		2.2	2.2	2.6	1		2.6	2.6	2.4	2	0.255	2.6	2.2
Pica pica	3.5	2	0.198	3.7	3.4	3.5	1		3.5	3.5	3.6	5	0.167	3.8	3.4
Nu. caryocatactes						3.1	1		3.1	3.1	3.1	1		3.1	3.1
Co. monedula	3.7	3	0.227	3.9	3.5						3.7	4	0.186	3.9	3.5
Co. frugilegus															
Co. corone cx	5.1	5	0.16	5.4	5.0	5.4	5	0.29	5.7	5.0	5.2	15	0.304	5.7	4.6
Co. corone ce	5.1	1		5.1	5.1						5.3	2	0.198	5.4	5.1
Co. corax	6.7	1		6.7	6.7	7.4	3	0.22	7.7	7.3	7.1	6	0.498	7.7	6.4
Cy. olor						14.1	1		14.1	14.1	14.1	1		14.1	14.1
R. regulus						1.0	1		1.0	1.0	1.0	1		1.0	1.0

Appendix 4. Length of ulna

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	118.6	2	4.84	122.0	115.2	118.4	4	5.18	123.0	112.4	118.9	10	3.57	123.0	112.4
Ha. albicilla	261.8	5	14.86	286.0	248.0	246.3	4	15.35	261.5	230.0	254.9	9	16.31	286.0	230.0
Hi. pennatus											128.8	4	7.12	133.2	118.1
M. milvus	128.8	2	16.73	140.6	116.9	136.3	2	4.60	139.5	133.0	132.5	4	10.91	140.6	116.9
M. migrans						131.9	1		131.9	131.9	131.9	1		131.9	131.9
C. aeruginosus	137.0	1		137.0	137.0	119.6	4	2.11	121.9	117.4	122.8	6	7.17	137.0	117.4
C. cyaneus	105.6	5	2.33	107.9	101.7	101.7	5	10.38	120.2	95.6	103.9	13	6.61	120.2	95.6
C. pygargus						103.6	2	0.00	103.6	103.6	103.6	2	0.00	103.6	103.6
A. gentilis	116.1	6	3.87	121.5	112.9	104.1	5	4.68	109.8	100.4	110.7	11	7.45	121.5	100.4
A. nisus	71.6	8	1.88	75.0	69.3	60.6	5	1.84	62.5	58.3	66.9	14	5.80	75.0	58.3
Aq. chrysaetos	223.7	5	5.61	230.5	215.0	208.9	4	2.18	211.0	206.0	217.1	9	8.86	230.5	206.0
B. buteo	122.4	5	3.34	125.9	117.5	117.3	6	3.73	120.7	110.9	120.3	14	4.36	127.7	110.9
B. lagopus	135.6	4	2.83	137.5	131.4	126.9	5	3.91	131.4	123.4	132.0	12	5.70	141.2	123.4
P. haliaetus	183.6	5	6.00	189.8	175.0	178.0	5	7.42	189.0	170.0	180.3	11	6.88	189.8	170.0
F. columbarius	56.6	5	0.96	57.9	55.2	52.1	5	1.21	53.6	50.3	54.5	16	2.49	57.9	50.3
F. peregrinus	102.1	5	2.09	103.6	98.9	86.5	6	2.09	89.8	84.4	93.0	14	7.63	103.6	84.4
F. rusticolus	117.5	5	5.52	121.5	108.0	110.2	5	5.94	120.0	104.5	114.0	11	6.29	121.5	104.5
F. subbuteo	67.4	1		67.4	67.4	61.8	1		61.8	61.8	63.2	3	3.66	67.4	60.5
F. tinnunculus	62.4	6	1.66	65.1	59.9	60.7	5	0.87	61.8	59.4	61.9	13	1.69	65.1	59.4
F. vespertinus	57.4	1		57.4	57.4	56.1	3	0.19	56.2	55.9	56.4	4	0.68	57.4	55.9
G. glandarius	49.3	1		49.3	49.3	50.9	2	1.86	52.3	49.6	50.4	4	1.33	52.3	49.3
Pe. infaustus	32.5	1		32.5	32.5	36.3	1		36.3	36.3	34.4	2	2.74	36.3	32.5
Pica pica	53.0	2	1.86	54.3	51.7	50.9	1		50.9	50.9	53.2	5	1.81	55.0	50.9
Nu. caryocatactes						49.6	1		49.6	49.6	49.6	1		49.6	49.6
Co. monedula	56.3	3	2.84	58.6	53.1	58.8	1		58.8	58.8	57.2	5	2.39	58.8	53.1
Co. frugilegus											80.3	2	2.57	82.2	78.5
Co. corone cx	79.9	5	3.41	82.7	75.7	83.7	5	2.52	86.2	80.2	81.3	15	3.06	86.2	75.7
Co. corone ce											79.4	1		79.4	79.4
Co. corax	113.0	1		113.0	113.0	114.4	1		114.4	114.4	111.3	4	3.49	114.4	106.4
Cy. olor						258.0	1		258.0	258.0	258.0	1		258.0	258.0
R. regulus						13.3	1		13.3	13.3	13.3	1		13.3	13.3

Appendix 5. Diameter D of ulna

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	5.8	2	0.389	6.1	5.6	5.8	4	0.411	6.2	5.3	5.9	10	0.348	6.4	5.3
Ha. albicilla	10.6	5	0.877	11.5	9.3	10.5	4	0.640	11.3	10.0	10.5	9	0.736	11.5	9.3
Hi. pennatus											5.3	4	0.303	5.8	5.1
M. milvus	6.4	2	0.276	6.6	6.2	6.2	1		6.2	6.2	6.3	3	0.215	6.6	6.2
M. migrans						5.7	1		5.7	5.7	5.7	1		5.7	5.7
C. aeruginosus	5.6	1		5.6	5.6	5.1	4	0.429	5.7	4.7	5.1	6	0.422	5.7	4.7
C. cyaneus	4.9	5	0.416	5.3	4.2	4.6	5	0.574	5.5	4.0	4.8	13	0.438	5.5	4.0
C. pygargus						4.1	2	0.283	4.3	3.9	4.1	2	0.283	4.3	3.9
A. gentilis	6.4	6	0.127	6.6	6.2	5.4	5	0.303	5.8	5.2	5.9	11	0.530	6.6	5.2
A. nisus	3.9	8	0.132	4.0	3.7	3.3	5	0.106	3.4	3.2	3.6	14	0.325	4.0	3.2
Aq. chrysaetos	10.5	5	0.615	11.0	9.7	9.8	4	0.716	10.7	8.9	10.2	9	0.724	11.0	8.9
B. buteo	5.9	5	0.392	6.5	5.5	5.2	6	0.356	5.9	4.9	5.5	14	0.441	6.5	4.9
B. lagopus	6.2	4	0.308	6.4	5.8	5.8	5	0.395	6.3	5.2	6.0	12	0.458	6.9	5.2
P. haliaetus	7.3	5	0.279	7.7	7.0	6.9	5	0.479	7.6	6.5	7.1	11	0.395	7.7	6.5
F. columbarius	3.4	5	0.228	3.8	3.2	3.2	5	0.148	3.4	3.0	3.3	16	0.230	3.8	3.0
F. peregrinus	5.8	5	0.301	6.3	5.5	5.2	6	0.144	5.4	5.1	5.5	14	0.345	6.3	5.1
F. rusticolus	7.0	5	0.270	7.4	6.7	6.7	5	0.480	7.5	6.4	6.8	11	0.382	7.5	6.4
F. subbuteo	4.4	1		4.4	4.4	3.6	1		3.6	3.6	3.8	3	0.448	4.4	3.6
F. tinnunculus	3.5	6	0.195	3.7	3.2	3.5	5	0.150	3.8	3.4	3.5	13	0.161	3.8	3.2
F. vespertinus	3.0	1		3.0	3.0	3.0	3	0.104	3.2	3.0	3.0	4	0.095	3.2	3.0
G. glandarius	3.2	1		3.2	3.2	3.1	2	0.092	3.2	3.0	3.1	4	0.151	3.2	2.9
Pe. infaustus	2.3	1		2.3	2.3	2.2	1		2.2	2.2	2.2	2	0.049	2.3	2.2
Pica pica	3.6	2	0.233	3.7	3.4	3.8	1		3.8	3.8	3.6	5	0.153	3.8	3.4
Nu. caryocatactes						2.8	1		2.8	2.8	2.8	1		2.8	2.8
Co. monedula	3.9	3	0.393	4.3	3.5	3.7	1		3.7	3.7	3.9	5	0.292	4.3	3.5
Co. frugilegus											4.8	2	0.035	4.9	4.8
Co. corone cx	4.8	5	0.119	5.0	4.7	5.2	5	0.304	5.6	4.9	5.0	15	0.378	5.6	4.1
Co. corone ce											4.8	1		4.8	4.8
Co. corax	6.5	1		6.5	6.5	6.9	3	0.320	7.2	6.6	6.6	6	0.502	7.2	5.7
Cy. olor						11.0	1		11.0	11.0	11.0	1		11.0	11.0
R. regulus						0.7	1		0.7	0.7	0.7	1		0.7	0.7

Appendix 6. Diameter d of ulna

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	6.3	2	0.035	6.3	6.3	5.8	4	0.414	6.4	5.4	5.9	10	0.370	6.4	5.4
Ha. albicilla	10.4	5	0.770	11.8	9.8	9.8	4	1.043	11.3	8.8	10.1	9	0.907	11.8	8.8
Hi. pennatus											5.6	4	0.287	6.0	5.3
M. milvus	6.4	2	0.205	6.6	6.3	5.9	1		5.9	5.9	6.2	3	0.326	6.6	5.9
M. migrans						5.6	1		5.6	5.6	5.6	1		5.6	5.6
C. aeruginosus	5.6	1		5.6	5.6	5.1	4	0.366	5.7	4.9	5.2	6	0.366	5.7	4.9
C. cyaneus	4.8	5	0.481	5.4	4.1	4.6	5	0.466	5.3	4.0	4.8	13	0.448	5.4	4.0
C. pygargus						4.1	2	0.035	4.2	4.1	4.1	2	0.035	4.2	4.1
A. gentilis	6.5	6	0.222	6.9	6.3	5.5	5	0.384	6.1	5.2	6.1	11	0.593	6.9	5.2
A. nisus	4.0	8	0.122	4.1	3.8	3.3	5	0.139	3.5	3.1	3.7	14	0.346	4.1	3.1
Aq. chrysaetos	10.2	5	0.579	10.8	9.5	10.0	4	0.411	10.5	9.5	10.1	9	0.497	10.8	9.5
B. buteo	5.9	5	0.209	6.1	5.6	5.4	6	0.287	6.0	5.2	5.7	14	0.331	6.1	5.2
B. lagopus	6.1	4	0.364	6.6	5.7	5.8	5	0.189	6.0	5.6	6.1	12	0.423	7.0	5.6
P. haliaetus	7.1	5	0.589	7.9	6.4	7.2	5	0.296	7.6	7.0	7.2	11	0.424	7.9	6.4
F. columbarius	3.4	5	0.251	3.8	3.2	3.1	5	0.199	3.4	2.9	3.4	16	0.249	3.8	2.9
F. peregrinus	6.5	5	0.156	6.8	6.4	5.6	6	0.501	6.3	4.9	6.0	14	0.512	6.8	4.9
F. rusticolus	7.3	5	0.405	7.9	6.8	6.8	5	0.657	7.9	6.3	7.0	11	0.575	7.9	6.3
F. subbuteo	3.7	1		3.7	3.7	3.7	1		3.7	3.7	3.7	3	0.058	3.8	3.7
F. tinnunculus	3.4	6	0.297	3.7	3.0	3.5	5	0.295	4.0	3.2	3.5	13	0.299	4.0	3.0
F. vespertinus	3.1	1		3.1	3.1	3.3	3	0.058	3.4	3.3	3.3	4	0.118	3.4	3.1
G. glandarius	3.1	1		3.1	3.1	3.1	2	0.170	3.2	3.0	3.1	4	0.115	3.2	3.0
Pe. infaustus	2.1	1		2.1	2.1	2.2	1		2.2	2.2	2.2	2	0.064	2.2	2.1
Pica pica	3.4	2	0.092	3.4	3.3	3.6	1		3.6	3.6	3.5	5	0.148	3.7	3.3
Nu. caryocatactes						3.0	1		3.0	3.0	3.0	1		3.0	3.0
Co. monedula	3.6	3	0.314	4.0	3.3	4.1	1		4.1	4.1	3.7	5	0.306	4.1	3.3
Co. frugilegus											4.9	2	0.057	4.9	4.9
Co. corone cx	4.9	5	0.139	5.1	4.7	5.2	5	0.199	5.4	4.9	5.0	15	0.257	5.4	4.6
Co. corone ce											4.9	1		4.9	4.9
Co. corax	6.4	1		6.4	6.4	6.9	3	0.299	7.2	6.7	6.5	6	0.513	7.2	5.7
Cy. olor						11.0	1		11.0	11.0	11.0	1		11.0	11.0
R. regulus						0.8	1		0.8	0.8	0.8	1		0.8	0.8

Appendix 7. Length of carpometacarpus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	58.2	2	1.237	59.1	57.3	58.7	4	2.107	60.7	55.8	58.7	10	1.686	60.7	55.8
Ha. albicilla	120.6	5	6.092	130.8	114.7	118.3	5	7.617	128.5	109.6	119.5	10	6.620	130.8	109.6
Hi. pennatus											61.8	1		61.8	61.8
M. milvus	65.7	1		65.7	65.7	71.9	2	0.042	71.9	71.8	69.8	3	3.557	71.9	65.7
M. migrans						65.3	1		65.3	65.3	65.3	1		65.3	65.3
C. aeruginosus	69.7	1		69.7	69.7	61.7	4	1.565	63.8	60.4	63.9	7	3.885	69.7	60.4
C. cyaneus	57.6	5	2.467	60.3	54.2	55.2	5	4.823	63.9	52.9	56.7	13	3.381	63.9	52.9
C. pygargus						53.2	2	0.495	53.5	52.8	53.2	2	0.495	53.5	52.8
A. gentilis	63.9	5	2.070	67.2	61.7	58.2	5	2.521	61.4	55.5	61.0	10	3.733	67.2	55.5
A. nisus	39.4	8	1.464	41.6	37.1	33.1	5	0.470	33.9	32.6	36.7	14	3.338	41.6	32.6
Aq. chrysaetos	108.0	4	3.788	111.7	103.2	101.0	4	1.276	102.9	100.0	104.5	8	4.582	111.7	100.0
B. buteo	61.9	5	1.841	64.3	59.4	59.0	6	1.628	60.6	56.8	60.5	14	2.108	64.3	56.8
B. lagopus	70.3	4	1.298	71.8	68.9	66.0	5	1.572	68.0	63.8	68.6	12	2.729	72.7	63.8
P. haliaetus	89.5	5	3.729	94.0	84.3	86.7	5	4.324	92.0	81.4	87.6	11	4.282	94.0	81.4
F. columbarius	33.9	5	0.686	34.5	32.8	31.9	5	0.662	32.8	31.1	33.0	16	1.295	34.9	30.8
F. peregrinus	61.8	3	1.255	63.2	60.7	53.7	5	0.781	54.6	52.6	56.7	11	3.897	63.2	52.6
F. rusticolus	72.4	5	1.117	73.5	70.8	66.8	5	3.810	72.8	62.7	69.2	11	4.025	73.5	62.7
F. subbuteo	40.8	1		40.8	40.8						38.9	2	2.652	40.8	37.1
F. tinnunculus	36.3	6	1.058	37.8	34.7	34.8	6	1.130	36.1	32.8	35.8	14	1.403	38.3	32.8
F. vespertinus	32.4	1		32.4	32.4	32.5	2	0.636	33.0	32.1	32.5	3	0.454	33.0	32.1
G. glandarius	26.9	1		26.9	26.9	28.0	2	0.120	28.1	27.9	27.7	4	0.566	28.1	26.9
Pe. infaustus	19.1	1		19.1	19.1	20.2	1		20.2	20.2	19.7	2	0.750	20.2	19.1
Pica pica	29.7	2	2.645	31.6	27.9	29.0	2	0.884	29.6	28.4	30.1	6	1.714	31.9	27.9
Nu. caryocatactes						28.2	1		28.2	28.2	28.2	1		28.2	28.2
Co. monedula	36.2	1		36.2	36.2	35.4	3	1.446	36.9	34.0	35.8	5	1.124	36.9	34.0
Co. frugilegus											49.6	2	1.937	51.0	48.2
Co. corone cx	49.1	5	2.344	52.0	46.6	51.9	5	1.655	53.4	49.5	50.2	15	2.066	53.4	46.6
Co. corone ce	50.3	1		50.3	50.3						49.9	2	0.615	50.3	49.5
Co. corax	65.3	1		65.3	65.3	71.4	3	1.044	72.3	70.3	69.1	6	3.240	72.3	64.9
Cy. olor						132.6	1		132.6	132.6	132.6	1		132.6	132.6
R. regulus						7.6	1		7.6	7.6	7.6	1		7.6	7.6

Appendix 8. Diameter D of carpometacarpus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	10.1	2	0.141	10.2	10.0	9.9	4	0.284	10.2	9.6	10.1	10	0.599	11.2	9.1
Ha. albicilla	17.2	5	1.360	19.2	15.5	16.6	5	0.920	17.5	15.1	16.9	10	1.131	19.2	15.1
Hi. pennatus											9.5	3	0.421	9.8	9.0
M. milvus	10.3	2	2.333	12.0	8.7	10.9	2	0.064	10.9	10.9	10.6	4	1.391	12.0	8.7
M. migrans						10.9	1		10.9	10.9	10.9	1		10.9	10.9
C. aeruginosus	8.6	1		8.6	8.6	8.5	4	0.252	8.7	8.1	8.5	7	0.187	8.7	8.1
C. cyaneus	8.6	5	0.655	9.2	7.5	7.8	5	1.086	9.5	6.5	8.2	13	0.861	9.5	6.5
C. pygargus						7.1	2	0.035	7.2	7.1	7.1	2	0.035	7.2	7.1
A. gentilis	9.5	5	0.549	10.2	8.9	8.3	5	0.362	8.7	7.8	8.9	10	0.766	10.2	7.8
A. nisus	6.4	8	0.256	6.8	6.0	5.5	5	0.160	5.7	5.3	6.0	14	0.521	6.8	5.3
Aq. chrysaetos	16.7	4	0.797	17.3	15.5	15.6	4	0.876	16.5	14.8	16.1	8	0.961	17.3	14.8
B. buteo	9.5	5	0.695	10.1	8.3	8.7	6	0.640	9.5	7.7	9.0	14	0.685	10.1	7.7
B. lagopus	9.8	4	0.670	10.3	8.8	9.4	5	0.623	10.0	8.4	9.7	12	0.728	11.2	8.4
P. haliaetus	10.5	5	0.506	11.2	9.8	10.5	5	0.812	11.3	9.5	10.5	11	0.637	11.3	9.5
F. columbarius	5.3	5	0.246	5.6	5.1	5.0	5	0.125	5.1	4.8	5.2	16	0.256	5.6	4.8
F. peregrinus	9.2	3	0.681	10.0	8.7	8.1	5	0.272	8.4	7.7	8.5	11	0.614	10.0	7.7
F. rusticolus	10.9	5	0.228	11.2	10.7	10.1	5	0.272	10.5	9.8	10.5	11	0.430	11.2	9.8
F. subbuteo	6.4	1		6.4	6.4						6.2	2	0.354	6.4	5.9
F. tinnunculus	5.5	6	0.337	6.1	5.1	5.5	6	0.136	5.7	5.3	5.5	14	0.284	6.1	5.1
F. vespertinus	5.0	1		5.0	5.0	4.9	3	0.104	5.0	4.8	4.9	4	0.095	5.0	4.8
G. glandarius	4.9	1		4.9	4.9	5.1	2	0.219	5.2	4.9	5.0	4	0.164	5.2	4.9
Pe. infaustus	3.8	1		3.8	3.8	4.0	1		4.0	4.0	3.9	2	0.141	4.0	3.8
Pica pica	5.1	2	0.028	5.2	5.1	5.1	2	0.297	5.3	4.9	5.2	6	0.214	5.5	4.9
Nu. caryocatactes						4.7	1		4.7	4.7	4.7	1		4.7	4.7
Co. monedula	5.7	1		5.7	5.7	5.7	3	0.411	6.1	5.3	5.7	5	0.313	6.1	5.3
Co. frugilegus											7.6	2	0.163	7.8	7.5
Co. corone cx	7.6	5	0.367	8.0	7.0	8.5	5	0.362	8.9	8.1	8.0	15	0.541	8.9	7.0
Co. corone ce	7.7	1		7.7	7.7						7.5	2	0.410	7.7	7.2
Co. corax	10.3	1		10.3	10.3	11.0	3	0.789	11.8	10.3	10.7	5	0.664	11.8	10.3
Cy. olor						12.2	1		12.2	12.2	12.2	1		12.2	12.2
R. regulus						1.8	1		1.8	1.8	1.8	1		1.8	1.8

