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The Impact of Body Mass on Morphological Integration in Avian Skeletons (Aves, Fringillidae; Carduelinae, Fringillinae)

Renate VAN DEN ELZEN[1)] & Hans L. NEMESCHKAL[2)]
[1)]Zoological Researchmuseum Alexander Koenig, Bonn, Germany
[2)]Department of Theoretical Biology, University of Vienna, Austria

Abstract. The dependence of the individual and of correlated skeletal variables of Carduelinae and Fringillinae upon body mass (=size) was tested by means of multiple regression and single linkage R-cluster analyses. The most obvious result is the significantly high degree of body mass dependences of all individual variables within the three functional complexes feeding, hind limb locomotion and flying. Elimination of body mass as a measure of size decoupled several units of correlated variables. Nevertheless the general robustness of units was strong but the removal of "size" had an impact on the extent of morphological integration, measurable as agglomeration level of variable units. Body mass (size) in our sample thus influenced the quantity rather than the quality of morphological integration. The key feature in fringilline/carduelinе skeletal morphology – coevolution of skull and hind limb traits – thus appears to be relatively unconstrained by size.

Keywords. Size, ecomorphology, functional complexes, biological roles, skeletal morphology, developmental genetics.

1. INTRODUCTION

1.1. The role of body size in avian morphology

Body size has been identified as an important factor driving the diversification and evolution of organisms. OLSON & MILLER (1958, 1999), e. g. quantified size as a strong integrative force of morphology, FAIRBAIRN (1997) identified its role in sexual dimorphism, KLINGENBERG & SPENCE (1997) analyzed its function in life-history evolution. BONNER (2004) proposed a third size dependent rule besides the already well known "weight-strength-rule" and "weight-surface-area-rule". His "weight-complexity-rule" explains that increase and decrease in size of organisms are strongly related to increase and decrease in complexity in general, from differentiation of cell types to the social organization of organisms.

These examples implement size as a morphological key feature in the organization of life, at all hierarchical levels from the individual to species (BARBOSA et al. 2000; BONNER 2004; CHERNOFF & MAGWENE 1999; PETERS 1993).

Size, as the physical magnitude of objects, can be quantified using either measures or weights. Linear length measures are used to seize both the two dimensional area as well as the three dimensional volume, whereas weight quantifies the proportionality to volume alone. Measures widely accepted to represent overall size of organisms include also factors like the first principal component (BOOKSTEIN *et al.* 1985; ZELDITCH & FINK 1995; LEISLER & WINKLER 2006), landmarks or ratios. BJÖRKLUND & MERILÄ (1993), e.g. used orthogonal rotation to remove size from species mean vectors, LEISLER (1980) calculated the cube root of a compound measurement of the body core skeleton (sternum length plus pelvis length plus coracoid length) times (sternum width plus pelvis width) times height of crista sterni as measure for "body size", following HOERSCHELMANN (1966).

For the characterization of volume, body mass is the adequate measure. Several rules explaining the constructional constraints on morphology are related to body mass: The "weight-strength-rule" already mentioned above, explains why e.g. longer arms, wings and legs have to be proportionally thicker than shorter ones, the "weight-surface-area-rule" describes physiological relations of e.g. gas diffusion in large versus small lung surfaces. These are geometric growth laws, that explain the change of proportions – so-called allometric relations – within a biological organism. The underlying process is differential growth during development brought about by differences in the growth rates of the various parts (WADDINGTON 1966).