Appendix 9. Diameter d of carpometacarpus

Species	Female					Male					All				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	5.0	2	0.354	5.3	4.8	4.8	4	0.118	5.0	4.7	4.9	10	0.236	5.3	4.7
Ha. albicilla	9.4	5	0.720	10.6	8.8	9.3	5	0.750	10.2	8.3	9.4	10	0.696	10.6	8.3
Hi. pennatus											4.5	3	0.140	4.6	4.4
M. milvus	5.7	2	0.000	5.7	5.7	5.4	2	0.177	5.6	5.3	5.6	4	0.189	5.7	5.3
M. migrans						4.9	1		4.9	4.9	4.9	1		4.9	4.9
C. aeruginosus	5.3	1		5.3	5.3	4.6	4	0.100	4.8	4.6	4.7	7	0.277	5.3	4.5
C. cyaneus	4.4	5	0.338	4.8	3.9	4.2	5	0.696	5.3	3.5	4.3	13	0.480	5.3	3.5
C. pygargus						3.5	2	0.177	3.7	3.4	3.5	2	0.177	3.7	3.4
A. gentilis	5.4	5	0.114	5.5	5.3	4.8	5	0.297	5.3	4.5	5.1	10	0.381	5.5	4.5
A. nisus	3.1	8	0.121	3.3	2.9	2.7	5	0.072	2.8	2.6	3.0	14	0.253	3.3	2.6
Aq. chrysaetos	8.5	4	0.298	9.0	8.3	8.2	4	0.451	8.7	7.6	8.3	8	0.404	9.0	7.6
B. buteo	4.8	5	0.271	5.3	4.6	4.4	6	0.297	4.8	4.1	4.6	14	0.314	5.3	4.1
B. lagopus	5.2	4	0.443	5.7	4.7	4.7	5	0.094	4.9	4.6	5.1	12	0.431	5.8	4.6
P. haliaetus	5.9	5	0.367	6.3	5.3	5.8	5	0.329	6.2	5.4	5.8	11	0.328	6.3	5.3
F. columbarius	2.7	5	0.217	3.1	2.5	2.3	5	0.114	2.5	2.2	2.6	16	0.234	3.1	2.2
F. peregrinus	4.9	3	0.225	5.1	4.7	4.3	5	0.308	4.6	3.9	4.6	11	0.348	5.1	3.9
F. rusticolus	5.7	5	0.137	5.9	5.5	5.5	5	0.254	5.8	5.2	5.6	11	0.218	5.9	5.2
F. subbuteo	3.3	1		3.3	3.3						3.1	2	0.177	3.3	3.0
F. tinnunculus	2.8	6	0.191	3.1	2.6	2.8	6	0.162	3.0	2.6	2.8	14	0.169	3.1	2.6
F. vespertinus	2.5	1		2.5	2.5	2.6	3	0.000	2.6	2.6	2.5	4	0.050	2.6	2.5
G. glandarius	2.5	1		2.5	2.5	2.5	2	0.191	2.6	2.4	2.5	4	0.112	2.6	2.4
Pe. infaustus	1.8	1		1.8	1.8	1.7	1		1.7	1.7	1.8	2	0.085	1.8	1.7
Pica pica	2.8	2	0.113	2.9	2.8	2.6	2	0.311	2.9	2.4	2.8	6	0.222	3.0	2.4
Nu. caryocatactes						2.4	1		2.4	2.4	2.4	1		2.4	2.4
Co. monedula	3.3	1		3.3	3.3	3.1	3	0.325	3.4	2.8	3.1	5	0.245	3.4	2.8
Co. frugilegus											3.9	2	0.014	3.9	3.9
Co. corone cx	4.1	5	0.359	4.7	3.9	4.1	5	0.162	4.3	3.9	4.1	15	0.300	4.7	3.3
Co. corone ce	4.0	1		4.0	4.0						4.1	2	0.071	4.1	4.0
Co. corax	5.6	1		5.6	5.6	5.9	3	0.259	6.2	5.7	5.8	5	0.249	6.2	5.6
Cy. olor						9.9	1		9.9	9.9	9.9	1		9.9	9.9
R. regulus						0.7	1		0.7	0.7	0.7	1		0.7	0.7

Appendix 10. Length of carina sterni

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	63.8	5	2.49	67.4	60.6	63.0	4	2.40	65.1	59.6	63.3	13	2.28	67.4	59.6
Ha. albicilla	139.5	6	10.44	157.1	128.9	138.9	5	10.59	148.5	125.6	139.2	11	9.97	157.1	125.6
Hi. pennatus											59.5	5	3.04	63.1	55.5
M. milvus	77.3	2	24.43	94.6	60.1	65.6	4	2.22	67.5	62.6	69.5	6	12.62	94.6	60.1
M. migrans						57.5	1		57.5	57.5	57.5	1		57.5	57.5
C. aeruginosus	59.9	5	3.65	64.3	55.3	54.1	5	2.41	57.4	51.5	56.7	12	3.98	64.3	51.5
C. cyaneus	49.3	5	4.14	53.5	42.5	49.3	5	4.53	57.1	45.9	49.6	13	3.63	57.1	42.5
C. pygargus	42.5	3	3.18	45.8	39.5	42.1	4	2.40	44.6	39.4	42.3	7	2.51	45.8	39.4
A. gentilis	88.8	6	3.44	93.1	85.4	78.0	5	5.47	84.1	70.6	83.9	11	7.07	93.1	70.6
A. nisus	54.2	8	2.03	56.9	51.3	44.4	5	1.20	45.4	42.4	50.0	14	5.24	56.9	42.4
Aq. chrysaetos	115.1	7	3.94	120.3	108.3	112.1	5	6.60	121.2	102.7	113.9	12	5.17	121.2	102.7
B. buteo	59.0	5	2.00	62.1	56.9	55.7	6	2.38	58.6	52.0	57.1	14	2.47	62.1	52.0
B. lagopus	64.5	5	2.79	67.4	61.5	60.1	5	2.23	62.3	56.8	62.8	13	3.16	67.4	56.8
P. haliaetus	79.8	5	3.87	83.3	73.6	74.7	6	3.15	80.2	71.4	76.6	12	4.29	83.3	71.4
F. columbarius	42.0	5	1.52	43.5	39.6	39.3	5	1.84	42.0	37.5	40.6	15	2.31	43.8	37.5
F. peregrinus	78.1	6	4.18	85.1	73.0	68.0	6	3.08	70.9	62.9	72.1	15	6.00	85.1	62.9
F. rusticolus	88.8	5	1.02	90.1	87.7	82.3	5	3.06	86.1	79.0	85.7	11	3.87	90.1	79.0
F. subbuteo	43.6	6	1.66	45.6	41.3	45.3	5	1.62	46.7	42.9	44.4	12	1.72	46.7	41.3
F. tinnunculus	35.1	6	1.50	36.6	32.5	33.9	6	2.08	36.8	31.2	34.7	14	1.86	37.5	31.2
F. vespertinus	32.0	3	2.83	34.8	29.1	32.4	5	0.53	33.2	31.9	32.2	8	1.58	34.8	29.1
G. glandarius	33.9	1		33.9	33.9	35.4	2	0.72	35.9	34.9	35.2	4	1.01	36.1	33.9
Pe. infaustus	24.2	1		24.2	24.2	25.6	1		25.6	25.6	24.9	2	1.00	25.6	24.2
Pica pica	39.1	3	1.89	40.9	37.1	37.8	2	3.97	40.6	35.0	39.4	7	2.51	42.0	35.0
Nu. caryocatactes						36.0	1		36.0	36.0	36.0	1		36.0	36.0
Co. monedula	43.2	1		43.2	43.2	41.1	4	2.33	43.1	37.9	41.5	5	2.23	43.2	37.9
Co. frugilegus											54.4	2	4.21	57.4	51.4
Co. corone cx	51.5	5	2.20	54.2	49.2	56.2	5	2.30	59.1	53.2	53.9	13	2.98	59.1	49.2
Co. corone ce	54.9	1		54.9	54.9						53.2	2	2.48	54.9	51.4
Co. corax	78.2	2	0.87	78.8	77.6	79.4	3	2.36	81.9	77.2	76.2	7	5.42	81.9	65.2
Cy. olor						215.0	1		215.0	215.0	215.0	1		215.0	215.0
R. regulus						9.6	1		9.6	9.6	9.6	1		9.6	9.6

Appendix 11. Diameter D of carina sterni

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	19.6	5	0.699	20.3	18.5	19.6	4	0.822	20.5	18.7	19.5	13	0.776	20.5	18.2
Ha. albicilla	33.9	6	2.088	37.1	31.1	34.0	5	3.624	40.0	30.4	33.9	11	2.728	40.0	30.4
Hi. pennatus											17.3	5	1.259	19.0	15.5
M. milvus	26.0	2	4.907	29.4	22.5	18.9	4	1.170	20.1	17.4	21.3	6	4.350	29.4	17.4
M. migrans						17.6	1		17.6	17.6	17.6	1		17.6	17.6
C. aeruginosus	17.1	5	0.562	18.0	16.5	14.8	5	0.458	15.6	14.4	15.9	12	1.389	18.0	14.2
C. cyaneus	16.6	5	1.725	17.9	13.6	15.9	5	0.680	17.0	15.4	16.4	13	1.148	17.9	13.6
C. pygargus	15.6	3	0.966	16.5	14.6	13.8	4	0.206	14.0	13.5	14.6	7	1.133	16.5	13.5
A. gentilis	26.2	6	1.653	29.3	24.6	23.6	5	1.646	25.9	21.9	25.0	11	2.077	29.3	21.9
A. nisus	17.3	8	0.746	18.1	16.1	13.6	5	0.727	14.7	12.8	15.7	14	2.034	18.1	12.8
Aq. chrysaetos	28.2	7	1.120	30.1	27.0	27.2	5	2.919	31.6	24.6	27.8	12	2.012	31.6	24.6
B. buteo	17.8	5	0.422	18.1	17.1	17.2	6	0.834	18.3	15.9	17.6	14	0.834	19.3	15.9
B. lagopus	17.8	5	0.706	19.0	17.3	16.9	5	1.187	18.7	15.5	17.6	13	1.090	19.4	15.5
P. haliaetus	28.3	5	0.956	29.6	27.0	27.7	6	1.585	30.2	25.4	28.0	12	1.254	30.2	25.4
F. columbarius	15.2	5	0.521	15.9	14.5	13.6	5	0.540	14.2	12.9	14.7	15	1.079	16.6	12.9
F. peregrinus	26.5	6	2.342	29.5	24.0	23.5	6	1.546	24.6	20.9	24.9	15	2.222	29.5	20.9
F. rusticolus	28.1	5	4.765	31.1	19.8	28.1	5	0.927	29.4	27.2	28.3	11	3.167	31.1	19.8
F. subbuteo	16.2	6	0.620	17.2	15.6	15.9	5	0.563	16.3	14.9	16.0	12	0.591	17.2	14.9
F. tinnunculus	13.5	6	0.589	14.4	12.5	13.7	6	1.144	15.2	12.3	13.7	14	0.924	15.2	12.3
F. vespertinus	12.2	3	1.531	13.9	11.0	11.6	5	0.404	12.1	11.2	11.8	8	0.918	13.9	11.0
G. glandarius	10.9	1		10.9	10.9	11.8	2	0.700	12.3	11.3	11.4	4	0.623	12.3	10.9
Pe. infaustus	7.8	1		7.8	7.8	8.5	1		8.5	8.5	8.1	2	0.509	8.5	7.8
Pica pica	14.7	3	1.293	15.9	13.3	13.4	2	1.287	14.3	12.5	14.3	7	1.137	15.9	12.5
Nu. caryocatactes						12.4	1		12.4	12.4	12.4	1		12.4	12.4
Co. monedula	17.2	1		17.2	17.2	14.9	4	1.713	16.6	13.2	15.4	5	1.798	17.2	13.2
Co. frugilegus											19.7	2	0.672	20.2	19.2
Co. corone cx	18.4	5	0.427	18.8	17.7	19.8	5	1.311	21.9	18.8	19.1	13	1.027	21.9	17.7
Co. corone ce	18.3	1		18.3	18.3						18.5	2	0.318	18.7	18.3
Co. corax	25.7	2	1.089	26.5	25.0	25.4	3	0.451	25.9	25.0	24.9	7	1.275	26.5	22.6
Cy. olor						44.6	1		44.6	44.6	44.6	1		44.6	44.6
R. regulus						3.6	1		3.6	3.6	3.6	1		3.6	3.6

Appendix 12. Length of femur

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	57.7	5	1.603	59.3	55.1	57.9	5	2.445	60.7	54.6	57.7	14	1.803	60.7	54.6
Ha. albicilla	125.1	6	6.542	136.0	118.1	122.7	5	8.038	132.5	113.6	124.0	11	6.986	136.0	113.6
Hi. pennatus											68.6	4	3.511	71.6	64.7
M. milvus	79.3	2	12.084	87.8	70.8	67.7	4	0.959	68.6	66.6	71.6	6	8.100	87.8	66.6
M. migrans						61.4	1		61.4	61.4	61.4	1		61.4	61.4
C. aeruginosus	76.4	5	1.012	77.5	75.2	69.8	5	0.940	70.9	68.6	72.9	12	3.521	77.5	68.6
C. cyaneus	67.2	5	7.977	71.3	53.0	63.4	5	6.092	70.3	53.6	66.3	13	6.354	71.3	53.0
C. pygargus	54.2	3	1.089	55.1	53.0	51.8	4	1.226	53.5	50.6	52.8	7	1.642	55.1	50.6
A. gentilis	87.9	6	3.389	92.1	84.5	78.2	5	2.920	81.3	75.2	83.5	11	5.898	92.1	75.2
A. nisus	52.9	8	1.591	55.8	51.1	45.5	5	0.711	46.5	44.7	49.7	14	3.989	55.8	44.7
Aq. chrysaetos	130.4	5	2.455	133.0	127.2	125.5	5	3.998	131.1	121.9	127.9	10	4.031	133.0	121.9
B. buteo	74.7	5	1.830	76.3	71.8	71.8	6	3.007	74.5	65.9	73.1	14	2.871	76.3	65.9
B. lagopus	82.1	5	1.271	83.6	80.1	76.0	5	2.821	79.0	71.5	79.7	13	3.701	84.4	71.5
P. haliaetus	77.1	5	1.979	79.2	74.3	75.5	6	2.917	78.7	71.2	76.2	12	2.445	79.2	71.2
F. columbarius	45.8	5	1.069	46.9	44.2	43.6	5	0.645	44.4	42.7	44.7	16	1.511	46.9	41.9
F. peregrinus	71.6	6	1.523	73.3	69.6	62.4	6	1.574	64.8	60.0	66.6	15	4.699	73.3	60.0
F. rusticolus	89.0	5	1.518	90.7	87.1	83.1	5	3.665	89.2	79.5	86.0	11	3.865	90.7	79.5
F. subbuteo	44.7	6	1.459	47.0	42.9	42.9	5	0.429	43.4	42.5	43.7	12	1.464	47.0	42.1
F. tinnunculus	44.9	6	1.620	47.8	43.2	44.5	6	0.898	45.6	43.0	44.7	14	1.337	47.8	43.0
F. vespertinus	36.2	3	1.400	37.9	35.4	36.0	5	1.320	38.1	34.6	36.1	8	1.252	38.1	34.6
G. glandarius	38.3	1		38.3	38.3	38.5	1		38.5	38.5	38.4	3	0.085	38.5	38.3
Pe. infaustus	30.8	1		30.8	30.8	33.5	1		33.5	33.5	32.2	2	1.923	33.5	30.8
Pica pica	43.4	2	1.966	44.8	42.0	40.4	2	1.068	41.2	39.6	42.8	6	2.213	44.8	39.6
Nu. caryocatactes						38.5	1		38.5	38.5	38.5	1		38.5	38.5
Co. monedula	38.4	1		38.4	38.4	36.9	4	1.707	38.6	35.0	37.4	6	1.557	38.6	35.0
Co. frugilegus											50.4	2	2.100	51.9	49.0
Co. corone cx	52.9	5	1.526	54.6	50.9	55.3	5	0.906	56.4	54.0	53.7	15	1.646	56.4	50.9
Co. corone ce	52.0	1		52.0	52.0						52.0	1		52.0	52.0
Co. corax	68.9	2	2.489	70.6	67.1	71.8	3	2.555	74.8	70.1	69.9	7	2.611	74.8	67.1
Cy. olor						104.0	1		104.0	104.0	104.0	1		104.0	104.0
R. regulus						9.7	1		9.7	9.7	9.7	1		9.7	9.7

Appendix 13. Diameter D of femur

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	6.7	5	0.096	6.9	6.7	6.3	5	0.178	6.5	6.1	6.5	14	0.382	7.5	6.1
Ha. albicilla	13.5	6	1.089	15.2	12.4	13.0	5	1.104	14.2	11.6	13.3	11	1.064	15.2	11.6
Hi. pennatus											6.1	4	0.169	6.3	5.9
M. milvus	7.5	2	1.280	8.4	6.6	6.4	4	0.287	6.8	6.2	6.7	6	0.825	8.4	6.2
M. migrans						5.6	1		5.6	5.6	5.6	1		5.6	5.6
C. aeruginosus	6.3	5	0.139	6.5	6.1	5.6	5	0.236	6.0	5.4	5.9	12	0.447	6.5	5.2
C. cyaneus	5.4	5	0.704	6.0	4.2	4.8	5	0.986	6.3	3.6	5.2	13	0.767	6.3	3.6
C. pygargus	4.2	3	0.050	4.3	4.2	4.0	4	0.193	4.1	3.7	4.1	7	0.180	4.3	3.7
A. gentilis	8.5	6	0.308	8.9	8.1	6.9	5	0.499	7.8	6.5	7.7	11	0.902	8.9	6.5
A. nisus	4.1	8	0.238	4.5	3.8	3.3	5	0.206	3.5	3.1	3.7	14	0.472	4.5	3.1
Aq. chrysaetos	13.6	5	0.444	14.1	13.2	13.0	5	0.719	13.9	12.3	13.3	10	0.633	14.1	12.3
B. buteo	6.7	5	0.207	6.9	6.4	6.2	6	0.393	6.8	5.6	6.5	14	0.390	6.9	5.6
B. lagopus	6.9	5	0.426	7.4	6.3	6.2	5	0.293	6.6	5.9	6.6	13	0.521	7.5	5.9
P. haliaetus	7.6	5	0.467	8.0	6.9	7.6	6	0.327	8.1	7.2	7.5	12	0.386	8.1	6.9
F. columbarius	3.7	5	0.255	3.9	3.3	3.5	5	0.143	3.7	3.4	3.6	16	0.185	3.9	3.3
F. peregrinus	6.4	6	0.205	6.7	6.3	5.7	6	0.238	6.1	5.4	6.1	15	0.404	6.7	5.4
F. rusticolus	8.4	5	0.284	8.6	8.0	7.7	5	0.637	8.8	7.1	8.0	11	0.606	8.8	7.1
F. subbuteo	3.9	6	0.303	4.3	3.5	3.6	5	0.079	3.7	3.5	3.7	12	0.268	4.3	3.5
F. tinnunculus	3.6	6	0.226	3.8	3.2	3.7	6	0.173	3.9	3.4	3.6	14	0.189	3.9	3.2
F. vespertinus	3.0	3	0.076	3.1	2.9	2.8	5	0.089	3.0	2.8	2.9	8	0.103	3.1	2.8
G. glandarius	3.3	1		3.3	3.3	3.2	1		3.2	3.2	3.2	3	0.044	3.3	3.2
Pe. infaustus	2.4	1		2.4	2.4	2.5	1		2.5	2.5	2.4	2	0.099	2.5	2.4
Pica pica	3.7	2	0.163	3.8	3.6	3.4	2	0.233	3.5	3.2	3.6	6	0.217	3.8	3.2
Nu. caryocatactes						3.0	1		3.0	3.0	3.0	1		3.0	3.0
Co. monedula	3.3	1		3.3	3.3	3.3	4	0.254	3.5	3.0	3.3	6	0.198	3.5	3.0
Co. frugilegus											4.4	2	0.049	4.4	4.4
Co. corone cx	4.5	5	0.120	4.6	4.3	4.7	5	0.134	4.9	4.5	4.6	14	0.247	4.9	3.9
Co. corone ce	4.5	1		4.5	4.5						4.5	1		4.5	4.5
Co. corax	6.4	2	0.177	6.5	6.3	6.7	3	0.483	7.3	6.4	6.4	7	0.458	7.3	5.7
Cy. olor						13.2	1		13.2	13.2	13.2	1		13.2	13.2
R. regulus						0.7	1		0.7	0.7	0.7	1		0.7	0.7