In small bodied flying vertebrates, flight imposes identical physical constraints on the flying organism that lead to a functional symmetry in body sizes (MAURER et al.,

2004). The body plan of birds is primarily constrained by the weight-strength-rule, that regulates flying ability. In extant species 22 kg is the limit for take off; the worldwide tiniest bird is the Bee Hummingbird, *Mellisuga helenae,* found in Cuba and weighing from 1,6–1,9 g (CHAI 1999). The most successful clade in modern birds, the passerines (or perching birds, Passeriformes) have miniaturized to an average body mass minimum of 4,5 g in some tropical species (Black-faced Flycatcher Warbler, *Abroscopus schisticeps,* Broad-billed Flycatcher Warbler, *Tickellia hodgsoni,* Cuban Gnatcatcher, *Polioptila lembeyei*; DUNNING 1993). The heaviest and thus largest song bird, the Raven, *Corvus corax,* from Alaska weighs 1.240 g. Perching birds successfully evolved and radiated within any terrestrial habitat –with exception of the polar regions where their occurrence is physiologically constrained by the weight-surface-area-rule.

1.2. Key features of the carduelid skeleton

Our paper focuses on the impact of body mass on the architecture of the avian skeleton, taking the song bird subfamilies Fringillinae and Carduelinae as a case study. Morphological diversity in skeletal elements in this phylogenetic entity (clade, monophylum) is mostly confined to changes in overall size (BJÖRKLUND 1991, 1994; VAN DEN ELZEN & NEMESCHKAL 1986, 2006; NEMESCHKAL & VAN DEN ELZEN 1990, VAN DEN ELZEN & NEMESCHKAL 2006). Differentiations in shape are (despite their unquestioned ecological importance) only expressed as an insignificant portion of the total variation. Whereas three shape axes explained only 9,3 % of variance, the size axis accounted for 85,5 % of variance (VAN DEN ELZEN & NEMESCHKAL 2006). The observed pattern has been identified as a general rule in passerine birds by BJÖRKLUND (1994, 2006). "….making species to be larger or smaller copies of each other, all moving up and down a common line of allometry". Mapping of skeletal variables along the first principal components (NEMESCHKAL & VAN DEN ELZEN 1990) revealed, that morphological diversification in Fringillinae and Carduelinae focuses on variables of the beak. Thus, morphological change in these subfamilies is mainly reflected in feeding mechanisms.

In terms of ecomorphology, a discipline taking the biological role of morphological structures under consideration (BOCK & VON WAHLERT 1965), elements of the avian skeleton belong to three different functional complexes: skeletal elements of the skull and beak are allied to the feeding complex, wing bones, pectoral elements and bones of the shoulder girdle represent the flying apparatus and skeletal elements of pelvis and legs the hindlimb locomotion complex. In the carduelid skeleton, nevertheless, units of covarying variables (UCCs) contain combinations other than proposed by the functional complexes described above. These UCCs were detected to reflect units carrying out common biological roles. Besides a more or less undisturbed module of the "flying complex", formed solely by wing bones plus elements of the shoulder girdle, the variables of the feeding and hindlimb locomotion complexes were united in one single common cluster, and demonstrate the superimposure of feeding on hindlimb locomotion.

In search of additional modern approaches in the study of morphological integration, CHERNOFF & MAGWENE (1999) propose a hierarchical framework for integrative hypotheses: Morphological variables are judged as integrated at the broadest, i. e. the uppermost inclusive level due to their covariation with size. At a less inclusive level variables covary due to developmental and/or functional associations and at still lower levels due to anatomical (spatial) associations. Starting out from physics we may assume that changes of singular parts from a macroscopical physical (e. g., mechanical) system will be ruled by various law-dependencies when the whole system changes size (e.g., mass). As a consequence, we test in the current study the dependence of individual and correlated skeletal variables upon body mass taken as a measure of size.

1.3. Presumptions

Based upon our knowledge from preceding analyses (VAN DEN ELZEN, NEMESCHKAL & CLASSEN 1987, NEMESCHKAL & VAN DEN ELZEN 1990, NEMESCHKAL, VAN DEN ELZEN & BRIESCHKE 1992, VAN DEN ELZEN & NEMESCHKAL 2006) our hypotheses are that:

1. a significant dependence of skeletal variables on body mass exists. It is expected to differ between variables and to be highest in beak elements;
2. thus the three theoretical functional complexes -feeding, hindlimb locomotion, flying- differ in their size dependence;
    a. variables of the feeding apparatus – showing highest morphological differentiation between species – should exhibit the largest amount of size dependence,
    b. elements of the hindlimb locomotion complex and of the flying apparatus are thought to show lesser dependence, as of lesser interspecific variability.
3. units of variables (UCCs) are also expected to be size dependent, elimination of "size" is thought to decouple variables within units; decoupling is expected to occur particularly within "mixed" variable units of beak and hindlimb osteometrics.

2. MATERIAL AND METHODS

In 313 specimens, representing 43 species (Table 1), 42 equivalent skeletal variables (measurements of bone lengths, widths and depths) were taken, as described in detail in NEMESCHKAL (1999). Twenty measurements stem from the feeding apparatus, 13 represent the flying apparatus and 9 hindlimb locomotion (Table 2).

Firstly, centroids of 43 species over 42 variables were built from the log scaled original data matrix consisting of 313 specimens. This procedure was essential, because body mass data were available as species means only. Morphological variation between species was then quantified by the total variance of species centroids. Body mass variation in the actual fringilline-cardueline sample ranges from a maximum of 54 g in the Hawfinch *Coccothraustes coccothraustes* to a minimum of 9 g in neotropical siskins (Table 1). To test hypotheses about size impact, linear regression analysis was applied. Log transformed species means of body mass were taken as predictor variable and each of the 42 skeletal measurements as criterion variable. The 42 resulting residuals are used as the variables under study – the variables corrected for body mass (= variables of which size was partialized out; BCM). The coefficients of determination between body mass and original variables (Table 2) were tested for significance using random bootstrap (1000 replicates each; for computer programme package see NEMESCHKAL (1999)). They are figured as profiles of variance (Figs 1, 2). Single linkage R-cluster analyses were chosen to figure correlations of original data (Figure 3- BO; based upon the variable intercorrelation matrix between species means for original data) and correlations data corrected for body mass (Fig. 3- BCM; variable intercorrelation matrix between species means for body mass adjusted data). Units of correlated variables were taken into account, when they agglomerated at the uppermost quartile ($r^2 > 0.924$) in the original dataset **and** reappeared in the size corrected dataset again. E-units are stable clusters with topological identity of variable positions in both the R-cluster analyses of original data and the body mass corrected data set. S-units are less stable units built of identical variables but with topological differences between analyses of original and size corrected variables.

3. RESULTS

The most obvious findings are on the one hand the significantly high degree of body mass correlation of all individual variables (Fig. 1) and on the other hand the robustness of several covarying variable units found in both the original and the "residual" data set, adjusted for body mass (Fig. 2).