Appendix 14. Diameter d of femur

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	5.9	5	0.204	6.3	5.7	5.6	5	0.186	5.9	5.4	5.8	14	0.296	6.3	5.4
Ha. albicilla	12.8	5	1.245	14.4	11.5	12.3	5	1.325	13.9	10.7	12.5	10	1.236	14.4	10.7
Hi. pennatus											6.4	4	0.428	6.9	6.0
M. milvus	7.1	2	0.813	7.7	6.6	6.0	4	0.307	6.5	5.8	6.4	6	0.722	7.7	5.8
M. migrans						5.4	1		5.4	5.4	5.4	1		5.4	5.4
C. aeruginosus	6.3	5	0.152	6.6	6.2	5.6	5	0.122	5.7	5.4	5.9	12	0.442	6.6	5.4
C. cyaneus	5.3	5	0.747	5.7	4.0	4.7	5	0.764	5.7	3.6	5.1	13	0.720	5.7	3.6
C. pygargus	4.3	3	0.132	4.4	4.2	3.9	4	0.217	4.1	3.6	4.1	7	0.249	4.4	3.6
A. gentilis	7.9	6	0.346	8.4	7.5	6.4	5	0.473	7.0	5.8	7.2	11	0.869	8.4	5.8
A. nisus	4.0	8	0.164	4.3	3.7	3.2	5	0.118	3.4	3.1	3.7	14	0.440	4.3	3.1
Aq. chrysaetos	12.5	5	0.517	12.9	11.7	12.4	5	0.693	13.1	11.5	12.4	10	0.583	13.1	11.5
B. buteo	6.0	5	0.640	6.5	5.0	6.0	6	0.371	6.5	5.5	6.1	14	0.454	6.5	5.0
B. lagopus	6.7	5	0.463	7.3	6.1	6.1	5	0.296	6.5	5.8	6.5	13	0.514	7.3	5.8
P. haliaetus	7.0	5	0.721	7.8	6.2	6.7	6	0.385	7.2	6.4	6.8	12	0.528	7.8	6.2
F. columbarius	3.5	5	0.195	3.6	3.2	3.0	5	0.175	3.2	2.9	3.3	16	0.257	3.6	2.9
F. peregrinus	6.6	6	0.114	6.8	6.5	5.6	6	0.353	6.0	5.2	6.1	15	0.544	6.8	5.2
F. rusticolus	7.9	5	0.236	8.1	7.5	7.1	5	0.536	8.0	6.6	7.5	11	0.531	8.1	6.6
F. subbuteo	3.6	6	0.258	4.0	3.2	3.4	5	0.045	3.5	3.4	3.5	12	0.208	4.0	3.2
F. tinnunculus	3.6	6	0.262	4.1	3.3	3.5	6	0.117	3.7	3.3	3.5	14	0.197	4.1	3.3
F. vespertinus	2.9	3	0.150	3.1	2.8	2.7	5	0.124	2.9	2.6	2.8	8	0.158	3.1	2.6
G. glandarius	2.9	1		2.9	2.9	2.8	1		2.8	2.8	2.8	3	0.107	2.9	2.7
Pe. infaustus	2.2	1		2.2	2.2	2.2	1		2.2	2.2	2.2	2	0.028	2.2	2.2
Pica pica	3.3	2	0.163	3.5	3.2	3.0	2	0.141	3.1	2.9	3.2	6	0.187	3.5	2.9
Nu. caryocatactes						2.9	1		2.9	2.9	2.9	1		2.9	2.9
Co. monedula	3.2	1		3.2	3.2	3.1	4	0.181	3.3	2.9	3.1	6	0.145	3.3	2.9
Co. frugilegus											4.0	2	0.028	4.0	4.0
Co. corone cx	4.2	5	0.205	4.5	4.1	4.4	5	0.186	4.5	4.1	4.3	14	0.262	4.5	3.6
Co. corone ce	4.2	1		4.2	4.2						4.2	1		4.2	4.2
Co. corax	5.7	2	0.205	5.8	5.5	6.2	3	0.290	6.4	5.9	5.9	7	0.385	6.4	5.4
Cy. olor						10.4	1		10.4	10.4	10.4	1		10.4	10.4
R. regulus						0.7	1		0.7	0.7	0.7	1		0.7	0.7

Appendix 15. Length of tibiotarsus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	89.5	2	4.10	92.4	86.6	87.8	4	5.03	93.6	81.6	88.4	10	3.39	93.6	81.6
Ha. albicilla	168.6	5	9.00	182.5	159.0	165.2	5	11.52	181.0	152.0	166.9	10	9.91	182.5	152.0
Hi. pennatus											95.9	2	4.96	99.4	92.4
M. milvus	103.0	2	19.22	116.6	89.5	84.5	2	0.21	84.6	84.3	93.7	4	15.44	116.6	84.3
M. migrans						78.9	1		78.9	78.9	78.9	1		78.9	78.9
C. aeruginosus	118.1	1		118.1	118.1	103.3	3	2.66	106.3	101.1	107.5	6	6.62	118.1	101.1
C. cyaneus	94.2	5	7.87	98.5	80.2	89.7	5	10.21	105.5	77.2	93.3	13	8.12	105.5	77.2
C. pygargus						78.0	3	2.86	79.7	74.7	78.0	3	2.86	79.7	74.7
A. gentilis	116.3	6	3.64	121.0	113.0	104.7	5	3.11	108.5	101.6	111.1	11	6.89	121.0	101.6
A. nisus	71.4	8	2.57	75.5	67.2	60.3	5	1.03	61.9	59.0	66.8	14	5.93	75.5	59.0
Aq. chrysaetos	169.7	5	2.64	173.0	167.0	163.2	4	2.26	166.0	161.0	166.8	9	4.14	173.0	161.0
B. buteo	101.4	5	1.90	104.3	99.6	98.9	5	3.76	103.4	93.3	100.4	13	3.37	106.3	93.3
B. lagopus	103.5	4	1.39	104.3	101.4	98.2	4	2.07	100.6	96.3	101.7	11	3.42	107.7	96.3
P. haliaetus	123.7	5	3.51	127.0	118.7	121.0	5	4.89	125.7	113.6	122.5	11	4.07	127.0	113.6
F. columbarius	57.9	5	1.10	59.3	56.5	54.6	5	1.03	55.7	53.1	56.4	16	2.05	59.4	53.1
F. peregrinus	91.5	5	2.64	94.6	88.5	78.5	6	2.07	81.9	75.4	84.4	13	6.70	94.6	75.4
F. rusticolus	107.6	5	2.34	109.8	104.8	99.9	5	4.44	107.1	95.0	104.0	11	5.06	109.8	95.0
F. subbuteo	60.0	1		60.0	60.0	54.9	2	0.50	55.2	54.5	55.8	4	2.88	60.0	53.5
F. tinnunculus	59.2	6	1.51	62.1	57.8	59.0	5	0.97	59.8	57.8	59.3	13	1.45	62.3	57.8
F. vespertinus	46.7	1		46.7	46.7	47.6	3	0.52	47.9	47.0	47.3	4	0.60	47.9	46.7
G. glandarius	60.2	1		60.2	60.2	61.7	2	2.84	63.7	59.7	61.2	4	1.78	63.7	59.7
Pe. infaustus	50.7	1		50.7	50.7	54.5	1		54.5	54.5	52.6	2	2.69	54.5	50.7
Pica pica	68.5	2	3.47	70.9	66.0	65.8	2	0.96	66.4	65.1	68.9	6	3.44	73.3	65.1
Nu. caryocatactes						57.1	1		57.1	57.1	57.1	1		57.1	57.1
Co. monedula	66.3	1		66.3	66.3	64.7	4	3.40	68.4	61.6	65.0	5	3.03	68.4	61.6
Co. frugilegus											86.8	2	3.23	89.1	84.5
Co. corone cx	85.9	4	5.61	92.0	79.6	90.3	5	2.53	93.5	87.2	88.3	14	3.82	93.5	79.6
Co. corone ce	87.6	1		87.6	87.6						87.6	1		87.6	87.6
Co. corax	110.3	1		110.3	110.3	114.3	2	3.27	116.6	112.0	112.8	5	2.40	116.6	110.3
Cy. olor						205.5	1		205.5	205.5	205.5	1		205.5	205.5
R. regulus						21.5	1		21.5	21.5	21.5	1		21.5	21.5

Appendix 16. Diameter D of tibiotarsus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	5.8	2	0.283	6.0	5.6	5.3	4	0.371	5.8	4.9	5.4	10	0.364	6.0	4.9
Ha. albicilla	11.2	5	1.029	12.8	9.9	11.1	5	0.974	12.2	9.9	11.2	10	0.947	12.8	9.9
Hi. pennatus											5.4	4	0.107	5.6	5.4
M. milvus	6.4	2	1.216	7.3	5.6	5.2	2	0.177	5.3	5.1	5.8	4	1.006	7.3	5.1
M. migrans						5.1	1		5.1	5.1	5.1	1		5.1	5.1
C. aeruginosus	5.4	1		5.4	5.4	4.9	3	0.076	5.0	4.9	5.1	6	0.266	5.5	4.9
C. cyaneus	4.7	5	0.645	5.2	3.6	4.2	5	0.850	5.5	3.2	4.5	13	0.667	5.5	3.2
C. pygargus						3.5	3	0.437	4.0	3.2	3.5	3	0.437	4.0	3.2
A. gentilis	7.4	6	0.401	7.9	7.0	6.1	5	0.476	6.7	5.6	6.8	11	0.829	7.9	5.6
A. nisus	3.7	8	0.291	4.2	3.3	2.9	5	0.181	3.2	2.8	3.4	14	0.503	4.2	2.8
Aq. chrysaetos	12.0	5	0.503	12.6	11.3	10.9	4	0.386	11.3	10.4	11.5	9	0.714	12.6	10.4
B. buteo	6.1	5	0.269	6.4	5.8	5.6	6	0.284	6.0	5.2	5.9	14	0.357	6.4	5.2
B. lagopus	6.4	4	0.333	6.7	5.9	5.8	5	0.429	6.6	5.5	6.1	12	0.424	6.7	5.5
P. haliaetus	7.1	5	0.471	7.6	6.6	7.1	5	0.406	7.4	6.4	7.1	11	0.408	7.6	6.4
F. columbarius	2.9	5	0.217	3.2	2.7	2.7	5	0.055	2.8	2.7	2.9	16	0.210	3.2	2.7
F. peregrinus	5.7	5	0.434	6.5	5.4	4.8	6	0.254	5.1	4.4	5.2	13	0.535	6.5	4.4
F. rusticolus	7.5	5	0.305	7.8	7.2	6.9	5	0.540	7.8	6.3	7.2	11	0.518	7.8	6.3
F. subbuteo	3.7	1		3.7	3.7	3.1	3	0.126	3.3	3.0	3.3	5	0.267	3.7	3.0
F. tinnunculus	3.3	6	0.195	3.7	3.2	3.3	5	0.217	3.7	3.1	3.3	13	0.183	3.7	3.1
F. vespertinus	2.7	1		2.7	2.7	2.8	3	0.229	3.0	2.6	2.7	4	0.194	3.0	2.6
G. glandarius	3.0	1		3.0	3.0	2.7	2	0.035	2.7	2.7	2.7	4	0.187	3.0	2.5
Pe. infaustus	2.1	1		2.1	2.1	2.4	1		2.4	2.4	2.2	2	0.148	2.4	2.1
Pica pica	3.1	2	0.375	3.4	2.9	3.2	2	0.170	3.3	3.1	3.2	6	0.208	3.4	2.9
Nu. caryocatactes						2.5	1		2.5	2.5	2.5	1		2.5	2.5
Co. monedula	3.3	1		3.3	3.3	3.1	4	0.115	3.2	2.9	3.1	5	0.128	3.3	2.9
Co. frugilegus											4.2	2	0.120	4.3	4.1
Co. corone cx	4.1	4	0.209	4.3	3.8	4.4	5	0.180	4.7	4.3	4.3	14	0.245	4.7	3.8
Co. corone ce	4.1	1		4.1	4.1						4.1	1		4.1	4.1
Co. corax	5.8	1		5.8	5.8	6.1	2	0.354	6.4	5.9	5.8	5	0.371	6.4	5.4
Cy. olor						11.6	1		11.6	11.6	11.6	1		11.6	11.6
R. regulus						0.7	1		0.7	0.7	0.7	1		0.7	0.7

Appendix 17. Diameter d of tibiotarsus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	5.1	2	0.283	5.3	4.9	4.8	4	0.193	5.0	4.5	4.8	10	0.245	5.3	4.5
Ha. albicilla	9.2	5	0.925	10.7	8.4	9.8	5	0.811	11.0	8.8	9.5	10	0.886	11.0	8.4
Hi. pennatus											5.1	4	0.304	5.5	4.8
M. milvus	5.7	2	0.481	6.0	5.4	4.7	2	0.247	4.9	4.5	5.2	4	0.664	6.0	4.5
M. migrans						4.3	1		4.3	4.3	4.3	1		4.3	4.3
C. aeruginosus	4.5	1		4.5	4.5	4.3	3	0.150	4.4	4.1	4.4	6	0.338	5.0	4.1
C. cyaneus	4.2	5	0.409	4.6	3.5	3.8	5	0.572	4.7	3.2	4.0	13	0.461	4.7	3.2
C. pygargus						3.1	3	0.304	3.3	2.7	3.1	3	0.304	3.3	2.7
A. gentilis	6.2	6	0.188	6.5	6.0	5.0	5	0.438	5.8	4.7	5.7	11	0.671	6.5	4.7
A. nisus	3.3	8	0.187	3.5	3.1	2.6	5	0.099	2.6	2.4	3.0	14	0.380	3.5	2.4
Aq. chrysaetos	9.3	5	0.504	10.0	8.9	8.9	4	0.744	9.8	8.0	9.2	9	0.620	10.0	8.0
B. buteo	5.3	5	0.167	5.5	5.1	5.5	6	1.238	7.8	4.0	5.4	14	0.785	7.8	4.0
B. lagopus	5.3	4	0.309	5.5	4.9	5.1	5	0.263	5.5	4.8	5.2	12	0.327	5.9	4.8
P. haliaetus	6.9	5	0.323	7.4	6.7	7.0	5	0.340	7.4	6.5	6.9	11	0.322	7.4	6.5
F. columbarius	2.9	5	0.175	3.2	2.7	2.7	5	0.175	2.9	2.4	2.9	16	0.214	3.2	2.4
F. peregrinus	5.6	5	0.529	6.5	5.2	4.7	6	0.383	5.3	4.2	5.1	13	0.583	6.5	4.2
F. rusticolus	6.4	5	0.254	6.7	6.2	5.7	5	0.488	6.5	5.1	6.1	11	0.480	6.7	5.1
F. subbuteo	3.4	1		3.4	3.4	2.9	3	0.058	3.0	2.9	3.0	5	0.235	3.4	2.8
F. tinnunculus	3.0	6	0.108	3.2	2.9	2.9	5	0.096	3.1	2.8	3.0	13	0.153	3.4	2.8
F. vespertinus	2.5	1		2.5	2.5	2.6	3	0.126	2.7	2.5	2.6	4	0.111	2.7	2.5
G. glandarius	2.6	1		2.6	2.6	2.6	2	0.049	2.6	2.5	2.6	4	0.031	2.6	2.5
Pe. infaustus	1.8	1		1.8	1.8	2.0	1		2.0	2.0	1.9	2	0.163	2.0	1.8
Pica pica	3.2	2	0.304	3.4	3.0	2.8	2	0.410	3.1	2.5	3.1	6	0.315	3.4	2.5
Nu. caryocatactes						2.2	1		2.2	2.2	2.2	1		2.2	2.2
Co. monedula	2.7	1		2.7	2.7	2.9	4	0.155	3.2	2.8	2.9	5	0.186	3.2	2.7
Co. frugilegus											3.7	2	0.141	3.8	3.6
Co. corone cx	3.8	4	0.121	3.9	3.6	4.0	5	0.135	4.1	3.8	3.8	14	0.176	4.1	3.5
Co. corone ce	3.7	1		3.7	3.7						3.7	1		3.7	3.7
Co. corax	4.8	1		4.8	4.8	5.5	2	0.460	5.9	5.2	5.2	5	0.483	5.9	4.6
Cy. olor						8.9	1		8.9	8.9	8.9	1		8.9	8.9
R. regulus						0.6	1		0.6	0.6	0.6	1		0.6	0.6

Appendix 18. Length of tarsometatarsus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	52.0	2	0.141	52.1	51.9	52.8	4	3.526	55.6	47.6	52.5	10	2.160	55.6	47.6
Ha. albicilla	100.3	5	4.865	107.8	96.5	97.5	5	7.381	106.4	86.6	98.9	10	6.082	107.8	86.6
Hi. pennatus											57.8	4	3.297	61.1	54.0
M. milvus	86.1	1		86.1	86.1	54.2	2	0.495	54.5	53.8	64.8	3	18.427	86.1	53.8
M. migrans						52.2	1		52.2	52.2	52.2	1		52.2	52.2
C. aeruginosus	93.1	1		93.1	93.1	83.2	3	1.838	85.2	81.7	86.1	6	4.485	93.1	81.7
C. cyaneus	71.5	5	6.073	75.8	61.0	70.1	5	8.157	82.3	59.5	71.6	13	6.089	82.3	59.5
C. pygargus						60.0	3	1.986	61.4	57.7	60.0	3	1.986	61.4	57.7
A. gentilis	82.9	5	3.131	87.5	79.4	78.5	4	1.927	79.9	75.8	80.9	9	3.410	87.5	75.8
A. nisus	60.3	8	2.469	62.9	55.1	54.5	5	0.954	56.1	53.8	57.8	14	3.549	62.9	53.8
Aq. chrysaetos	104.2	5	1.108	105.5	102.5	100.7	4	2.344	103.9	98.8	102.6	9	2.451	105.5	98.8
B. buteo	74.7	5	2.278	76.6	72.1	73.7	6	3.374	79.4	69.3	74.5	13	2.811	79.4	69.3
B. lagopus	69.3	4	1.671	70.4	66.8	67.9	4	1.706	69.5	66.0	68.8	11	1.602	70.4	66.0
P. haliaetus	52.7	5	1.600	54.9	51.0	51.4	5	1.591	53.4	49.2	52.4	11	1.858	55.4	49.2
F. columbarius	38.3	5	0.605	38.8	37.4	36.8	5	0.907	37.8	35.5	37.2	16	1.073	38.8	35.5
F. peregrinus	52.7	3	1.940	54.9	51.4	47.6	5	0.795	48.4	46.6	49.1	9	2.935	54.9	46.0
F. rusticolus	64.3	5	2.173	66.1	61.6	61.5	5	1.963	64.2	59.3	65.0	11	7.299	85.9	59.3
F. subbuteo	36.3	1		36.3	36.3	33.7	1		33.7	33.7	34.4	3	1.612	36.3	33.3
F. tinnunculus	40.1	6	0.645	41.3	39.5	40.9	5	1.030	41.9	39.6	40.4	13	0.977	41.9	39.0
F. vespertinus						28.9	3	0.180	29.1	28.7	28.9	3	0.180	29.1	28.7
G. glandarius	41.4	1		41.4	41.4	43.9	2	1.450	44.9	42.9	42.5	4	1.804	44.9	40.9
Pe. infaustus	35.8	1		35.8	35.8	38.2	1		38.2	38.2	37.0	2	1.683	38.2	35.8
Pica pica	48.4	2	1.817	49.7	47.1	46.7	2	2.595	48.5	44.9	49.0	6	2.780	52.2	44.9
Nu. caryocatactes						39.1	1		39.1	39.1	39.1	1		39.1	39.1
Co. monedula	44.1	1		44.1	44.1	43.3	4	2.009	45.3	41.4	43.5	5	1.777	45.3	41.4
Co. frugilegus											53.9	2	0.127	54.0	53.8
Co. corone cx	56.9	5	2.822	60.4	53.1	60.6	5	2.302	63.0	58.1	58.5	15	2.630	63.0	53.1
Co. corone ce	58.0	1		58.0	58.0						58.0	1		58.0	58.0
Co. corax	65.2	1		65.2	65.2	69.8	2	1.718	71.0	68.6	68.3	5	2.195	71.0	65.2
Cy. olor						111.1	1		111.1	111.1	111.1	1		111.1	111.1
R. regulus						17.1	1		17.1	17.1	17.1	1		17.1	17.1

Appendix 19. Diameter D of tarsometatarsus

Species	**Female**					**Male**					**All**				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	6.6	2	0.636	7.0	6.1	5.8	4	0.370	6.3	5.4	6.2	10	0.484	7.0	5.4
Ha. albicilla	11.7	5	1.192	13.6	10.4	11.6	5	1.114	13.4	10.6	11.6	10	1.088	13.6	10.4
Hi. pennatus											6.0	4	0.373	6.6	5.7
M. milvus	7.2	1		7.2	7.2	5.1	2	0.120	5.2	5.0	5.8	3	1.213	7.2	5.0
M. migrans						5.2	1		5.2	5.2	5.2	1		5.2	5.2
C. aeruginosus	4.3	1		4.3	4.3	4.4	4	0.238	4.8	4.3	4.4	7	0.389	5.2	4.0
C. cyaneus	3.8	5	0.430	4.3	3.2	3.1	3	0.721	3.9	2.5	3.5	11	0.539	4.3	2.5
C. pygargus						2.6	3	0.144	2.8	2.5	2.6	3	0.144	2.8	2.5
A. gentilis	6.5	5	0.459	7.2	6.1	5.3	5	0.331	5.7	5.0	5.9	10	0.741	7.2	5.0
A. nisus	2.9	8	0.285	3.5	2.6	2.2	5	0.121	2.4	2.1	2.6	14	0.429	3.5	2.1
Aq. chrysaetos	11.8	5	0.567	12.3	10.9	10.3	4	1.062	11.9	9.5	11.1	9	1.099	12.3	9.5
B. buteo	5.5	5	0.244	5.8	5.2	5.2	6	0.517	6.0	4.6	5.4	13	0.418	6.0	4.6
B. lagopus	6.4	4	0.739	7.5	5.9	5.3	4	0.436	5.9	5.0	5.9	11	0.745	7.5	5.0
P. haliaetus	9.3	5	0.788	10.2	8.1	9.1	5	0.573	10.0	8.4	9.1	11	0.655	10.2	8.1
F. columbarius	2.8	5	0.288	3.1	2.3	2.4	5	0.167	2.7	2.2	2.6	16	0.255	3.1	2.2
F. peregrinus	5.8	3	0.275	6.2	5.7	4.8	5	0.208	5.1	4.6	5.1	9	0.552	6.2	4.6
F. rusticolus	7.4	5	0.449	7.8	6.7	6.8	5	0.750	8.0	6.2	7.1	11	0.637	8.0	6.2
F. subbuteo	3.0	1		3.0	3.0	2.6	1		2.6	2.6	2.7	3	0.312	3.0	2.4
F. tinnunculus	3.2	6	0.254	3.7	3.0	2.8	5	0.452	3.2	2.1	3.1	13	0.375	3.7	2.1
F. vespertinus						2.3	3	0.115	2.5	2.3	2.3	3	0.115	2.5	2.3
G. glandarius	2.4	1		2.4	2.4	2.1	2	0.099	2.2	2.1	2.2	4	0.146	2.4	2.1
Pe. infaustus	1.6	1		1.6	1.6	1.7	1		1.7	1.7	1.6	2	0.099	1.7	1.6
Pica pica	2.7	2	0.424	3.0	2.4	2.5	2	0.191	2.7	2.4	2.7	6	0.269	3.0	2.4
Nu. caryocatactes						2.2	1		2.2	2.2	2.2	1		2.2	2.2
Co. monedula	2.8	1		2.8	2.8	2.8	4	0.077	2.8	2.7	2.8	5	0.070	2.8	2.7
Co. frugilegus											3.7	1		3.7	3.7
Co. corone cx	3.8	5	0.170	4.1	3.6	4.1	5	0.228	4.4	3.8	3.9	15	0.259	4.4	3.5
Co. corone ce	3.9	1		3.9	3.9						3.9	1		3.9	3.9
Co. corax						5.8	2	0.318	6.1	5.6	5.9	3	0.232	6.1	5.6
Cy. olor						9.6	1		9.6	9.6	9.6	1		9.6	9.6
R. regulus						0.6	1		0.6	0.6	0.6	1		0.6	0.6