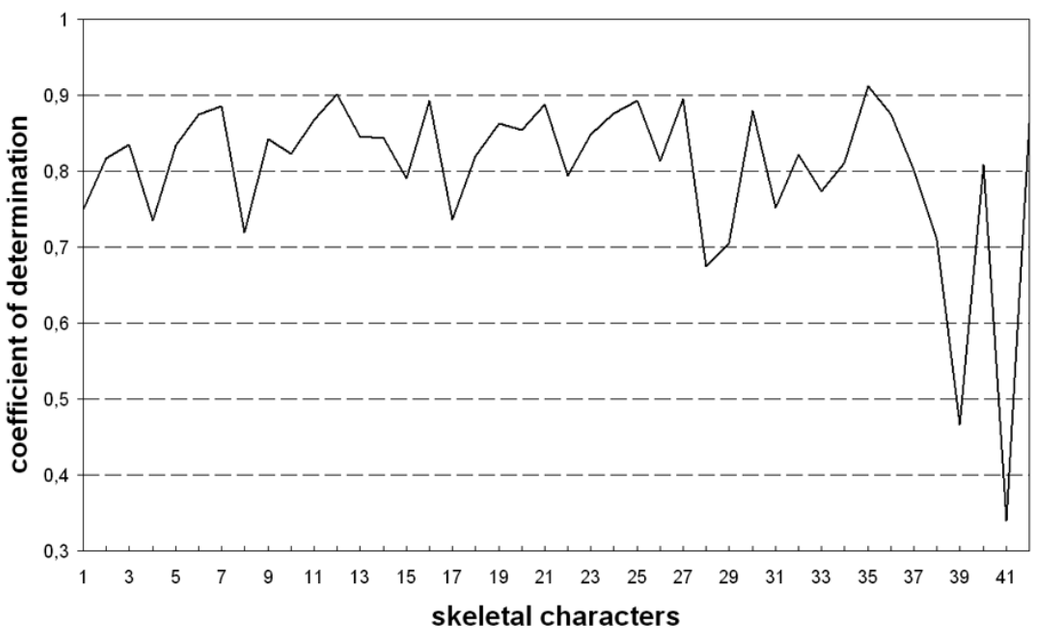


Fig. 1. Dependence of 42 skeletal characters on body mass as shown by coefficients of determination.

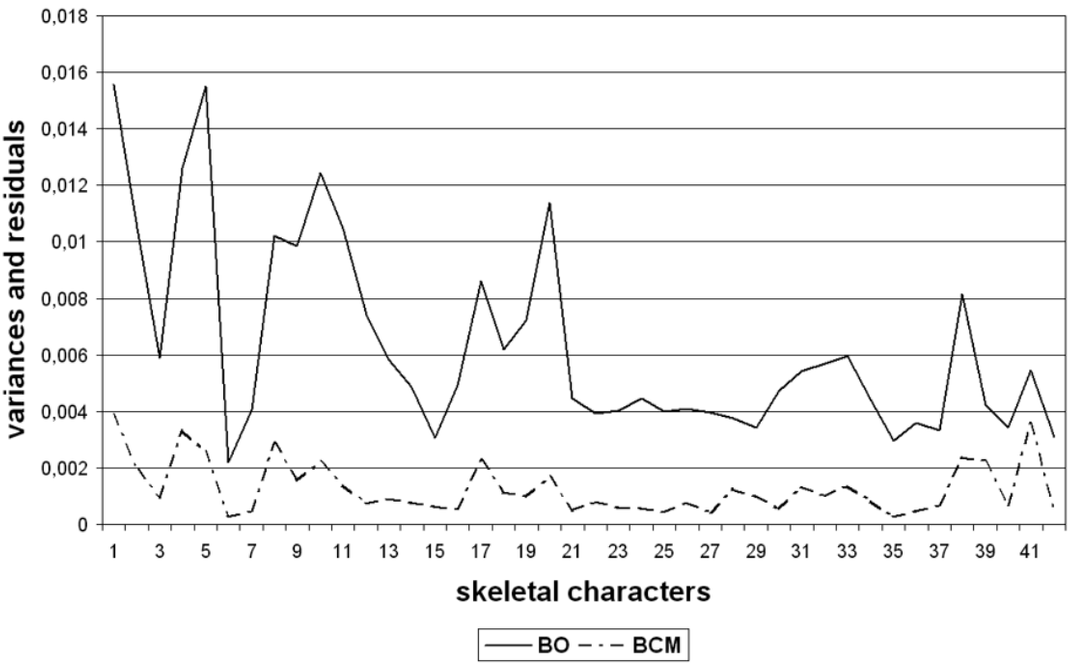
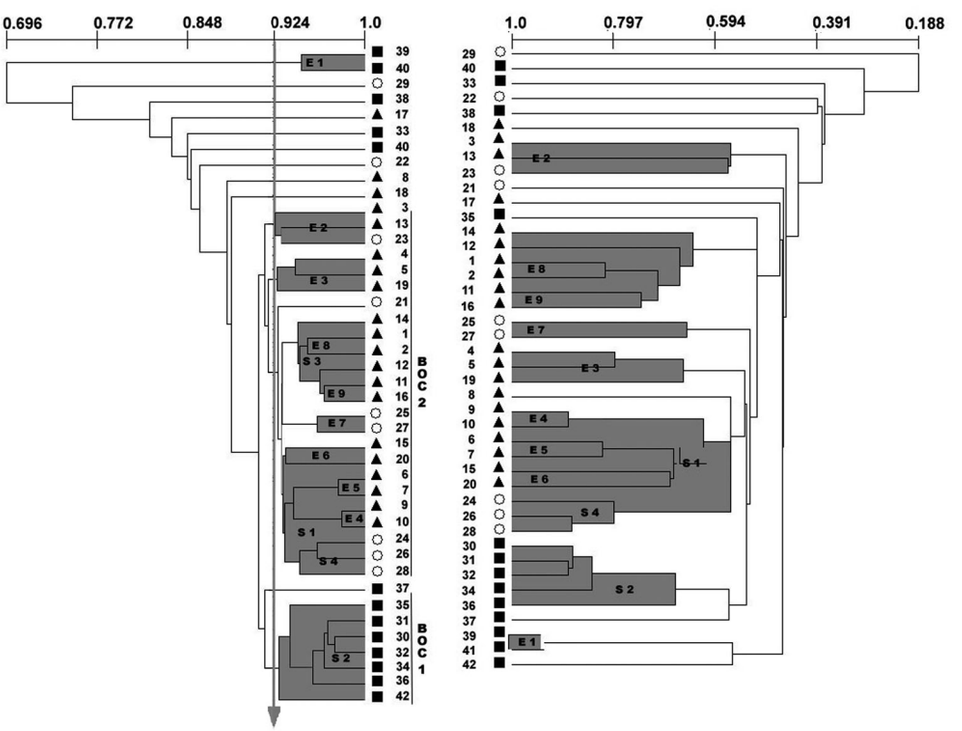