Appendix 20. Diameter d of tarsometatarsus

Species	Female					Male					All				
	Mean	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**	**Mean**	**n**	**S. D.**	**Max**	**Min**
	mm			*mm*	*mm*	*mm*			*mm*	*mm*	*mm*			*mm*	*mm*
P. apivorus	3.4	2	0.318	3.7	3.2	3.3	4	0.229	3.5	3.0	3.3	10	0.309	3.7	2.7
Ha. albicilla	10.4	5	4.298	17.9	7.2	8.7	5	0.835	9.6	7.7	9.5	10	3.052	17.9	7.2
Hi. pennatus											4.0	4	0.431	4.6	3.5
M. milvus	5.3	1		5.3	5.3	4.1	2	0.283	4.3	3.9	4.5	3	0.721	5.3	3.9
M. migrans						3.9	1		3.9	3.9	3.9	1		3.9	3.9
C. aeruginosus	4.3	1		4.3	4.3	3.6	4	0.108	3.7	3.5	3.7	7	0.349	4.3	3.4
C. cyaneus	3.1	5	0.442	3.5	2.5	2.6	3	0.454	3.1	2.2	3.0	11	0.439	3.5	2.2
C. pygargus						2.5	3	0.388	2.8	2.1	2.5	3	0.388	2.8	2.1
A. gentilis	5.5	5	0.276	5.8	5.1	4.2	5	0.206	4.6	4.0	4.9	10	0.719	5.8	4.0
A. nisus	2.3	8	0.737	4.1	1.8	1.7	5	0.106	1.9	1.7	2.0	14	0.626	4.1	1.6
Aq. chrysaetos	8.7	5	0.951	9.5	7.1	7.7	4	0.486	8.0	7.0	8.3	9	0.903	9.5	7.0
B. buteo	4.7	5	0.267	5.2	4.6	4.2	6	0.429	4.7	3.6	4.4	13	0.418	5.2	3.6
B. lagopus	4.8	3	1.011	5.6	3.7	4.5	4	0.242	4.7	4.1	4.6	10	0.530	5.6	3.7
P. haliaetus	4.4	5	0.214	4.7	4.2	4.3	5	0.164	4.6	4.1	4.4	11	0.218	4.8	4.1
F. columbarius	2.5	5	0.537	3.1	1.7	1.8	5	0.520	2.7	1.5	2.1	16	0.612	3.4	1.5
F. peregrinus	4.5	3	0.939	5.6	4.0	3.7	5	0.747	5.0	3.2	3.9	9	0.851	5.6	3.2
F. rusticolus	5.2	5	0.182	5.4	5.0	5.6	5	1.514	8.0	4.4	5.3	11	0.994	8.0	4.4
F. subbuteo	2.1	1		2.1	2.1	1.8	1		1.8	1.8	1.9	3	0.173	2.1	1.8
F. tinnunculus	2.1	6	0.218	2.6	2.0	2.4	5	0.429	2.9	1.9	2.3	13	0.312	2.9	1.9
F. vespertinus						1.6	3	0.050	1.7	1.6	1.6	3	0.050	1.7	1.6
G. glandarius	3.6	1		3.6	3.6	2.5	2	0.212	2.6	2.3	2.7	4	0.638	3.6	2.2
Pe. infaustus	1.6	1		1.6	1.6	2.1	1		2.1	2.1	1.8	2	0.346	2.1	1.6
Pica pica	2.5	2	0.247	2.7	2.3	2.2	2	0.007	2.2	2.2	2.5	6	0.258	2.8	2.2
Nu. caryocatactes						2.0	1		2.0	2.0	2.0	1		2.0	2.0
Co. monedula	2.6	1		2.6	2.6	2.5	4	0.064	2.6	2.4	2.5	5	0.064	2.6	2.4
Co. frugilegus											3.1	1		3.1	3.1
Co. corone cx	3.4	5	0.190	3.7	3.3	3.5	5	0.296	4.0	3.3	3.4	15	0.282	4.0	2.7
Co. corone ce	3.3	1		3.3	3.3						3.3	1		3.3	3.3
Co. corax						4.1	2	0.064	4.2	4.1	4.1	3	0.059	4.2	4.1
Cy. olor						8.8	1		8.8	8.8	8.8	1		8.8	8.8
R. regulus						0.5	1		0.5	0.5	0.5	1		0.5	0.5

Appendix 21. Latin, English and Swedish names

Species included in the allometric analysis are marked with an asterisk.

Latin name	**English name**	**Swedish name**
Pernis apivorus (Linné 1758) *	Honey Buzzard	Bivråk
Haliaeetus albicilla (Linné 1758) *	White-tailed Eagle	Havsörn
Hieraaetus pennatus (J F Gmelin 1788)	Booted eagle	Dvärörn
Milvus milvus (Linné 1758) *	Red Kite	Glada
Milvus migrans (Boddaert 1783)	Black Kite	Brun glada
Circus aeruginosus (Linné 1758) *	Marsh Harrier	Brun kärrhök
Circus cyaneus (Linné 1766) *	Hen Harrier	Blå kärrhök
Circus pygargus (Linné 1758) *	Montagu's Harrier	Ängshök
Accipiter gentilis (Linné 1758) *	Goshawk	Duvhök
Accipiter nisus (Linné 1758) *	Sparrow Hawk	Sparvhök
Aquila chrysaetos (Linné 1758) *	Golden Eagle	Kungsörn
Buteo buteo (Linné 1758) *	Common Buzzard	Ormvråk
Buteo lagopus (Pontoppidan 1763) *	Rough-legged Buzzard	Fjällvråk
Pandion haliaetus (Linné 1758) *	Osprey	Fiskgjuse
Falco columbarius (Linné 1758) *	Merlin	Stenfalk
Falco peregrinus (Tunstall 1771) *	Peregrine	Pilgrimsfalk
Falco rusticolus (Linné 1758) *	Gerfalcon	Jaktfalk
Falco subbuteo (Linné 1758) *	Hobby	Lärkfalk
Falco tinnunculus (Linné 1758) *	Kestrel	Tornfalk
Falco vespertinus (Linné 1766) *	Red-footed Falcon	Aftonfalk
Garrulus glandarius (Linné 1758)	Jay	Nötskrika
Perisoreus infaustus (Linné 1758)	Siberian jay	Lavskrika
Pica pica (Linné 1758)	Magpie	Skata
Nucifraga caryocatactes (Linné 1758)	Nutcracker	Nötkråka
Corvus monedula (Linné 1758)	Jackdaw	Kaja
Corvus frugilegus (Linné 1758)	Rook	Råka
Corvus corone cornix (Linné 1758)	Crow	Kråka
Corvus corone corone (Linné 1758)	Black crow	Svartkråka
Corvus corax (Linné 1758)	Raven	Korp
Cygnus olor (J. F. Gemlin 1789)	Swan	Knölsvan
Regulus regulus (Linné 1758)	Gold crest	Kungsfågel

II

The Reversed Sexual Size Dimorphism of Scandinavian raptors

By Per Florén.

Abstract

The reversed sexual size dimorphism of many birds of prey is well known. The method normally used when comparing morphological characters is to calculate the difference in size in percentage of the total size of the character. With this method it is not possible to differentiate between differences caused by the difference in mass (size) itself and differences caused by ecological adaptations. In this article a new method will be presented that makes it possible to do this. Regression analysis is used for this analysis, where a general trend line is calculated for each character. The characters, such as length and thickness of wing and leg skeletons of a species are then compared with these lines. Fourteen Scandinavian birds of prey are included in this study.

The results show that the legs in the female are proportionally shorter that in a geometrically similar male, with only a few exceptions. Or, when the legs are taken to be of similar length, the female has a proportionally larger trunk than the male. The most probable explanation is that the female need a larger trunk to be able to produce eggs and to stand starvation better.

The results also show that most bones have smaller diameter than expected from body mass, which is reasonable based on the shorter length. But for some species the bones have larger diameters indicating a need for stronger bones. For example *F. columbarius, B. lagopus, P. apivorus, C. aeruginosus* and *C. cyaneus* all have a tarsometatarsus with larger diameter *D* than expected from body mass. This could indicate a different behaviour, compared with the male, creating stronger forces acting on the foot and leg.

Introduction

Sexual size dimorphism is common among the majority of mammals and birds. In most species the male is larger than the female. Darwin (1871) suggested that sexual selection favours larger and therefore stronger males in the struggle for the females. But there are exceptions. For example, raptors show reversed sexual size dimorphism, although the degree of dimorphism differs. The species in this article span from about 10% to almost 70% difference in body mass between the sexes.

How can we understand the reason behind reversed sexual size dimorphism? It is most certain something that increases the fitness of species, otherwise it would not have been found in species from different groups, not closely related to each other. There are least three different types of explanations (Earhart & Johnson 1970, Balgooyen 1976, Synder & Wiley 1976, Nelson 1977, Newton 1979, and Walter 1979, Widén 1988):

1. **The need for a large sized female**, either to protect herself, her eggs, and nestlings from predators, or to be able to produce more and larger eggs, or to be able to withstand starvation in a better way, especially during incubation and

nestling. Fig. 1 shows an example of how the mass of the male and female Osprey (*P. haliaetus*) decreases during incubation and nestling.

2. **The need for a difference in size between the sexes** The difference in size permits the male and female to use different ecological niches in the same geographic area. The larger female hunts larger prey, the smaller male hunts smaller preys. Among mammals and birds of prey, the mass of the prey is about 10% of the body mass of the predator (Peters 1983, p. 110). In this way the couple can double the number of possible prey in the territory. Andersson and Norberg (1981) have shown that differences in size could increase the number of accessible prey in a certain area for a *F. peregrinus*.
3. **The need for a smaller sized male** The third explanation is based on sexual selection, but this time the female does not choose the male that is strongest in male to male fight, but the male that is strongest in the aerial manoeuvres. One example of this is the social behaviour of the Merlin (*F. columbarius*) characterised by for example power flying and power diving (Johnsgard 1990 p. 291). This would favour smaller and more agile males.

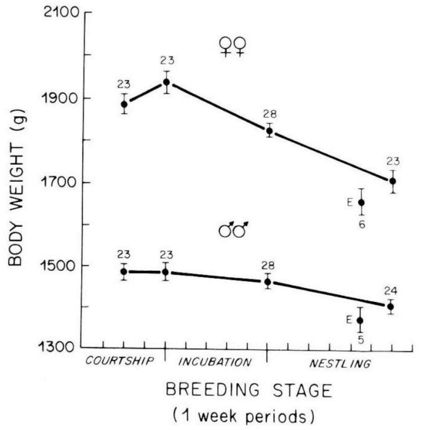

Figure 1. Seasonal mass change among Ospreys breeding in south-eastern Massachusetts. Means and standard errors are shown. From Pooke (1989, p. 125).

The explanations, of course, do not exclude each other; they could be true all three. Another interesting question is **how the male and female are different**. Is the female an isometric (all lengths increased with the same factor) enlargement of the male (or the male a smaller copy of the female) or are there other differences than just the size? If the reason for a larger female were, for example, the need to defend herself and her eggs, one would expect to find, for example, a relatively larger bill or larger claws. If the reason were to stand starvation better, one would expect to find a proportionally larger trunk with larger fat depots.

It had not been that complicated to compare males and females, if birds of prey of different sizes had been isometric, but as has been shown (Article I) they are not. The bones in the legs change in a different way with increased body mass, than the bones of the wings do. It is not proved, but seems reasonable to understand these changes as a response to the biomechanical demands the different sizes put on the skeleton. It is therefore reasonable to assume that these biomechanical demands are the same for both the male and the female. We can hence expect to see a "basic difference" in, for example, the diameter of humerus depending of the difference in size alone, between males and females. These “basic differences” are described in the allometric equations presented in Article I.

On top of these “basic difference” we may see differences depending on adaptations to the different ecological niches of the two sexes, if there are any. Some examples of what we might find if the sexes are adapted to different ecological niches and different roles are the following:

1. Based on the arguments for a **larger female**:
    a. **Better defence**, for example longer bill, claws etc. (This prediction can not be tested in this article.)
    b. **Better reproduction and digestive system, larger fat depots**: proportionally more trunk and shorter wing and leg bones. (This prediction will be tested in this article.)
2. Based on the arguments for a **difference in size**:
    a. **Adaptations that differentiate** the male from the female and make it possible for them to hunt for prey of different sizes in different habitats (for example more or less open spaces). (This prediction will be tested to some extent in this article.)
3. Based on the arguments for a **smaller, more agile, male**:
    a. **Better aerial manoeuvring** capacity indicates: proportionally larger wing area (broader and/or longer wings) resulting in lower wing loading, which gives the male the possibility to make sharper turns, or stronger wing muscles. (This prediction will be tested to some extent in this article.)

Material and methods

The material used is the same as in Article I, the only difference is that some species that had less then five specimen of each species and sex were excluded in this analyses (Table 1). Symbols, constants and variables used in this article are given in Table 2.

Table 1. Species, average mass and number of skeleton measured.

Species (Scientific and English names)		**Female**		**Male**	
		m kg	**n**	**m kg**	**n**
Pernis apivorus (Linné 1758)	Honey Buzzard	0.832	5	0.746	5
Haliaeetus albicilla (Linné 1758)	White-tailed Eagle	5.346	6	4.182	5
Circus aeruginosus (Linné 1758)	Marsh Harrier	0.716	5	0.550	5
Circus cyaneus (Linné 1766)	Hen Harrier	0.489	5	0.353	5
Accipiter gentilis (Linné 1758)	Goshawk	1.168	6	0.795	5
Accipiter nisus (Linné 1758)	Sparrow Hawk	0.258	8	0.154	5
Aquila chrysaetos (Linné 1758)	Golden Eagle	4.691	7	3.600	5
Buteo buteo (Linné 1758)	Common Buzzard	0.987	5	0.735	6
Buteo lagopus (Pontoppidan 1763)	Rough-legged Buzzard	1.035	5	0.850	5
Pandion haliaetus (Linné 1758)	Osprey	1.700	5	1.386	5
Falco columbarius (Linné 1758)	Merlin	0.195	5	0.165	5
Falco peregrinus (Tunstall 1771)	Peregrine	1.050	6	0.635	6
Falco rusticolus (Linné 1758)	Gerfalcon	1.693	5	1.090	5
Falco tinnunculus (Linné 1758)	Kestrel	0.215	6	0.173	6

Table 2. The symbols, constants and variables used in this article. The SI system is used but note that measurements of lengths sometimes, for practical reasons, are presented in mm. For a more throughout definition see Table 2 and Figs. 1.2, and 3 in Article I.

Symbol	Unit	Name
a	–	Allometric constant
b	–	Allometric exponent
D	mm	Diameter of bone
d	mm	Diameter of bone
Δ		Difference between male and female.
$\Delta\%$		Difference in percent between male and female.
l	mm	Length
L	mm	Measured length
L_{female}	mm	Measured length female
L_{male}	mm	Measured length male
$L_{expected}$	mm	Length of female expected from the allometric equation and the male length
m	kg	Body mass
m_{female}	kg	Body mass female
m_{male}	kg	Body mass male

Information about behaviour of the species was obtained from ornithological literature, for example Bruun et al. (1978), Brown et al. (1968), Cerny (1984), Cramp et al. (1985), Forsman (1984), Glutz et al. (1966-82), Hagen (1942, 1952), Haftorn (1971), and Rendahl (1935). Unfortunately very little research is done to identify differences in female and male behavioural ecology. Information on how they hunt or what they eat is almost never given separately for the two sexes.

Theory

The traditional way to compare the differences (e. g. Smith 1984b) between a male and a female of the same species is to calculate the difference (Δ) between, for example, the mass of the male (m_{male}) and the female (m_{female}):

$$\Delta=m_{female}-m_{male}, \qquad (1)$$

or, in percentage:

$$\Delta\%= (m_{female}-m_{male})/m_{male}= (m_{female}/m_{male})-1. \qquad (2)$$

This is simple to calculate and often helpful but does not help us to differentiate between differences caused by the biomechanical effects of different sizes and the differences caused by ecological adaptations. To be able to make this distinction we need to use the allometric relationships between body mass and lengths etc., identified in Article I. Based on the difference in body mass between male and female the expected differences in bone length and diameter can be calculated using the allometric relationship. Differences other than this could be due to differences in their ecology. The difference in any length, for example the length of humerus, between the male and the female, can be calculated based on the general allometric equation that describes the relationship between a length (L) and a mass (m), based on the experimental value for the exponent b (a is a constant).

$$L=a*m^{b} \tag{3}$$

Logarithm of eq. (3) gives us:

$$log\ (L)=\mathrm{b} * log\ (\mathrm{m}) + log\ (\mathrm{a}). \tag{4}$$

This is the equation for a straight line with the slope *b.* To be able to calculate the expected value ($L_{expected}$) of the length of the female, we need to find the constant log (a) that describes the straight line through the point (m_{male}, L_{male}) with the slope *b*,

$$\log\ (\mathrm{a}) = \log\ (\mathrm{L}_{\mathrm{male}}) - \mathrm{b} * \log\ (\mathrm{m}_{\mathrm{male}}). \tag{5}$$

The expected value of *L* for the female ($L_{expected}$) with the mass m_{female} can now be calculated using eq. (4 and 5),

$$\log\ (\mathrm{L}_{\mathrm{expected}}) = \mathrm{b} * \log\ (\mathrm{m}_{\mathrm{female}}) + \log\ (\mathrm{L}_{\mathrm{male}}) - \mathrm{b} * \log\ (\mathrm{m}_{\mathrm{male}}). \tag{6}$$

This can be rewritten as

$$\log\ (\mathrm{L}_{\mathrm{expected}}) = \mathrm{b} * \log\ (\mathrm{m}_{\mathrm{female}}) - \mathrm{b} * \log\ (\mathrm{m}_{\mathrm{male}}) + \log\ (\mathrm{L}_{\mathrm{male}}), \tag{7}$$

giving

$$\log\ (\mathrm{L}_{\mathrm{expected}}) = \mathrm{b} * \log\ (\mathrm{m}_{\mathrm{female}}/\mathrm{m}_{\mathrm{male}}) + \log\ (\mathrm{L}_{\mathrm{male}}). \tag{8}$$

If both sides are raised to the same exponent we get

$$(\mathrm{L}_{\mathrm{expected}}) = (\mathrm{m}_{\mathrm{female}}/\mathrm{m}_{\mathrm{male}})^{b*}\ (\mathrm{L}_{\mathrm{male}}). \tag{9}$$

The difference $\Delta\%_{\mathrm{exp}}$ between the expected length (based on the allometry of the whole group) of the female ($\mathrm{L}_{\mathrm{expected}}$) and the actual length ($\mathrm{L}_{\mathrm{female}}$) can be calculated from

$$\Delta\%_{\mathrm{exp}} = (L_{\mathrm{female}}/\ L_{\mathrm{expected}})\ \text{-}1 \tag{10}$$

Using equations (9) to eliminate ($L_{expected}$) the equation can be rewritten as

$$\Delta\%_{\mathrm{exp}} = \frac{L_{female}}{L_{male}\left(\dfrac{m_{female}}{m_{male}}\right)^{b}} - 1 \tag{11}$$

This means that if the result is positive, the real length (L_{female}) is longer than what is expected from the allometry of this measurement. If negative, it is smaller than expected.

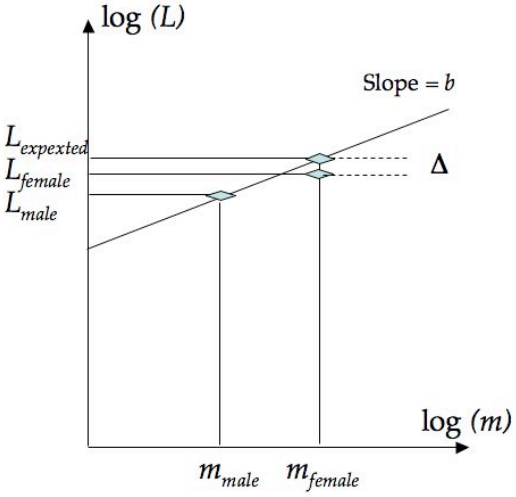

Figure 2. Illustration of the above equations, please see the text for further explanations.

We can now study the differences between male and female that remains after the general effects of differences in size is dealt with.

It has already been shown (see Article I) that the strength of bones and the density of bodies are almost constant. It is therefore reasonable to expect that thicker bones are stronger than thinner.

Results

The results of the comparisons between male and female of 14 species of Scandinavian birds of prey are presented below. The analysis is focused on how the female is different from what is expected, based on her mass and the allometric equations found in Article I. The differences identified have a reasonable probability to be caused by other reasons but biomechanical effects of general differences in size. Most likely they are caused by differences in the ecology of the two sexes. The presentation of the results is divided into groups based on some typical search behaviour of the species.

Group 1. Air-search, ground prey

Table 3 shows the differences in various morphological characters among species using air-searching for prey on the ground.

Pernis apivorus is a bird specialised in digging out bees and wasps from their underground nests. The wing bones of the female are shorter and have smaller diameter D than expected. For the diameter d humerus is significantly larger but not for the other two wing bones. The leg bones are shorter than expected but significantly larger in the diameter D.

Buteo buteo is a bird typically soaring around, or perching, searching for smaller animals such as mice, rats, frogs etc. The female's humerus and ulna are shorter and thicker (stronger) than expected. The leg bones are shorter and weaker than expected in most measurements.

Buteo lagopus is a close relative to *B. buteo* and have much in common, but there are two main differences:

1. *B. lagopus* lives in the mountains of northern Scandinavia; *B. buteo* lives in the southern part.
2. *B. lagopus* hover more frequent.

The humerus of the female has the expected length but has larger diameters, both *D* and *d*, which makes it stronger than expected. The lengths of ulna and carpometacarpus are both slightly shorter than expected, but where ulna is more slender (and lighter) in both *D* and *d*, whereas carpometacarpus is larger in *D* but not in *d*. The leg bones are almost as long as expected from allometry, and both femur and tarsometatarsus are stronger than expected.

Aquila chrysaetos prefers the northern Scandinavia, its mountains and woods. It eats both birds, mammals as well as carcasses. It catches the prey on the ground, or if it is a bird when this is taking off. The female has smaller bones in both wings and legs than expected in all measurements but two, namely *d* of carpometacarpus and *D* of tarsometatarsus.

Table 3. Differences in length (L) and diameters (D and d) of wing bones, leg bones and carina sterni between values expected from allometry and actual measurements. ***Hum*** *is humerus,* ***Cmc*** *is carpometacarpus,* ***Fem*** *is femur,* ***Tib*** *is tibiotarsus, and* ***Tmt*** *is tarsometatarsus.* ***HW*** *is the length of the hand wing;* ***WS*** *is the length of the wingspan. The difference in mass (m) is calculated according to eq. (2).*

Species		**Hum**	**Ulna**	**Cmc**	**Carina**	**Fem**	**Tib**	**Tmt**	**HW**	**WS**
Pernis apivorus	*L*	-3%	-4%	-6%	-2%	-3%	-2%	-5%	2%	-1%
	D	-4%	-4%	-4%	-3%	12%	15%	11%		
	d	12%	-4%	-4%		-4%	-4%	-5%		
	m	12%								
Buteo buteo	*L*	-5%	-8%	-6%	-5%	-5%	-7%	-6%	-4%	-5%
	D	2%	8%	-10%	-2%	4%	-11%	-13%		
	d	5%	8%	13%		-12%	-10%	9%		
	m	34%								
B. lagopus	*L*	0%	-1%	-1%	1%	1%	-1%	-3%	-1%	-2%
	D	6%	-7%	4%	0%	8%	-7%	9%		
	d	9%	-7%	-7%		7%	-7%	14%		
	m	22%								
Aquila chrysaetos	*L*	-4%	-4%	-3%	-7%	-5%	-4%	-4%	0%	-2%
	D	-10%	-9%	-3%	-3%	-3%	-2%	5%		
	d	-9%	-9%	2%		-3%	-9%	-1%		
	m	30%								

Group 2 Slow air-search, ground or water prey

Table 4 shows the differences in various morphological characters among two of the species using air-searching for prey on the ground or water.

Table 4. Differences in length (L) and diameters (D and d) of wing bones, leg bones and carina sterni between values expected from allometry and actual measurements. ***Hum*** *is humerus,* ***Cmc*** *is carpometacarpus,* ***Fem*** *is femur,* ***Tib*** *is tibiotarsus, and* ***Tmt*** *is tarsometatarsus.* ***HW*** *is the length of the hand wing;* ***WS*** *is the length of the wingspan. The difference in mass (m) is calculated according to eq. (2).*

Species		Hum	Ulna	CMC	Carina	Fem	Tib	Tmt	HW	WS
Circus	L	-1%	2%	3%	1%	0%	5%	5%	-4%	-2%
aeruginosus	D	-10%	10%	3%	6%	-10%	-10%	-12%		
	d	6%	10%	-9%		-10%	14%	-12%		
	m	30%								
C. cyaneus	L	-9%	-9%	-6%	-11%	-4%	-6%	-7%	0%	-3%
	D	3%	-11%	0%	-3%	-12%	10%	14%		
	d	-11%	-11%	-11%		-13%	-11%	-14%		
	m	39%								

Circus aeruginosus prefers lakes, sea bays, and creeks with reed, marshes and fields. It feeds on rodents, nestlings and can sometimes catch a coot or moorhen by surprise. When it is hunting it is flying on V-shaped wings at a height of 2-5 meters. Compared with what is expected from allometry the female has slightly longer ulna and carpometacarpus, and still the hand wing and the wingspan are slightly shorter than expected. The wing bones are stronger than expected for ulna and for diameter *d* of the humerus and for diameter *D* of the carpometacarpus. The leg bones are longer and significantly weaker than expected, except for the diameter *d* of the tibiotarsus.

Table 5. Differences in length (L) and diameters (D and d) of wing bones, leg bones and carina sterni between values expected from allometry and actual measurements. ***Hum*** *is humerus,* ***Cmc*** *is carpometacarpus,* ***Fem*** *is femur,* ***Tib*** *is tibiotarsus, and* ***Tmt*** *is tarsometatarsus.* ***HW*** *is the length of the hand wing;* ***WS*** *is the length of the wingspan. The difference in mass (m) is calculated according to eq. (2).*

Species		Hum	Ulna	CMC	Carina	Fem	Tib	Tmt	HW	WS
Haliaeetus	L	-5%	-4%	-6%	-9%	-6%	-6%	-3%	2%	1%
albicilla	D	-3%	1%	-8%	-6%	-9%	-9%	-11%		
	d	-2%	-8%	-8%		-2%	-18%	-1%		
	m	28%								
Pandion	L	-6%	-5%	-4%	-1%	-5%	-4%	-1%	-2%	-3%
haliaetus	D	-8%	-7%	2%	-5%	-8%	-8%	-10%		
	d	4%	-7%	-7%		-8%	-7%	-9%		
	m	22%								

Circus cyaneus is often found at swamps, mires and moors and other open areas. They usually eat smaller mammals like rodents, young rabbits, shrews and birds. Both wing and leg bones are shorter than expected and the length of the hand wing is as expected whereas the wingspan is slightly shorter. Humerus is larger in *D* but smaller in *d*, ulna and carpometacarpus has smaller diameters, except for carpometacarpus diameter *D* which is as expected. The leg bones are shorter and have smaller diameters than expected, with exception for tarsometatarsus and tibiotarsus diameters *D*.

Table 5 shows the differences between the male and the female in various morphological characters, among two other species using air-searching for prey on the ground or water.

Haliaeetus albicilla prefers to live in archipelagos, rivers and larger lakes. Sometimes it can be found in the Scandinavian mountains. Its prey varies significantly and includes fish, birds and nestlings, small mammals and carcasses (most common for individuals living in the mountains). Both its wing and bone skeletons are shorter and weaker than expected (except for ulna diameter *D*), while the hand wing and wingspan is slightly longer than expected.

Pandion haliaetus in Scandinavia prefers to live in larger lakes and archipelagos with sweet and clear water. Its prey is fish swimming near the surface and it hovers often in the search for it. Both wing and bone skeleton are shorter and weaker than expected, with two exceptions: the diameter *d* of humerus and diameter D of carpometacarpus.

Group 3 Air-search, sneak attack, ground prey

Table 6 shows the differences in various morphological characters among species using air-searching and sneak attack for prey on the ground.

Table 6. Differences in length (L) and diameters (D and d) of wing bones, leg bones and carina sterni between values expected from allometry and actual measurements. ***Hum*** *is humerus,* ***Cmc*** *is carpometacarpus,* ***Fem*** *is femur,* ***Tib*** *is tibiotarsus, and* ***Tmt*** *is tarsometatarsus.* ***HW*** *is the length of the hand wing;* ***WS*** *is the length of the wingspan. The difference in mass (m) is calculated according to eq. (2).*

Species		**Hum**	**Ulna**	**Cmc**	**Carina**	**Fem**	**Tib**	**Tmt**	**HW**	**WS**
Accipiter gentilis	L	-5%	-5%	-4%	-1%	0%	-3%	-5%	0%	-1%
	D	-3%	5%	9%	-2%	-2%	0%	-1%		
	d	-1%	2%	-13%		14%	5%	25%		
	m	47%								
Accipiter nisus	L	-5%	-5%	-2%	2%	-2%	0%	-3%	1%	0%
	D	2%	12%	0%	6%	9%	9%	16%		
	d	3%	12%	-17%		8%	-17%	-21%		
	m	68%								

Accipiter gentilis is the larger of the two hawks in Scandinavia. It prefers to live in old spruce-woods where it feeds on birds (forest birds, crows and pigeons) and smaller mammals like hare and squirrel. The humerus is shorter and more slender than expected whereas the two distal wing bones (ulna and carpometacarpus) are thicker in diameter *D* than expected. The leg bones are somewhat shorter than expected but the most significant difference is the increased diameter *d*, especially for tarsometatarsus.

Accipiter nisus is a smaller hawk, living in smaller woods with mixed species of trees. It feeds on smaller birds (titmice, sparrows and larks) and, in the winter, rodents. It is known for its ability to make sneak-attacks flying just above or around houses or vegetation. Its humerus and ulna are both shorter and thicker than expected, especially the ulna. The lengths of the leg bones are a little shorter than expected, but their diameter *D* is larger. The diameters *d* for both humerus and ulna are larger than expected, whereas they are significantly smaller (and hence weaker and lighter) in tibiotarsus and tarsometatarsus.

Group 4 Air-search, air prey

Table 7 shows the differences in various morphological characters among species using air-searching for prey.

Falco columbarius is a small falcon living in the northern mountains in areas where there are a large amount of smaller birds during the summer. It often uses a sneak-attack flying near the ground. If necessary it can follow the prey in the air. Sometimes the male and female hunts together. The difference between the sexes is relatively small regarding the lengths of both the bones in the wings and legs. The wing bones of the female are slightly longer than expected and the leg bones shorter. The strength of both wing and leg bones are a few percent below expected with two exceptions, the diameter *D* of tarsometatarsus and the cross sectional diameter *d* of carpometacarpus, which, on the other hand, are much thicker and therefore stronger than expected.

Table 7. Differences in length (L) and diameters (D and d) of wing bones, leg bones and carina sterni between values expected from allometry and actual measurements. ***Hum*** *is humerus,* ***Cmc*** *is carpometacarpus,* ***Fem*** *is femur,* ***Tib*** *is tibiotarsus, and* ***Tmt*** *is tarsometatarsus.* ***HW*** *is the length of the hand wing;* ***WS*** *is the length of the wingspan. The difference in mass (m) is calculated according to eq. (2).*

Species		**Hum**	**Ulna**	**Cmc**	**Carina**	**Fem**	**Tib**	**Tmt**	**HW**	**WS**
F. colum-	*L*	1%	2%	0%	1%	-1%	0%	-2%	4%	2%
baris	*D*	-6%	-6%	-6%	2%	-6%	-6%	38%		
	d	-6%	-6%	41%		-7%	-6%	-7%		
	m	18%								
F. pere-	*L*	-6%	-5%	-4%	-5%	-1%	0%	-3%	0%	-1%
grinus	*D*	-6%	1%	-6%	3%	-18%	-2%	-6%		
	d	-3%	-16%	4%		-5%	0%	-1%		
	m	65%								
F. rusti-	*L*	-7%	-11%	-8%	-8%	-7%	-7%	-8%	-4%	-5%
colus	*D*	-5%	-14%	-6%	-11%	-16%	-4%	-19%		
	d	-3%	-14%	3%		-5%	-15%	-32%		
	m	55%								

Falco peregrinus is the typical air-attacking bird. It can live in most parts of Scandinavia but prefers habitats with steep mountainsides and open space with rich bird-life. It strikes its prey in the air from above with high speed (over 200 km/h has been documented). It hits its prey with its feet or with its breast. In some cases the prey loses its conscious at first strike, sometimes repeated attacks is needed. The female has shorter wing bones and just slightly shorter leg bones. Most diameters follow the same pattern, with two exceptions, the cross sectional diameter d of ulna and diameter D of femur, which are significantly smaller than expected.

Falco rusticolus is like *F. peregrinus* a bird-hunter, hunting in the air, but it is focused on a different habitat, the Scandinavian mountains (over the tree line) and has a different favourite prey, the ptarmigan. It can use both sneak-attack and hunt its prey until this is exhausted. Its wing bones are both shorter and thinner (weaker) than expected, especially the ulna. The leg bones are shorter and thinner/weaker than expected, especially the carpometacarpus diameter d.

Group 5 Air-search (hovering), ground prey

Table 8 shows the differences in various morphological characters among species using hovering air-searching for prey on the ground.

Falco tinnunculus has a way of living quite different from to the other falcons described here. It is specialised on hovering over open areas looking for small mammals, preferably rodents, like the field vole, which it caches with its feet.

Its wing bones are shorter, but much thinner than expected, especially the ulna (except for the diameter D of carpometacarpus). The leg bones are shorter and thinner than expected with exception for the cross sectional diameter d of the femur, which is significantly thicker/stronger than expected.

Table 8. Differences in length (L) and diameters (D and d) of wing bones, leg bones and carina sterni between values expected from allometry and actual measurements. ***Hum*** *is humerus,* ***Cmc*** *is carpometacarpus,* ***Fem*** *is femur,* ***Tib*** *is tibiotarsus, and* ***Tmt*** *is tarsometatarsus.* ***HW*** *is the length of the hand wing;* ***WS*** *is the length of the wingspan. The difference in mass (m) is calculated according to eq. (2).*

Species		**Hum**	**Ulna**	**Cmc**	**Carina**	**Fem**	**Tib**	**Tmt**	**HW**	**WS**
F. *tinnunculus*	L	-5%	-7%	-5%	-5%	-5%	-7%	-8%	-2%	0%
	D	-8%	-30%	11%	-12%	-8%	-8%	-10%		
	d	-8%	-30%	-7%		22%	-7%	-10%		
	m	24%								

Discussion

The general picture

Figure 3 shows how the length L and the diameter D relate to the expected length and diameter of the bones of the female wing and leg.

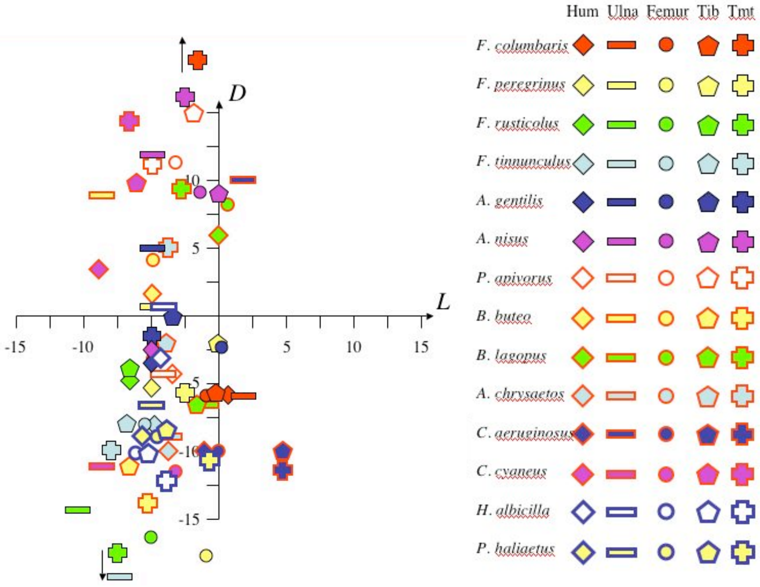

*Figure 3. Illustration of how the length L and diameter D of humerus (**Hum**), ulna, femur, tibiotarsus (**Tib**) and tarsometatarsus (**Tmt**) of the female relates to the expected values.*

The waste majority of data is found to the left of the Y-axis, which means that almost every bone in every female bird is shorter than expected when compared to the body mass. In other words, if the female were a geometrically enlargement of the male, then her legs should have been longer than they actually are. Or, when the legs of the female and the male are taken to be of similar lengths, the body size of the female is still larger than that of the male, because they are not geometrically similar. Thus, it is especially the trunk that has become larger in the female. This supports the hypotheses that one reason for a larger female is to be able to produce more eggs and/or stand starvation better.

The species do not have the same type of deviation from the expected values for the different bones. The falcons, together with sea eagle and osprey, are relatively well clustered down and to the left. Remaining species have their data points well spread over the left half of the diagram.

The families are not very well clustered either. Particularly the hawks, buzzards and harriers have their different measurements spread over the diagram.

The wing skeleton

Figure 4 shows how the length *L* and the diameter *D* relate to the expected length and diameter of the bones of the female wing including carina sterni.

If we compare the variation of data for the humerus and the ulna it is obvious that ulna has a much wider distribution, both in *L* and in *D*. Humerus may perhaps be more problematic to change in dimension due to the loadings from the flight muscles.

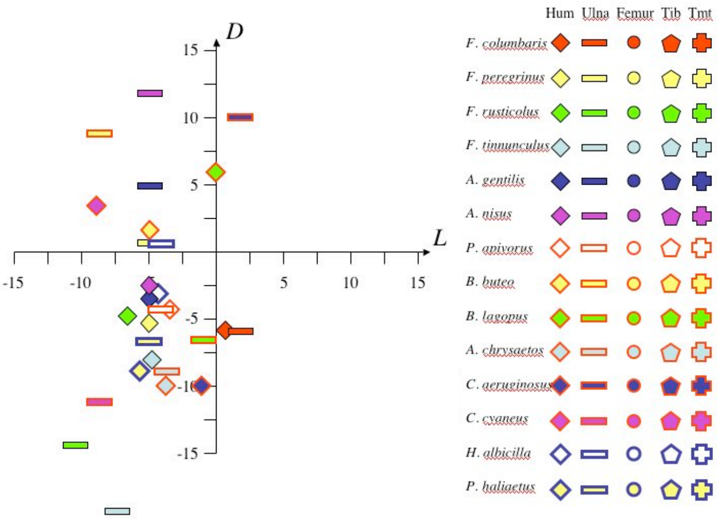

*Figure 4. Illustration of how the length L and diameter D humerus (**Hum**), ulna, of the female relates to the expected values.*

One exception from the over all pattern is *Circus aeruginosus,* which has an ulna that is slightly longer and significantly stronger than expected (diameter *D* is 10% thicker than expected). Another exception is *Falco columbarius,* which is the only species where the female has longer and thinner humerus and ulna, which probably indicates weaker wing bones.

Buteo lagopus has a humerus that is stronger than expected (diameter *D* is 6% thicker than expected). *Accipiter nisus, B. buteo*, and *A. nisus* do all have ulnas with a diameter D that is 5% or more over what is expected.

Circus cyaneus, *F. rusticolus*, and *F. tinnunculus* do all have ulnas with a diameter D that is more than 10% or less than expected. The reason for the much lower value for the diameter *D* of the ulna of *F. tinnunculus* may be an adaptation to decrease the wing mass and thus the inertia of the wing and the energy needed for hovering.

In general, falcons (together with *P. haliaetus* and *H. albicilla*) have wing skeletons with shorter and thinner bones than expected. Hawks, harriers and buzzards tend to have shorter but thicker wing bones, but they differ more from each other (they are much more spread over the diagram).

Leg skeleton

Figure 5 shows how the length *L* and the diameter *D* relate to the expected length and diameter of the bones of the female leg.

The bones of the female leg are, as we can see from Figure 5, more differentiated (compared to the wing bones), with both larger and smaller diameters *D* than expected. Only three measurements are longer then expected, namely the humerus of *B. lagopus*, which has larger diameter too, and the tibiotarsus and tarsometatarsus of *C. aeruginosus*, which also has smaller diameter than expected.

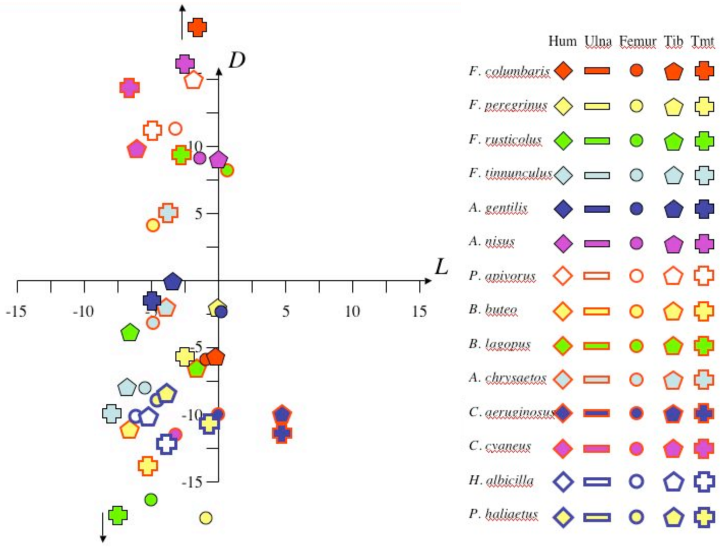

*Figure 5. Illustration of how the length L and diameter D femur, tibiotarsus (**Tib**) and tarsometatarsus (**Tmt**) of the female relates to the expected values.*

C. cyaneus, *A. nisus* and *F. columbarius* all have a tarsometatarsus that is more than 10% larger in diameter D than expected, especially *F. columbarius*. All of the leg bones of *Pernis apivorus* are more than 10% thicker than expected. This could indicate that, although the relatively small difference in body mass (12%), the female of *P. apivorus* can dig out things that the male cannot. If this is correct, it supports the idea of male and female having two different ecological niches. Unfortunately no data has been found to support these hypotheses.