Fig. 2. Comparison of variance profiles. Variance of original characters (BO) occur in the upper line and residuals for characters corrected for body mass (BCM) at the bottom.



Figs 3. Single linkage R-cluster analysis of original data (BO; left) and of body mass corrected data (BCM; right). Black squares indicate measures of the pectoral girdle and forelimbs, black triangles mark skull measurements and open circles measures of the pelvic girdle and hindlimbs. Clusters are explained in the text.

3.1. Influence of body mass on individual variables

All 42 variables are correlated with body mass at a high significance level ($p < 0.001$) as revealed by random bootstrap procedures. The degree of correlation with "size", measured by coefficients of determination (COD) between (log transformed) original data of species means and body mass, is highest in coracoid length (variable number 35; COD=0,91), post orbital length (12; 0,90) and equal at COD= 0,89 in tibiotarsus width (27), total skull length (16) and synsacrum length (21). The largest amount of body mass independence exhibit carpometacarpus (41) and ulna lengths (39; COD= 0,34 and 0,47) as well as tarsometatarsus length (No 28) and width (29; COD= 0,70, resp. 0,67) and proximal end width of the humerus (38; COD= 0,71). Skull variables in general reveal the highest correlation with body mass, hindlimb and forelimb variables indicate a larger variation in their correlation with body mass.

A comparison of variance profiles of original and size corrected skeletal variables (Fig. 2) confirms and strengthens these findings: The relatively higher variances in the original variables appear smoothened in the size corrected residuals (BCM; bottom line in fig. 2), indicating that the largest amount of total variance between species is due to a "size factor", measurable by body mass. This especially holds true for skull variables (skeletal variables 1–20) and less for hindlimb and forelimb measures (skeletal variables 24–29, 37–42).

3.2. Influence of body mass on united variables

The single linkage cluster analysis of original data (Fig. 3) extracted two main units fused at a high level, several disintegrated variables and one isolated variable set (E1). The module BOC 1 is composed of the variables of the flying apparatus, mainly its "engine-supporting" part, including measures of sternum, coracoid and scapula. Wing measures that represent "flight performance" are highly disintegrated, only humerus length (37) and carpometacarpus width (42) are included. The second main module BOC 2 combines skull and hindlimb measures.