F. rusticolus and *F. peregrinus* both have a femur that is more than 15% thinner than expected. The former has a tarsometatarsus that is even less in diameter D compared with what is expected.

Notes about some of the birds

Pandion haliaetus

Both wing and bone skeletons are shorter and weaker than expected, with two exceptions, the diameter *d* of humerus and diameter D of carpometacarpus. The reason for this adaptation could perhaps be the frequent hovering, which would demand low wing mass for low inertia.

Circus aeruginosus and *C. cyaneus*

The *C. aeruginosus* female is quite different from the other species.

The humerus is of expected length but smaller in diameter, and ulna is longer and has larger diameter than expected from the isometric scaling.

The leg bones are thinner and shorter (except for the femur that is of expected length), giving the female taller and weaker legs. In the female of *C. cyaneus*, on the other hand, all bones are shorter than expected. Ulna and femur have lower values for the diameter *D*, whereas humerus, tibiotarsus and tarsometatarsus are thicker. Although *C.*

aeruginosus and *C. cyaneus* belong to the same family, their ulna, tibiotarsus, and tarsometatarsus have the absolute opposite deviations from what is expected.

Buteo lagopus

Can the differences between *B. buteo* and *B. lagopus* in flight-style be the reason behind relatively longer wing bones of the *lagopus*? The humerus, for example, is longer and stronger than expected from allometry, not as for *B. buteo* and *P. apivorus*. The leg bones are almost as long as expected from allometry, and both femur and tarsometatarsus are stronger than expected. Reason for this strength is difficult to understand.

Accipiter gentilis

The most significant difference is the increased diameter *d* of the leg bones, which can be interpreted as an adjustment to loads that increase more than expected from body mass, and perhaps from other directions than normal. Furthermore, the two distal wing bones (ulna and carpometacarpus) are thicker (diameter *D*) than expected, which perhaps can be a response to the risk of colliding with trees and branches in the forest habitat where it hunts.

Falco columbarius

This is the only species where the female has a slightly longer and slightly thinner humerus and ulna than expected from the trends for the females. This means that this species does not follow the general pattern for females with larger fraction of body mass compared to leg and wing bone length (see above). For some reason it is more close to the male in its proportions.

The femur and tibiotarsus are as expected in length, but more slender. But the tarsometatarsus is 38% larger in diameter *D*! This could indicate that the female more often catches prey on the ground, compared to the male.

Conclusion

This new method to compare the skeletons in males and females, to see how they differ from each other, is both useful and gives several suggestions for further research. In some cases the deviations from the general trend line for a particular character for the whole group can be explained by what is already known about the behaviour of the species. In other cases more research is needed, research that relates morphology to differences in the behaviour of males and females.

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III

Ecomorphology of the locomotor apparatus of Scandinavian raptors

By Per Florén

Abstract

The scope of ecomorphology is to identify how differences in morphologic characters, for example length and diameter of wing bones of different species, can be explained, based on the ecology of each species. To identify these differences can be complicated enough if the species are of the same size, and even more complicated, if they differ significantly in body mass. One way to handle this problem is to use the allometric equation (see article I) to establish the general relation between body mass and the character that one wants to study. The allometric equation give us a typical size of our character for every given body mass. One can now compare the same character of each species and calculate the difference between the "typical size" calculated from the allometric equation and the actual size. In this article, wing and leg skeletons, from 14 Scandinavian raptors are compared with the allometric line of each character. The results are used to test 10 predictions about how the different species would be expected to differ from the general picture, based on typical flight style and hunting behaviour.

It is shown that soaring birds have relatively longer humerus and smaller carina sterni whereas actively flying birds have shorter humerus and larger carina sterni, just as predicted. Frequently hovering birds, on the other hand, did not have shorter wing bones as was predicted, neither had fast flying birds like *F. peregrinus* lower carina sterni.

"Hitters", birds catching their food by hitting their prey with speed, typically falcons, did indeed have shorter and thicker tibiotarsus and tarsometatarsus, as predicted, but did not have longer femur. "Grabbers", birds using reaching not impulse to catch their prey, where divided into fast "fast grabbers" typically hawks and "slow grabbers" typically harriers. Both types of "grabbers" were found to have relatively longer tibiotarsus and tarsometatarsus and "slow grabbers" had smaller than expected diameters of these bones. On the other hand showed it impossible to verify the prediction that "fast grabbers" would have larger diameters of tibiotarsus and tarsometatarsus than expected. "Diggers" (*P. apivorus)* finally confirmed the prediction of shorter and thicker tarsometatarsus.

Introduction

The scoop of ecological morphology is to examine and analyse how morphological differences between species and sexes can be understood in an ecological context. Doing this, one problem that arises is: How do we differentiate between characteristics, for example a bone diameter, that primarily is caused by ecological reasons and the characteristics caused by the animal's general size. Of cause size itself is a part of the ecological adaptation but when the size is given, what consequences does it bring?

One way to solve this problem is to use the allometric equation (see Article I) to find the relationship between body mass and the actual measurement. This is done for a wider group of animals, in this case Scandinavian birds of prey. Based on this it is general trend line it is possible to calculate, from body mass, what lengths and diameters one would expect; this is the length and diameter typical for this group of species and this body mass.

Material and methods

The material used are the same as that used in Article I. Only those species where there are at least five specimen of each species and sex were compared here (Table 1). Symbols, constants and variables used are defined in Table 2.

Table 1. Species, average mass and number of skeleton measured, m is body mass and n is number of species.

Species (Scientific and English names)		**Female**		**Male**	
		m (kg)	**n**	**m (kg)**	**n**
Pernis apivorus (Linné 1758)	Honey Buzzard	0.832	5	0.746	5
Haliaeetus albicilla (Linné 1758)	White-tailed Eagle	5.346	6	4.182	5
Circus aeruginosus (Linné 1758)	Marsh Harrier	0.716	5	0.550	5
Circus cyaneus (Linné 1766)	Hen Harrier	0.489	5	0.353	5
Accipiter gentilis (Linné 1758)	Goshawk	1.168	6	0.795	5
Accipiter nisus (Linné 1758)	Sparrow Hawk	0.258	8	0.154	5
Aquila chrysaetos (Linné 1758)	Golden Eagle	4.691	7	3.600	5
Buteo buteo (Linné 1758)	Common Buzzard	0.987	5	0.735	6
Buteo lagopus (Pontoppidan 1763)	Rough-legged Buzzard	1.035	5	0.850	5
Pandion haliaetus (Linné 1758)	Osprey	1.700	5	1.386	5
Falco columbarius (Linné 1758)	Merlin	0.195	5	0.165	5
Falco peregrinus (Tunstall 1771)	Peregrine	1.050	6	0.635	6
Falco rusticolus (Linné 1758)	Gerfalcon	1.693	5	1.090	5
Falco tinnunculus (Linné 1758)	Kestrel	0.215	6	0.173	6

Table 2. The symbols, constants and variables used in this article. The SI system is used but note that measurements of lengths sometimes, for practical reasons, are presented in mm. For a more throughout definition see Table 2 and Figs. 1.2, and 3 in Article I.

Symbol	**Unit**	**Name**
a	–	Allometric constant
b	–	Allometric exponent
D	mm	Diameter of bone
d	mm	Diameter of bone
Δ		Difference between male and female.
$\Delta\%$		Difference in percent between male and female.
l	mm	Length
L	mm	Measured length
$L_{expected}$	mm	Length of female expected from the allometric equation and the male length
m	kg	Body mass

Information about the behaviour of the species was retrieved from ornithological literature, for example Brown et al (1968), Bruun et al. (1978), Brüll (1984), Cerny (1984), Cramp et al. (1985), Fiuczynski (1988), Forsman (1984), Gerdhage et al. (1988), Glutz et al. (1966-82), Goslow (1971), Haftorn (1971), Hagen (1942, 1952), Johnsgard P A (1990), Lindberg (1975), Marcström et al. (1990), Monneret (1987), Petterson (1997), Poole (1989), Porter et al. (1986), and Rendahl (1935). The subject of animal mechanics is treated for example in Norberg (1979, 1981) and the connection between lifestyle of the birds and their morphology in, for example, Norberg and Norberg (1986).

Theory

The typical relationship between a length (l), for example the length of humerus, or diameter (D) of ulna, and body mass (m) for a group of related species, can be calculated based on the general allometric equation:

$$l=a*m^b \tag{1}$$

(see Article I). With the experimental values for the constant a and the exponent b given, it is possible to calculate the typical length of, for example humerus, for a given body mass. This is the expected length ($L_{expected}$) this bone would have, if the species had followed the allometric relationship between mass and length for the actual group. This is sometimes referred to as the "Criterion of subtraction" see Smith (1980, 1984 a and b) for a deeper penetration of the theory and history of this method.

We can now calculate how the actual length L differs from the expected length ($L_{expected}$). One way to do this is to calculate the difference in percentage ($\Delta\%$) between the expected and the actual length:

$$\Delta\% = \frac{L - L_{\mathrm{exp}ected}}{L_{\mathrm{exp}ected}} = \frac{L}{L_{\mathrm{exp}ected}} - 1. \tag{2}$$

Substituting $L_{expected}$ with eq. (1) we get

$$\Delta\% = \frac{L}{am^b} - 1, \tag{2}$$

where m is the measured mass of the species, L is the measured length, and where a and b are constants from the allometric equation for the given measurement and group of species. A positive value of $\Delta\%$ means that the measured length L is longer then expected, a negative means that it is shorter. The values for $\Delta\%$ were calculated with values for a and b from Article I, using Excel, and the results are presented below.

Predictions

Bone tissue in general has the same strength in different birds (se Article I), therefore, the thicker a bone is the stronger it could be expected to be. Strength related to bending or buckling is not only dependent of how thick the bone is but it is also dependent of the form of the bone's cross sectional area, the largest diameter should have the same orientation as the maximum bending force. A bone can thus be expected to have larger difference between the diameter *D* and *d* the larger, and more predictable, the bending force is. Predictable direction of force is often, but not always the same as muscle force.

Comparing males and females, it is important to remember that all bone measurements (*L*) are related to the general relationship between masses (*m*) and bones. This means that it is not possible to determine if a species and a sex has an absolute "over-weight" or "under-length". If, for example, the female of one species has a heavier body than expected from the general allometric relationship (either from large fat-reserves, larger muscles, or because of the weight of the organs needed for the production of eggs), this will show up as an "under-length" of all length measurements, not as an "overweight".

Predictions about the wing bones

For birds that frequently is gliding and/or soaring (eagles, harriers and buzzards), with no or little flapping, the most favourable, from an energy-point-of-view, is to have *Musculus pectoralis major* (the muscle acting downwards on the humerus) attached as far away from the body trunk as possible (Pennycuick 1978). For birds flying actively (falcons, hawks), the point of attachment should be placed as near the body trunk as possible. If we assume that the point of attachment is placed on the same fraction of the humerus, it would be favourable for soaring birds to have a longer humerus than expected from changes in body size, and for actively flying birds to have a shorter humerus.

For hovering birds, like *F. tinnunculus, P. haliaetus* and, to a lesser degree, *B. lagopus* (and perhaps birds flying very slowly) it is important to keep the inertia of the wing as low as possible (Norberg 1990). Because bone tissue is somewhat heavier than muscles, skin and feathers it is expected to be favourable with shorter wing bones than expected from changes in body size, especially for humerus and ulna.

The carina sterni is the bone where the flight-muscles are attached to the body. Although not a general rule (the size of the muscle related to the size of the carina sterni differs much between birds of different families), the size of the area of carina sterni (length *L* multiplied by diameter *D*) and the strength of the flight-muscle might be correlated between closely related birds. Birds characterised by active flying, hovering, short (vertical) take offs and flying with heavy prey are expected to have larger flight muscles than average, and therefore larger carina sterni.

Birds flying faster than average, for example *F. peregrinus,* need to minimize body drag (Norberg 1990). Fast flyers can therefore be expected to have a carina sterni with more of a "low profile", that is larger length and smaller diameter *D*.

The wing area and the aspect ratio (how slender the wing is) of the wings have large influence of the flight performance (Norberg 1990). Large wing area related to what is expected from body mass will give the bird a lower wing loading (mass/wing area) and this means better ability to make tight turns, whereas high aspect ratios means, for example, better flight economy. The problem is that the wing area and the aspect ratio of the wing are not in a simple way related to the size of wing bones. One species could have short humerus and ulna, but long feathers, whereas another species may have long wing bones and relatively short feathers.

Predictions about the leg bones

The skeleton of the legs has to be designed to meet the impulse created from both ruff landings and attacks on prey. The load created by the impulse is increasing with larger difference in speed between the bird and the prey, or between the bird and the landing place. The harder the landing place (rock is harder, small branches and water are less hard) the larger the impulse will be, for a given speed. When the strike hits the bones in the leg, the impulse from the foot first meets the tarsometatarsus and this bone will have to withstand the highest loading, during a short period of time. When the impulse is transferred to tibiotarsus and femur the impulse is partly absorbed by muscles and the peak force is somewhat smaller and somewhat more predictable. Based on this, it is reasonable to predict that tarsometatarsus has a wider range variation in diameter D and d compared to tibiotarsus and femur.

Femur probably works as a shock absorber; a longer femur can absorb a more power full shock, as the distal end of femur can move a longer distance for a given angular movement in the hip joint. Based on this we can predict that longer femur will be found among those birds having larger impulse-load at landing and prey catching.

When birds of prey catch their prey their techniques can be divided into four main categories:

1. "**Hitters**" who use speed and impulse, which is typical for, among others, *F. peregrinus, F. rusticolus, F. columbarius*, *P. haliaetus,* and *A. chrysaetos*.
2. "**Fast grabbers**" who use speed and reaching, but not impulse, to catch the prey, which is typical for, among others, *A. gentilis, A. nisus*, and *H. albicilla.*
3. "**Slow grabbers**" who use reaching, but nether impulse nor speed, which is typical for, among others, *C. aeruginosus C. cyaneus, F. tinnunculus, B. buteo,* and *B. lagopus*.
4. "**Diggers**" who is digging out insects from the ground, which is typical for *P. apivorus*.

Of cause there are species combining different methods on different prey or in different situations. *A. nisus*, for example, often starts with an attack from above, if this is unsuccessful it tries to reach the prey hiding in the vegetation with its long legs and toe. *H. albicilla* can hunt in a number of different ways, both hitting (birds and sometimes fish), slow grabbing (carrion) and fast grabbing (fish). The above characterisations are compiled from descriptions in the ornithological literature referred to above and have to be regarded as preliminary.

"**Hitters**" can be expected to have stronger (thicker and shorter) tibiotarsus and tarsometatarsus (and probably longer femur to absorb the shock) than expected from body mass. "Diggers" should be expected to have even shorter and thicker leg bones. As the distance between the foot and trunk is mainly created by the tibiotarsus and tarsometatarsus (as the femur normally is orientated in an other direction), birds that can benefit from a long distance between foot and trunk, for example "grabbers", can be expected to have long tarsometatarsus and tibiotarsus.

"**Fast grabbers**" can be expected to have larger diameters in their leg bones, based on the risk of high impulse using high speed close to prey and/or ground.

"**Slow grabbers**" can be expected to have long and slender tibiotarsus and tarsometatarsus to increase reach (and probably shorter femur due to small impulse due to low speed impact).

"**Diggers**" can be expected to have shorter (using muscle force more effectively) and stronger leg bones than expected.

Predictions in short

Predictions (if nothing else is said, the predictions are made for a species and sex related to the group as a whole):

1. **Soaring and gliding birds** is expected to have longer humerus, **active flyers to have shorter**.
2. **Hovering birds** are expected to have shorter wing bones, especially humerus and ulna.
3. Birds characterised by **active flying, hovering**, short (vertical) take offs and flying with heavy prey is expected to have **larger** than average **surface** (surface $\propto l*D$) of carina sterni.
4. **Fast flyers** are expected to have larger length and **smaller diameter** of carina sterni making the bird more streamlined.
5. "**Hitters**" can be expected to have shorter and **thicker tarsometatarsus and tibiotarsus**.
6. The larger the impulse at landing/prey catching, typical for "**hitters**", the **longer** the **femur** can be expected to be, to absorb the impulse.
7. Both fast and slow "**grabbers***" can be expected to have **longer tarsometatarsus and tibiotarsus**.
8. "**Fast grabbers**" can be expected to have **larger diameters in tibiotarsus and tarsometatarsus**, especially if hunting over ground.
9. "**Slow grabbers**" can be can be expected to have **longer and more slender tibiotarsus and tarsometatarsus** (and probably shorter femur).
10. **Diggers** can be expected to have **shorter and stronger leg bones**.
11. **Tarsometatarsus** can be expected to have a **wider range variation** in diameter D and d compared to tibiotarsus and femur.
12. Bones loaded with a more **predictable direction of load,** most probable a muscle force, can be expected to have **larger difference between the diameter D and d.**

In this article prediction 1-10 will be tested.

Results and Discussion

The differences between the actual, measured lengths and diameters and the lengths expected from the allometric relationships are presented below. Positive values indicate that the actual measurement is larger than expected from changes in body mass (m). For each species a few comments are made to point out differences compared with the expected values. Some commented results are supported by scientific data; other comments are more like suggestions for further research.

The presentation of the differences is divided into a number of groups. The groups are not primarily systematic but focused on the lifestyle, mainly the birds' way of hunting.

Group 1 Air-search, ground prey

Pernis apivorus

The differences between the actual, measured lengths and diameters for *P. apivorus* and the lengths expected from the allometric relationships is presented in Tables 3 and 4.

Table 3. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Pernis apivorus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	7%	1%	-7%	-4%	-19%	-8%	-18%
	D	4%	5%	9%	-3%	8%	5%	31%
	d	3%	3%	4%		-2%	-2%	-26%
M	*L*	10%	5%	-2%	-2%	-16%	-6%	-14%
	D	8%	9%	13%	0%	-4%	-9%	18%
	d	-8%	7%	8%		2%	2%	-22%

Table 4. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Pernis apivorus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for > 20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	L	+	0	–	–	– –	–	– –
	D	+	+	+	0	+	+	+ + +
	d	0	0	+		0	0	– – –
M	L	+	+	0	0	– –	–	– –
	D	+	+	+ +	0	–	–	+ +
	d	–	+	+		0	0	– – –

P. apivorus is a bird specialised in digging out bees and wasps from their underground nests. Humerus is longer than expected from body weight, which make soaring less energy demanding, and the diameter *D* is larger than expected, probably making the bone stronger than expected in the ordinary direction. Carina sterni comes close to what is expected. Shorter leg bones can indicate that strength is more important than reach, and with shorter bones the maximum digging force produced is increased. The tarsometatarsus is thicker, than expected, in *D*-dimension and thinner in *d*, increasing the strength in the main direction, and decreasing it in the perpendicular direction. This suggests that the forces acting on the leg are stronger and more predictable in direction.

Buteo buteo

B. buteo is a bird typically soaring around, or sitting on a stump or fence, searching for smaller animals as mice, rats, frogs etc. How it relates to the allometric relationships is described in Table 5 and 6.

The bones in the wing skeleton are as expected or just below. There are only two exceptions: the length of the male ulna and the perpendicular diameter *d* of carpometacarpus. Carina sterni is smaller than expected. The bones in the leg skeleton are as expected or, for the male slightly longer whereas the female has somewhat smaller diameter *d* for femur and humerus. Tarsometatarsus is the only bone that is more significantly different from what is expected. It is longer than expected, smaller (the female) or as expected (male) in the diameter *D*, and considerable thicker in the diameter *d*. This indicates a bone that is better at reaching and snatching prey, but with lower strength than expected in the *D* direction. On the other hand it is stronger in the *d* direction, indicating more unpredictable loads.

Table 5. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Buteo buteo. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	-3%	-3%	-7%	-17%	-1%	-1%	13%
	D	-3%	-1%	-8%	-17%	1%	-2%	-14%
	d	-3%	-2%	-3%		-9%	-8%	14%
M	*L*	2%	5%	-1%	-12%	5%	7%	20%
	D	-5%	-9%	2%	-15%	-3%	10%	-1%
	d	-7%	-10%	-13%		3%	2%	5%

Table 6. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Buteo buteo. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for > 20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	0	0	–	– –	0	0	+ +
	D	0	0	–	– –	0	0	– –
	d	0	0	0		–	–	+ +
M	*L*	0	+	0	– –	+	+	+ +
	D	–	–	0	– –	0	+	0
	d	–	–	– –		0	0	+

Buteo lagopus

B. lagopus, is a close relative to *B. buteo* and they have much in common. There are two main differences: *B. lagopus* lives in the mountains of northern Scandinavia; *B. buteo* lives in the southern part, and *B. lagopus* hover more frequent than its relative. The allometric relationships of the skeletons in *B. lagopus* are described in Tables 7 and 8.