The two main modules BOC 1 and BOC 2 are composed of two different types of subsets: Robustness is observed in nine smaller units (E1–E9), where only two to three variables are coupled. Similar structure is maintained after correction for size in four units (S1–S4), including three to 17 variables as well as including several of the stable units (E4–E9). Whereas, for example, femur length (24) and tibiotarsus length (26) are next neighbours in the S4 cluster in BO, in BCM tibiotarus length (26) and tarsometatarsus length (28) are agglomerated at the highest level. The larger S1 and S2 units also include some of the smaller, topologically stable E units: E4–E6 always occur within S1, E8–E9 within S3, S4 is always part of S1.

BOCs identified in the R-cluster analysis of original data are to a great extent also found in the analysis of body mass corrected data (Fig. 3). Again in the body mass corrected data analysis, a main cluster composed of engine-supporting variables from the flight complex (S2 in BOC1, fig. 3) opposes a main cluster structured by a mixture of skeletal elements of the feeding and hind limb locomotion apparatus characters. The main differences to the original data analysis are the rather low agglomerative level (coefficients of determination in the "size-corrected" dataset being two to three times lower than in the original dataset), reduction of the involved variable units and some changes in variable topology. BOC2, that was composed of S1 (including S4), S3, E2, E3 and E7 in the original dataset, comprises in the size corrected data set only S1 (including S4) and E3, the remaining components – units S3, E2 and E7 – are clustered at lower agglomeration levels.

Subcluster S1 differs in its hierarchical structure of agglomeration levels of E units and arrangement of variables within S clusters. In S2 sternum length (30), keel length (32) and keel depth (31) are differently arranged, in S3 post orbital length (12), and within S4 femur-, tibiotarsus and tarsometatarsus lengths (24, 26, 28) changed their position along branches.

In both illustrations of single linkage R-cluster analyses (Fig. 3), E1 shows up as a more or less disintegrated unit. It consists of measures of ulna (39) and carpometacarpus lengths (41), which are tied together at a relatively high agglomeration level, especially in the analysis of "size-corrected" data, in which both measures are combined with carpometacarpus width (42).

4. DISCUSSION

4.1. Size and morphological integration

Do these results confirm or contradict our predictions and expectations of hypotheses on morphological integration? Corroborating our first assumption, a general body mass dependence was identified at a high significance level for all individual characters within all three classical functional complexes. "Size" could thus be confirmed as a strong integrative force in cardueline and fringilline skeletal morphology. Variability was, as assumed in our second hypothesis, relying to a greater extent on body mass in skull and beak measurements than in characters allied to the other functional complexes. Elimination of "size", decoupled,

Table 1. List of species under study, their body masses and information sources. Sources: DU= Dunning 1993; RE= labels of specimens at ZFMK, Bonn; RO= McLean 1988; WA= Ward 2003.

Species	**body mass in g**	**sources**
Fringilla montifringilla	24	DU
Fringilla coelebs	21,4	DU
Coccothraustes coccothraustes	54	DU
Pyrrhula pyrrhula	21,8	DU
Pinicola enucleator	56,4	DU
Loxia curvirostra	40,38	DU
Chloris chloris	27,8	DU
Chloris sinica	31,3	DU
Acanthis flammea	13	DU
Carduelis carduelis	15,6	DU
Linaria cannabina	15,3	DU
Agriospiza flavirostris	15,4	DU
Rhodospiza obsoleta	25,5	DU
Spinus spinus	14,5	DU
Spinus cucullatus	9	RE
Spinus barbatus	16,6	DU
Spinus xanthogaster	12,7	DU
Spinus yarrellii	9,5	RE
Spinus psaltria	9,5	DU
Serinus pusillus	11,6	DU
Serinus serinus	11,2	DU
Serinus syriacus	12,1	BE
Serinus canicollis	13,8	DU
Serinus citrinella	12	DU
Alario alario	11,8	RO
Serinus canaria	12,97	DU, RE
Ochrospiza reichenowi	11,5	RE
Ochrospiza atrogularis	11,4	DU
Ochrospiza leucopygia	9	RE
Ochrospiza mozambica	10,6	DU
Ochrospiza dorsostriata	14,4	DU
Ochrospiza xanthopygia	10	RE
Crithagra gularis	15,5	DU
Crithagra striolata	22,4	DU
Crithagra albogularis	25,9	DU
Crithagra donaldsoni buchanani	24	DU
Crithagra sulphurata	19,2	DU
Serinops flaviventris	16,3	DU
Crithagra mennelli	15,3	RO
Crithagra burtoni	29,9	DU
Dendrospiza hyposticta	15	DU
Dendrospiza scotops	15,4	RO
Pseudochloroptila totta	13,4	WA