The wing bones are slightly longer and the humerus is more slender than expected. This is in contradiction with the prediction that hovering birds should minimize the mass of the wing, at least the distal parts. Carina sterni is smaller than expected. The bones in the leg are longer or as expected and the diameters are both as expected as well as larger and smaller.

Table 7. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Buteo lagopus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	**Var**	**Hum**	**Ulna**	**Cmc**	**Carina**	**Fem**	**Tib**	**Tmt**
F	*L*	4%	6%	3%	-10%	7%	-1%	3%
	D	-4%	-3%	1%	-18%	-1%	-4%	1%
	d	-5%	-4%	-4%		4%	-10%	12%
M	*L*	4%	7%	5%	-11%	6%	1%	7%
	D	-10%	4%	-3%	-18%	-9%	4%	-8%
	d	-12%	3%	3%		-3%	-3%	-2%

Table 8. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Buteo lagopus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for > 20%.

Sex	**Var**	**Hum**	**Ulna**	**Cmc**	**Carina**	**Fem**	**Tib**	**Tmt**
F	*L*	+	+	0	–	+	0	0
	D	–	0	0	– –	0	–	0
	d	–	–	–		+	–	+ +
M	*L*	+	+	+	– –	+	0	+
	D	–	+	0	– –	–	+	–
	d	– –	0	0		0	0	0

Aquila chrysaetos

A. chrysaetos prefers the northern Scandinavia, its mountains and woods. It eats both birds, mammals as well as carcasses. It catches the prey on the ground, or if it is a bird when it is taking off. Tables 9 and 10 show how its skeleton differs from the allometric relationships.

The lengths of the wing bones are shorter than expected, or as expected (the male humerus and ulna). The diameters are larger, or as expected, for the male and smaller or as expected for the female. Carina sterni is as expected or, mostly, smaller than expected.

The leg bones are longer than expected (except for the female tibiotarsus). The femur is both longer and stronger which could indicate a better shock absorber and/or better possibilities to reach the prey. Tarsometatarsus is longer and more slender (in the *D* diameter), indicating better reach and less strength.

Table 9. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Aquila chrysaetos. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	**Var**	**Hum**	**Ulna**	**Cmc**	**Carina**	**Fem**	**Tib**	**Tmt**
F	*L*	-7%	-7%	-8%	-9%	4%	0%	5%
	D	-7%	-4%	1%	-15%	8%	6%	-4%
	d	-6%	-5%	1%		3%	-5%	0%
M	*L*	-3%	-3%	-5%	-2%	10%	4%	10%
	D	3%	5%	4%	-12%	12%	8%	-9%
	d	4%	4%	-2%		6%	4%	0%

Table 10. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Aquila chrysaetos. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for >20%.

Sex	**Var**	**Hum**	**Ulna**	**Cmc**	**Carina**	**Fem**	**Tib**	**Tmt**
F	*L*	–	–	–	–	+	0	+
	D	–	–	0	– –	+	+	–
	d	–	–	0		0	–	0
M	*L*	0	0	–	0	+	+	+
	D	0	+	+	– –	++	+	–
	d	+	+	0		+	+	0

Circus aeruginosus

C. aeruginosus prefer lakes, sea bays, and creeks with reed, marshes and fields. It feeds on rodents, nestlings and can sometimes catch a coot or moorhen by surprise. When it is hunting it is flying on V-shaped wings at a height of 2-5 meters. Its characteristics are presented in Tables 11 and 12.

The wing bones are all significantly longer than expected, and has diameters as expected, or slightly above (stronger), with exceptions for the female humerus (smaller *D*) and male carpometacarpus (significantly larger *d*). This gives *C. aeruginosus* a wing skeleton that is much longer than expected, but not that much stronger. This gives *C. aeruginosus* an ideal skeleton for slow flight (long wings, large wing area, low wing loading) and (probably) a low energy demand, because of the more distal point of attachment of the flight muscle. Carina sterni is shorter to significantly shorter than expected.

Femur and tibiotarsus are significantly longer than expected and femur stronger, especially in the male. Tarsometatarsus is much longer than expected and weaker in the D-dimension but stronger in d. This gives the bird long legs, not very strong, but built for good reach, perhaps to be able to snatch prey, and perhaps to facilitate landing with the long wings?

Table 11. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Circus aeruginosus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	16%	24%	18%	-5%	12%	28%	52%
	D	-4%	10%	3%	-14%	-2%	-7%	-20%
	d	9%	9%	9%		4%	3%	6%
M	*L*	18%	21%	15%	-6%	12%	22%	45%
	D	7%	1%	1%	-19%	9%	3%	-9%
	d	3%	-1%	20%		16%	-9%	20%

Table 12. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Circus aeruginosus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for >20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	+ +	+ + +	+ +	–	+ +	+ + +	+ + +
	D	–	+	0	– –	0	–	– –
	d	+	+	+		+	0	+
M	*L*	+ +	+ + +	+ +	–	+ +	+ + +	+ + +
	D	+	0	0	– –	+	0	–
	d	0	0	+ +		+ +	–	+ +

Circus cyaneus

C. cyaneus is often found at swamps, mires and moors and other open areas. On the menu we find smaller mammals as rodents, young rabbits, shrews and birds. Its characteristics are presented in Tables 13 and 14.

Table 13. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Circus cyaneus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	10%	12%	12%	-11%	11%	16%	28%
	D	12%	5%	18%	-5%	-5%	8%	-3%
	d	8%	3%	0%		1%	-6%	-5%
M	*L*	20%	23%	20%	1%	16%	23%	37%
	D	9%	17%	17%	-3%	8%	-2%	-15%
	d	21%	16%	13%		16%	6%	11%

Table 14. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Circus cyaneus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for > 20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	+	+ +	+ +	– –	+ +	+ +	+ + +
	D	+ +	+	+ +	–	–	+	0
	d	+	0	0		0	–	–
M	*L*	+ +	+ + +	+ +	0	+ +	+ + +	+ + +
	D	+	+ +	+ +	0	+	0	– –
	d	+ + +	+ +	+ +		+ +	+	+ +

C. cyaneus shares the long wing bones and leg bones with *C. aeruginosus,* but *C. cyaneus* has larger diameters, and is probably stronger, in most characters. The female carina sterni is smaller than expected, the male is as expected. The bones of the leg are all significantly longer than expected, especially the tarsometatarsus. The male femur is stronger, and the male tarsometatarsus is weaker in the *D*-direction but stronger in the *d*-dimension.

Group 2 Air-search, water prey

Haliaetus albicilla

H. albicilla prefers to live in archipelagos, rivers and larger lakes. Sometimes it can be found in the Scandinavian mountains. Its prey varies significantly and includes fish, birds and nestlings, small mammals and carcasses (most common for individuals living in the mountains). Its characteristics are presented in Tables 15 and 16.

Table 15. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Haliaetus albicilla. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	5%	4%	-1%	5%	-4%	-5%	-2%
	D	1%	1%	-3%	0%	-5%	-8%	-10%
	d	5%	-9%	-4%		-2%	-10%	4%
M	*L*	10%	8%	5%	15%	2%	1%	1%
	D	4%	0%	5%	7%	5%	1%	2%
	d	6%	-1%	5%		0%	10%	5%

Table 16. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Haliaetus albicilla. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for >20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	+	+	0	+	–	–	0
	D	0	0	0	0	–	–	–
	d	+	–	–		0	–	+
M	*L*	+	+	+	+ +	0	0	0
	D	+	0	+	+	+	0	0
	d	+	0	+		0	+	+

The wing bones are all somewhat longer than expected, with exception for the female carpometacarpus. The diameters are as expected, or close to. The longer humerus verifies prediction 1, stating that soaring and gliding birds should be expected to have longer distance between shoulder joint and the point of attachment of the muscle *pectoralis major*. Carina sterni is somewhat larger than expected. The leg bones are close to what is expected, but the female has bones somewhat shorter and weaker than expected.

Pandion haliaetus

P. haliaetus in Scandinavia prefers to live in larger lakes and archipelagos with fresh and clear water. Its prey is fish swimming near the surface. *P. haliaetus* often hovers in headwind. Its characteristics are presented in Tables 17 and 18.

All the bones of the wing are longer then allometry, the male ulna significantly longer. The diameters are nearly as expected. Carina sterni is shorter, but significantly larger (*D*). The bones of the legs are shorter than expected, except for the male tibiotarsus that is slightly longer, and for tarsometatarsus that is significantly shorter. Femur has diameters smaller than expected and tarsometatarsus is significantly stronger in the *D*-dimension and, in addition, significantly weaker in the perpendicular dimension. These legs don't have to be outstretched, and the load on tarsometatarsus comes always in the main direction (*D*-dimension).

Table 17. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Pandion haliaetus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	5%	16%	11%	-8%	-14%	2%	-30%
	D	-1%	-5%	-7%	12%	-7%	-8%	18%
	d	2%	-6%	-4%		-15%	6%	-29%
M	*L*	12%	23%	16%	-7%	-10%	6%	-29%
	D	7%	2%	-9%	18%	0%	0%	31%
	d	-2%	1%	4%		-8%	14%	-22%

Table 18. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Pandion haliaetus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for >20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	+	+ +	+ +	–	– –	0	– – –
	D	0	–	–	+ +	–	–	+ +
	d	0	–	–		– –	+	– – –
M	*L*	+ +	+ + +	+ +	–	–	+	– – –
	D	+	0	–	+ +	0	0	+ + +
	d	0	0	+		–	+ +	– – –

Group 3 Air-search, sneak attack, ground prey

Accipiter gentilis

A. gentilis is the larger of the two hawks in Scandinavia. It prefers to live in old spruce-woods where it feeds on birds (forest birds, crows and pigeons) and smaller mammals like hares and squirrels. Its characteristics are presented in Tables 19 and 20.

Table 19. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Accipiter gentilis. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	-11%	-14%	-9%	18%	10%	7%	20%
	D	3%	-7%	-3%	15%	7%	7%	-5%
	d	4%	7%	-8%		13%	4%	27%
M	*L*	-7%	-10%	-6%	19%	11%	10%	26%
	D	6%	-11%	-12%	17%	10%	7%	-5%
	d	5%	5%	5%		-1%	-1%	1%

Table 20. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Accipiter gentilis. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for >20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	– –	– –	–	+ +	+	+	+ +
	D	0	–	0	+ +	+	+	–
	d	+	+	–		+ +	+	+ + +
M	*L*	–	–	–	+ +	+ +	+	+ + +
	D	+	– –	– –	+ +	+	+	–
	d	+	+	+		0	0	0

The wing bones are shorter than expected, especially the female ulna. The diameters are somewhat larger for the *d*-dimension, except for the female carpometacarpus, whereas the *D*-dimension is shorter than expected or nearly so, except for the female humerus. Carina sterni is both significantly longer and higher than expected.

The leg bones are longer, especially the tarsometatarsus, and somewhat thicker and stronger than expected (for the female the *D*-dimension is significantly thicker), with exception for the male *d*-dimension and the tarsometatarsus *D*-measurement. Comparing the data for tarsometatarsus it could be suggested that the female hits the ground harder than the male and that the male has more use for a good reach.

Accipiter nisus

A. nisus is a little hawk, living in smaller woods with mixed species of trees. It feeds on small birds (titmice, sparrows and larks) and, in the winter, rodents. It is known for its ability to make sneak-attacks flying just above or around houses or bushes. Its characteristics are presented in Tables 21 and 22.

Table 21. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Accipiter nisus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	-4%	-1%	-5%	25%	8%	8%	27%
	D	2%	5%	-2%	12%	-2%	11%	-1%
	d	13%	3%	-6%		6%	-11%	-14%
M	*L*	1%	4%	-3%	23%	11%	8%	31%
	D	0%	-6%	-2%	6%	-10%	2%	-15%
	d	10%	-8%	14%		-2%	7%	9%

Table 22. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Accipiter nisus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for > 20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	–	0	–	+ + +	+	+	+ + +
	D	0	+	0	+ +	0	+ +	0
	d	+ +	0	–		+	– –	– –
M	*L*	0	+	0	+ + +	+ +	+	+ + +
	D	0	–	0	+	–	0	– –
	d	+	–	+ +		0	+	+

Humerus is close to average, but somewhat stronger than expected. The female ulna is shorter but thicker and the male ulna is longer but more slender. The female carpometacarpus is shorter and weaker whereas the male is as long as expected, but stronger in the *d*-dimension. The increased strength for humerus in the *d*-dimension may indicate more unpredictable loads on this bone. Carina sterni is significantly longer and higher. The leg bones are longer than expected, especially the tarsometatarsus, which make possible a better reach for of the bird when grabbing a prey.

Group 4 Air-search, air prey

Falco columbaris

F. columbarius is a small falcon living in the northern mountains in areas where there are a lot of smaller birds during the summer. It often uses a sneak-attack flying near the ground. If necessary it can follow the prey in the air. Sometimes the male and female hunts together. Its characteristics are presented in Tables 23 and 24.

Table 23. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Falco columbaris. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	-12%	-12%	-8%	7%	3%	-3%	-13%
	D	-9%	-14%	-10%	7%	9%	-7%	14%
	d	0%	-15%	4%		-11%	-2%	-3%
M	*L*	-13%	-14%	-8%	6%	4%	-3%	-12%
	D	-3%	-8%	-4%	4%	17%	-1%	-17%
	d	7%	-10%	-26%		-4%	5%	5%

Table 24. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Falco columbaris. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for >20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	– –	– –	–	+	0	0	– –
	D	–	– –	–	+	+	–	+ +
	d	0	– –	+		– –	0	0
M	*L*	– –	– –	–	+	+	0	– –
	D	0	–	–	+	+ +	0	– –
	d	+	–	– – –		–	+	+

The wing bones are shorter and generally more slender than expected, with exception for the cross sectional diameter *d* of the male humerus and the female carpometacarpus. A short humerus may be energetically favourable for active flight (see predictions above). Carina is slightly longer and higher than expected.

The two proximal leg bones are as expected, or slightly longer (male humerus). Tarsometatarsus is much shorter than expected, and for the female thicker and for the male thinner in the *D*-dimension and thicker in *d*. This could indicate that the female tarsometatarsus is loaded with larger forces than the male bone is.

Falco peregrinus

F. peregrinus is the typical air-attacking bird. It can live in most parts of Scandinavia but prefers habitats with steep mountain-sides and open space with rich bird-life. It strikes its prey in the air from above with high speed (over 200 km/h has been documented).

It hits its prey, not with its feet, but with its breast. In some cases the prey loses its conscious at first strike, sometimes repeated attacks are needed. Its characteristics are presented in Tables 25 and 26.

Table 25. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Falco peregrinus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	-22%	-21%	-9%	7%	-7%	-12%	-21%
	D	-5%	-3%	-10%	23%	-16%	-5%	0%
	d	-5%	-5%	-5%		3%	8%	11%
M	*L*	-17%	-17%	-5%	13%	-5%	-12%	-19%
	D	1%	-4%	-4%	19%	3%	-3%	7%
	d	-2%	14%	-9%		9%	8%	12%

Table 26. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Falco peregrinus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for > 20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	– – –	– – –	–	+	–	– –	– – –
	D	–	0	–	+ + +	– –	–	0
	d	–	–	–		0	+	+ +
M	*L*	– –	– –	–	+ +	–	– –	– –
	D	0	–	–	+ +	0	0	+
	d	0	+ +	–		+	+	+ +

The wing skeleton is generally significantly shorter (favourable for active flight, see prediction 1) and often more slender than expected. The male ulna is the exception having a diameter *d* larger than expected. The carina is both longer and higher than expected from body mass.

The leg bones are shorter, especially the female tarsometatarsus. The diameter d is as expected for the female femur, larger than expected for the other two leg bones of the female and for all leg bones of the male. The tarsometatarsus has the largest diameter *d* for both the male and the female. This indicates that there is no need for longer reach, but for stronger tarsometatarsus.

Falco rusticolus

F. rusticolus is like *F. peregrinus* a bird-hunter, hunting in the air, but it is focused on a different habitat, the Scandinavian mountains (over the tree line) and has different favourite prey, the ptarmigan. It can use both sneak-attack and it can hunt its prey until the prey is exhausted. Its characteristics are presented in Tables 27 and 28.

Table 27. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Falco rusticolus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	-21%	-26%	-11%	3%	-1%	-11%	-16%
	D	-11%	-5%	-7%	12%	-7%	5%	-8%
	d	-9%	-5%	-4%		-3%	-9%	-11%
M	*L*	-15%	-16%	-3%	11%	6%	-5%	-9%
	D	-6%	11%	-1%	26%	10%	10%	14%
	d	-6%	10%	-6%		2%	6%	31%

Table 28. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Falco rusticolus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for > 20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	– – –	– – –	– –	0	0	– –	– –
	D	– –	–	–	+ +	–	+	–
	d	–	–	–		0	–	– –
M	*L*	– –	– –	0	+ +	+	–	–
	D	–	+ +	0	+ + +	+	+	+ +
	d	–	+	–		0	+	+ + +

The bones of the wing are significantly shorter (with exception for the male ulna) and in most measurements somewhat more slender than expected (exception is here the male ulna). Carina is longer and higher, especially for the male. The female leg bones are all shorter, and shortest is the tarsometatarsus. Tarsometatarsus is more slender than expected, too. The male has somewhat longer femur but tibiotarsus and tarsometatarsus are shorter than expected. They male leg bones are all thicker than expected, especially the tarsometatarsus.

Group 5 Air-search, air prey or ground prey

Falco tinnunculus

F. tinnunculus has a way of living quit different from that of the other falcons described here. It has specialised on hovering over open areas when looking for small mammals, preferable rodents as field vole, which it caches with its feet. The hovering, as in other large birds, can only be performed in headwind, not still air. Its characteristics are presented in Tables 23 and 24.

The female wing bones are shorter, and often more slender, than expected, whereas the male bones are as expected in length, but thicker (with exception for the *D*-dimension of humerus and ulna). Carina sterni is shorter in the *L*-dimension and in *D*-dimension (female) or close to the average for the birds in this analysis (male). The leg bones are of average length, or shorter than expected, femur is stronger and the male carpometacarpus is much stronger.

Table 28. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Falco tinnunculus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	-7%	-8%	-6%	-14%	-3%	-5%	-11%
	D	-12%	-16%	5%	-10%	5%	-11%	9%
	d	-3%	-18%	1%		14%	-5%	-7%
M	*L*	-2%	-1%	-1%	-9%	2%	2%	-4%
	D	-5%	20%	-6%	3%	15%	-3%	21%
	d	5%	18%	9%		-6%	3%	3%

Table 29. Differences between actual and expected measurements of wing bones, leg bones, and carina sterni in Falco tinnunculus. Hum is humerus, Cmc is carpometacarpus, Fem is femur, Tib. is tibiotarsus, and Tmt. is tarsometatarsus. F is female and M is male. Deviations (negative or positive) from the allometric relation are indicated as follows: 0 for ≤3%; – and + for 4-10%; – – and + + for 11-20%; – – – and + + + for > 20%.

Sex	Var	Hum	Ulna	Cmc	Carina	Fem	Tib	Tmt
F	*L*	–	–	–	– –	0	–	– –
	D	– –	– –	+	–	+	– –	+
	d	0	– –	0		+ +	–	–
M	*L*	0	0	0	–	0	0	–
	D	–	+ +	–	0	+ +	0	+ + +
	d	+	+ +	+		–	0	0

Test of the predictions

The discussion will start with an overview of all measurements and how they differ from what is expected followed by tests of predictions 1-10.

All bones of all birds

Fig. 1 shows the deviations in percentage from expected values of length *L* and diameter *D* of all bones for all species.

There is a weak pattern that the measurements deviate either up and to the right or down and to the left, meaning that deviations more often tend to be longer and stronger or shorter and weaker, which is not very surprising. More interesting are species that deviate from this pattern:

1. *Pandion haliaetus* and *Pernis apivorus* both have tarsometatarsus much shorter and thicker than expected.
2. *Circus* and *Accipiter* both have tarsometatarsus much shorter and thinner than expected.

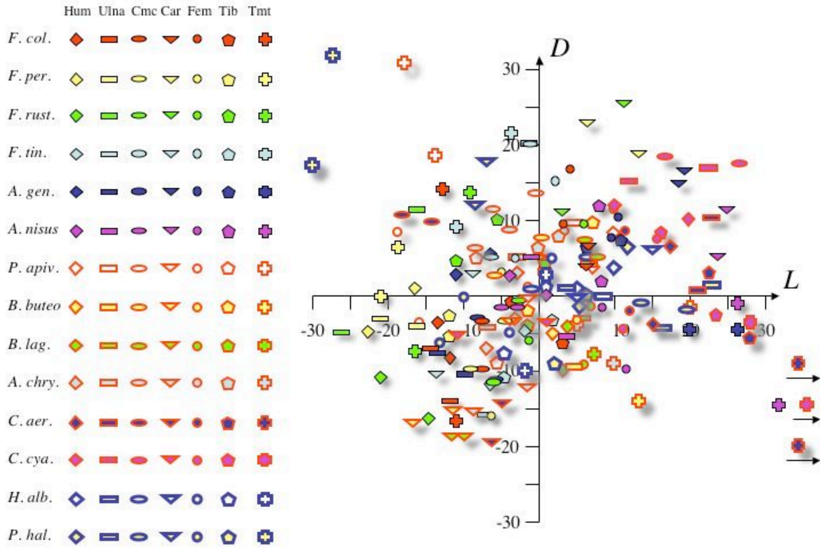

Figure 1. The deviations in percentage from expected values of length L and diameter D of all bones for all species. Male and female symbols are the same but each female symbol has a shadow.

It is easy to understand the short and thick tarsometatarsus of the digging *P. apivorus*, but more difficult to understand why the osprey has even shorter bone. The length of the bones in *Circus* can be understood as better reach of prey, when trying to grab it. But the extremely long and slender legs put great demands on the harrier to land with big caution to avoid fractures in the leg bones.

The bones of the wing

If we focus on the bones of the wing two groups differentiate themselves clearly (Fig. 2):

1. In *Falco* all the wing bones are shorter than expected.
2. In *Circus* and *P. haliaetus* all the wing bones are longer than expected. There is one exception namely the carpometacarpus of *C. aeruginosus,* which is found among the falcons to the left in the diagram.

The short bones of the falcons and the long bones of the osprey will be considered later. The long wing bones of Circus can be connected with both the long wings, the large wing area and gliding flight style.

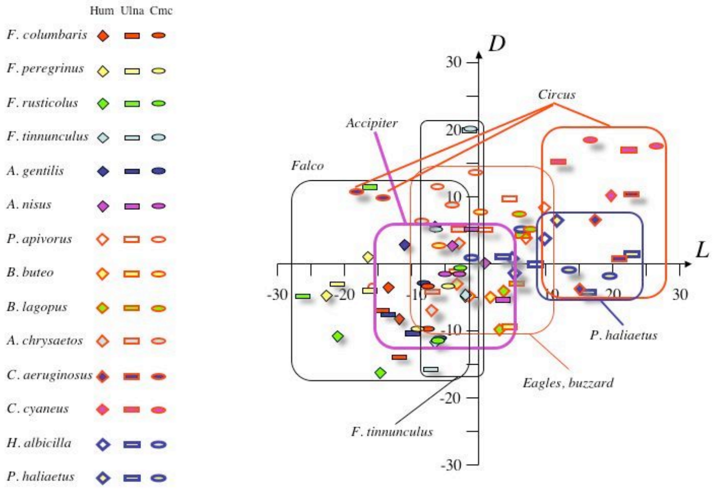

Figure 2. The deviations in percentage from expected values of length L and diameter D of all wing bones except carina sterni for all species. Male and female symbols are the same but each female symbol has a shadow.

The bones of the leg

Fig. 3 shows the deviations in percentage, from expected values of length *L* and diameter *D* of, the leg bones for all species.

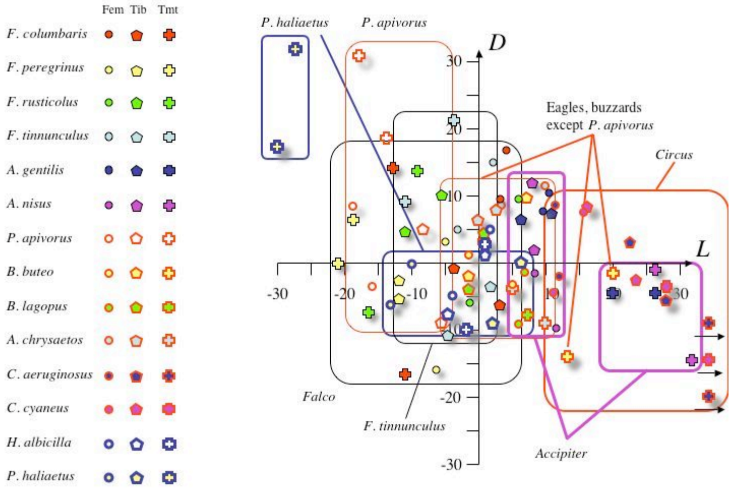

Figure 3. The deviations in percentage from expected values of length L and diameter D of allleg bones for all species. Male and female symbols are the same but each female symbol has a shadow.

We have already mentioned the short and thick bones of the osprey and the honey buzzard as well as the long and narrow bones of the harriers and hawks. The falcons are found to have around average diameter and below average length (Fig. 4). The eagles and buzzards are found in the middle of the diagram, except for the tarsometatarsus of *B. buteo*, which is longer and weaker than expected.

Prediction 1: Soaring birds – longer humerus, active flyers – shorter humerus

Fig 4 shows the deviations in percentage from expected values of length L and diameter D of humerus for all species.

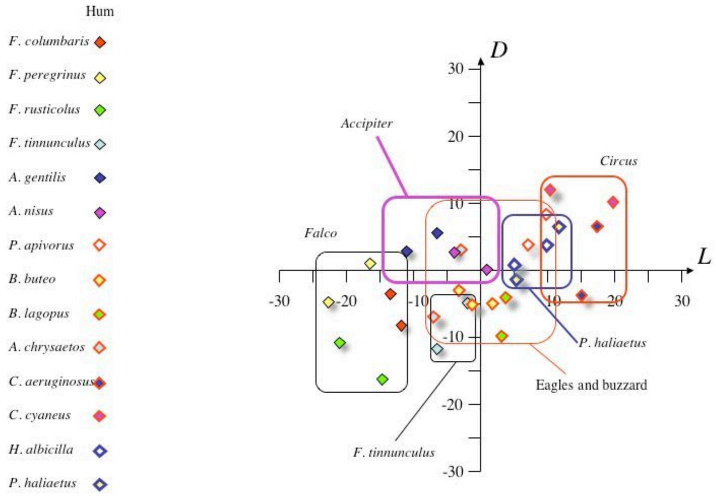

Figure 4. The deviations in percentage from expected values of length L and diameter D of humerus for all species. Male and female symbols are the same but each female symbol has a shadow.

The first prediction stated that soaring and gliding birds should be expected to have longer humerus, but active flyers shorter. This prediction is verified: the active flying falcons and hawks are found to the left, the soaring and gliding harriers to the right in the diagram (Fig. 4).

Prediction 2: Hovering birds – shorter humerus and ulna

Fig. 5 shows the deviations in percentage from expected values of length *L* and diameter *D* of the wing bones humerus and ulna for the hovering species *F. tinnunculus, B. lagopus and P. haliaetus*. The second prediction was that hovering birds are expected to have shorter wing bones, especially humerus and ulna, to decrease the inertia of the wing. This prediction is not verified for *B. lagopus* or *P. haliaetus*, but possibly for *F. tinnunculus*. But since the kestrel has longer bones than other falcons this verification could be debated. The result indicates that the inertia of the wing is not an important factor among these birds of prey.

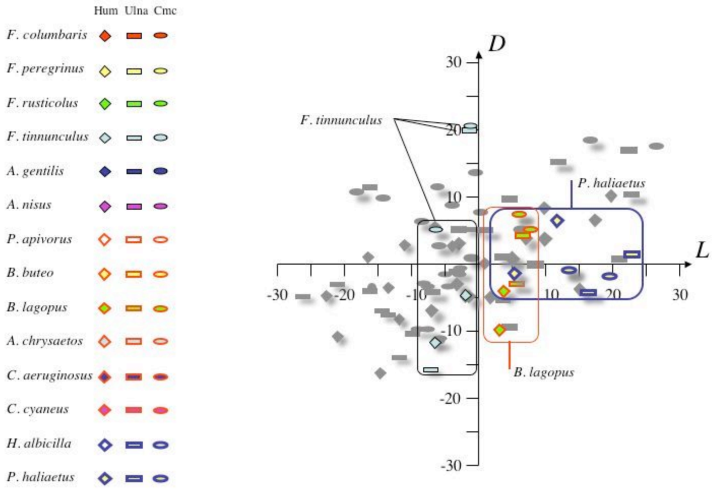

Figure 5. The deviations in percentage from expected values of length L and diameter D of humerus and ulna for the hovering species F. tinnunculus, B. lagopus and P. haliaetus. Male and female symbols are the same but each female symbol has a shadow.

Prediction 3: Active flyers – larger surface of carina sterni

This prediction is tested together with prediction 4 in the next paragraph.

Prediction 4: Fast flyers – longer and smaller diameter of carina sterni

Fig. 6 shows the deviations in percentage from expected values of length *L* and diameter *D* of carina sterni.

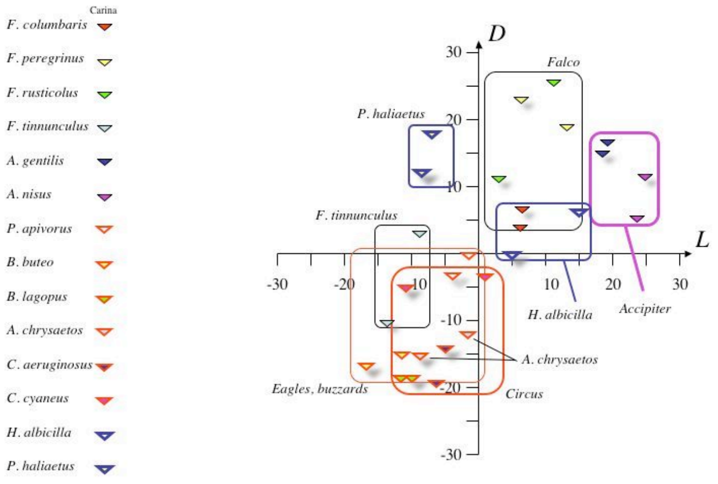

Figure 6. The deviations in percentage from expected values of length L and diameter D of carina sterni for all species. Male and female symbols are the same but each female symbol has a shadow.

Predictions 3 and 4 are the following:

3. Birds characterised by **active flying, hovering**, short (vertical) take offs and flying with heavy prey is expected to have **larger** than average **surface**

(surface ∝ l^*D) of carina sterni. (We would expect them to be found in the upper right quadrant of the diagram in Fig. 6.)

4. **Fast flyers** are expected to have larger length and **smaller diameter** of carina sterni making the bird more streamlined. (They should be expected to be found to the right and lower down in Fig. 6.)

Prediction 3 is verified with to exceptions:

1. The hovering *P. haliaetus* and *F. tinnunculus* do not have larger surface, again indicating hovering has not the impact that we have predicted.
2. *A. chrysaetos*, often described as an active flyer and not seldom having to take of with heavy preys, does not have larger surface of carina sterni.

Prediction 4 is not verified at all. The diameter *D* of carina sterni does not seem to be a problem in streamlining birds like *F. peregrinus*.

Prediction 5: "Hitters" – shorter and thicker tibiotarsus and tarsometatarsus

Prediction 5 says that "hitters" are expected to have shorter and thicker tibiotarsus and tarsometatarsus than the other species, because of the larger loads during impact. This prediction is verified. The majority of the "hitters" are found in the left half of the diagram and the other species in the right. But there are three exceptions:

1. The digging *P. apivorus* that have short and thick legs, see prediction 10, putting it in the same part of the diagram as the hitters, but for other reasons.
2. *F. tinnunculus* that have short and thick tarsometatarsus questioning the categorization that put it in the group of "grabbers".
3. For all of the falcons some of the leg bones are thinner, not thicker as is expected.

The most extreme "hitter" seems to be the osprey, at least regarding tarsometatarsus. The eagles (*P. haliaetus, and A. chrysaetos*) are closest to the "non hitters" having lengths and diameters close to what is expected from body mass.

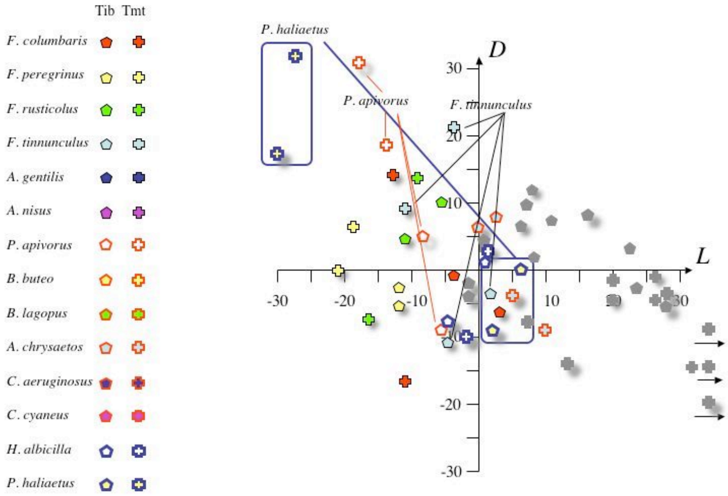

Figure 7. The deviations in percentage from expected values of length L and diameter D of tarsometatarsus and tibiotarsus, for "hitters" F. peregrinus, F. rusticolus, F. columbarius, P. haliaetus, and A. chrysaetos. Male and female symbols are the same but each female symbol has a shadow.

Prediction 6: "Hitters" – longer femur

Prediction 6 says that "hitters" can be expected to have longer femur. This prediction is, as can be seen in Fig. 8, not verified since the "hitters" does not have longer femur than the species in the other groups.

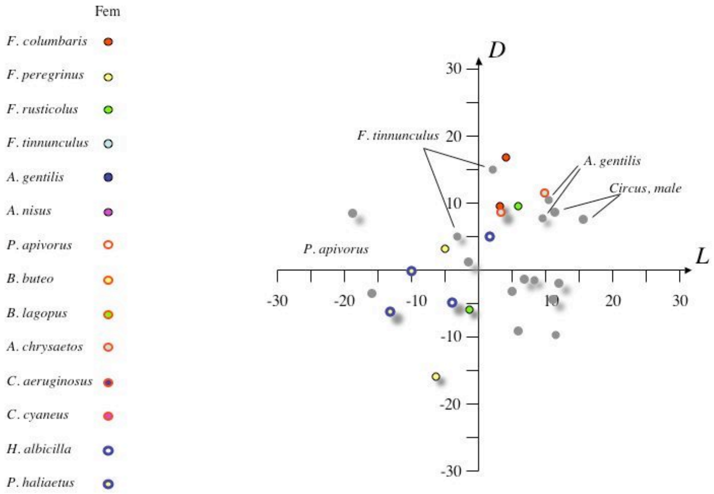

Figure 8. The deviations in percentage from expected values of length L and diameter D of femur, for "hitters" F. peregrinus, F. rusticolus, F. columbarius, P. haliaetus, and A. chrysaetos. Male and female symbols are the same but each female symbol has a shadow.

Prediction 7: "Grabbers" – longer tibiotarsus and tarsometatarsus

This prediction, saying that "grabbers" can be expected to have longer tibiotarsus and tarsometatarsus, is verified (Fig. 9) with three exceptions:

1. *A. chrysaetos*, which is supposed to be a "hitter", has longer tarsometatarsus than some of the "grabbers".
2. *F. tinnunculus,* have bones significantly shorter than predicted placing it among the "hitters". As has been discussed above, perhaps this species is grouped to the wrong group?
3. *H. albicilla, B. lagopus* and *B. buteo* have some of their leg bones of around average length, not longer as predicted for "grabbers".

The prediction is verified for *Accipiter* and *Circus* and for tarsometatarsus in *B. buteo*.

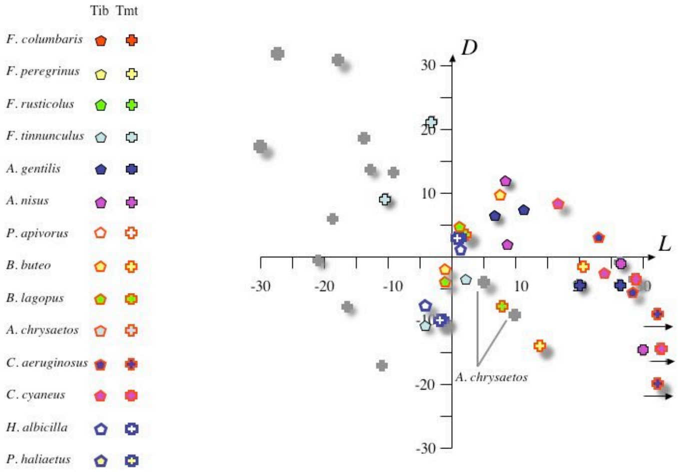

Figure 9. The deviations in percentage from expected values of length L and diameter D of tarsometatarsus and tibiotarsus, for "grabbers" A. gentilis, A. nisus, H. albicilla, C. aeruginosus C. cyaneus, F. tinnunculus, B. buteo, and B. lagopus. Male and female symbols are the same but each female symbol has a shadow.

Prediction 8: "Fast grabbers" – larger diameters of tarsometatarsus and tibiotarsus

This prediction, saying that "fast grabbers" can be expected to have larger diameters of tibiotarsus and tarsometatarsus, is not verified (Fig. 10) since the diameters in species of this group is distributed on both sides of the x-axis.

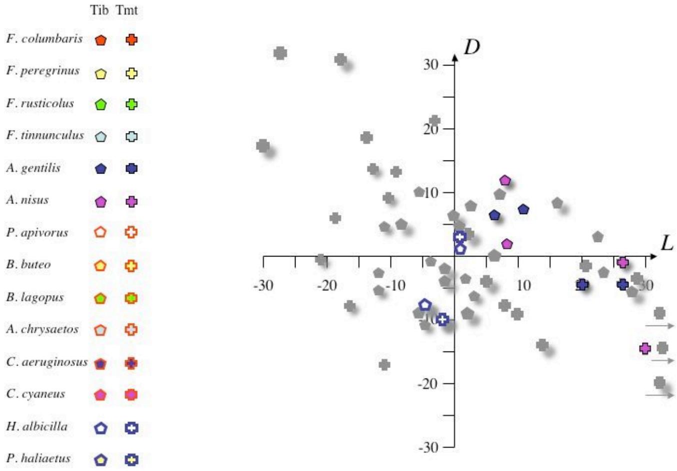

Figure 10. The deviations in percentage from expected values of length L and diameter D of tarsometatarsus and tibiotarsus, for "fast grabbers" A. gentilis, A. nisus, H. albicilla. Male and female symbols are the same but each female symbol has a shadow.

Prediction 9: "Slow grabbers" – tibiotarsus with smaller diameters

This prediction, saying that "slow grabbers" can be expected to have smaller diameters of tibiotarsus and tarsometatarsus, is not verified (Fig. 11), since the diameters of this group is distributed on both sides of the x-axis.

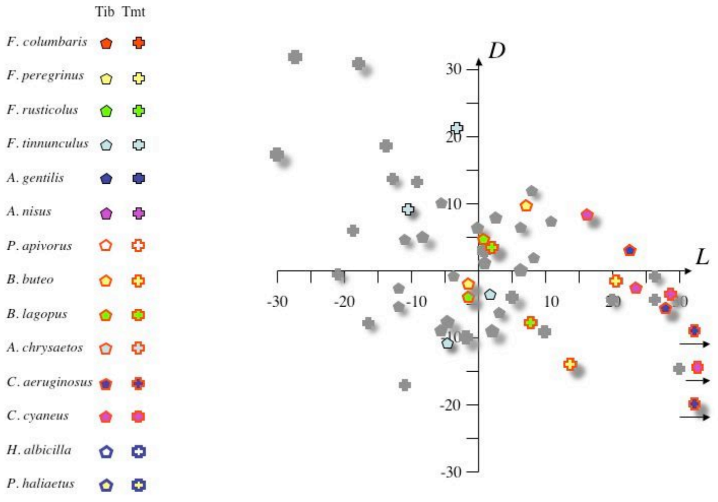

Figure 11. The deviations in percentage from expected values of length L and diameter D of tarsometatarsus and tibiotarsus, for "slow grabbers" C. aeruginosus C. cyaneus, F. tinnunculus, B. buteo, and B. lagopus. Male and female symbols are the same but each female symbol has a shadow.

Prediction 10: "Diggers" – shorter leg bones with larger diameter.

This prediction, saying that the larger loads that can be expected on the legs of digging birds should lead to larger diameters is verified for the tarsometatarsus for both sexes and for female tibiotarsus and femur, but not for male tibiotarsus and femur (Fig. 3).

Conclusions

Predictions 1 (soaring– longer humerus and active flyers – shorter) **and prediction 3** (active flyers – larger carina sterni) are verified for the species with more typical flight behaviour (*Falco, Accipiter* and *Circus*). But the situation is more problematic for buzzards (*Buteo* and *Pernis*) and eagles (*Aquila* and *Haliaetus*). These birds are mainly generalists and more problematic to characterise, *H. albicilla* for example has a carina sterni indicating active flying and a humerus indicating soaring. Either it was to optimistic or even wrong to categorize *Aquila* and *Haliaetus* as "hitters" and "fast grabbers" respectively, or the information the categorizing was based on was insufficient.

Predictions 2 (hovering birds – shorter wing bones) **and prediction 4** (fast flyers – lower carina sterni) were simply wrong. The falsification of prediction 2 indicates that the inertia of the wing is not an important criterion for selection for these birds. In the same way the falsification of prediction 4 indicates that a decrease of the parasite drag through a lower carina sterni is not any strong selective force in the evolution.

Prediction 5 (hitters – shorter and thicker tibiotarsus and tarsometatarsus) is verified where as **prediction 6** (hitters – longer femur) is not. It is obvious that birds of prey benefit from stronger tarsometatarsus and tibiotarsus, but not from longer femur.

Prediction 7 (grabbers – longer tibiotarsus and tarsometatarsus) **and prediction 9** (slow grabbers – smaller diameter) are both verified (with some exceptions) but not **prediction 8** (fast grabbers – larger diameter). Here too, it is the usual problem with buzzards

(*Buteo* but not for *Pernis* this time), eagles (*Aquila* and *Haliaetus*) and kestrel (*F. tinnunculus*). This indicates strong selection for long length, for all grabbers, but not for strength for the fast grabbers.

Prediction 10 (diggers – shorter and stronger foot and leg bones) is verified for tarsometatarsus of both sexes and for tibiotarsus and femur for the female.

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