as predicted in the third assumption, several units of correlated variables. Nevertheless, contradicting our expectations, displacement of variables from units or units from larger modules was low and robustness of units strong. Body mass (size) itself in our sample thus influenced the quantity rather than the quality of morphological integration and did not affect the key feature in fringilline/carduelinе skeletal morphology – coevolution of skull and hindlimb variables.

According to classical hypotheses on morphological integration, "size" is the uppermost integrative level, at deeper agglomerative levels, traits covary due to developmental or functional associations and at still deeper levels due to spatial adjacency (CHERNOFF & MAGWENE 1999) respectively morphological neighborhood (ALPATOV & BOSCHKO-STEPANENKO 1928). Indeed, in our study, removal of the first hierarchical layer "size", mostly effected the degree of morphological integration, measurable as agglomeration level of character units. Structure and relation of character compositions however remained to a great extent constant and robust. For variable units at the body mass reduced level, three types of trait correlations are identifiable: S-modules are subunits agglomerated at higher integrative levels within BOC1 and BOC2, the original, not body mass reduced, modules. E-modules that are not composed of characters from immediate morphological neighborhood or partial overlap (E4, E5, E9) can be assigned to two categories: Classical functional units (E2, E3, E6 and E7) are with one exception (E7) fused at lower agglomerative levels (below 0.6 COD) than the units of biological roles E1 and E8 (above 0.8 COD). Our findings thus corroborate the integrative hypotheses quoted above, that anatomical association is a primary integrative level in morphology.

4.2. Interpretation of the observed character modules

EBLE (2005) classifies four different kinds of modules in morphology:

1. modules due to structural relations,
2. modules of pleiotropic genotype-phenotype mappings,
3. developmental units (gene expressions, domains of epigenetic dynamics, regions with localized allometric growth) and
4. functional units.

We would like to extend the definition of the last category by modules accomplishing common biological roles (NEMESCHKAL et al. 1992) and thus differentiate between

4.a. mechanical functioning (like kinetics) and
4.b. biological functioning (like morphological traits used in e. g. feeding).

Units E4 (postorbital width and internasal width, 9, 10), E5 (skull width and interorbital maximal width, 6, 7) and E9 (premaxilla length and total skull length, 11, 16) may be explained by their immediate morphological neighbourhood and /or partial overlap ("rule of neighbourhood", ALPATOV & BOSCHKO-STEPANENKO 1928; structural relations EBLE 2005). Most of the other results allow for mechanical functional explanations, few for explanations of their biological roles. E2 is composed of two skull characters (caudal length of the mandible and quadratojugal length, 3, 13) and a pelvis measure (synsacrum distal length, 23). Whereas the first two skull variables are functional counterparts and act in seed husking, their –also body mass independent- correlation with a synsacrum length measure comes unawares. E3 combines two mandible depths (4, 5) with quadratum length (19), characters functioning in the kinetism of the avian skull, especially in lateral bill movements enhancing seed husking (NUIJENS & ZWEERS 1997). Also units E6 (skull height and premaxilla depth, 15, 20) and E7 (femur and tibiotarsus width, 25, 27) are easier to explain by constructional constraints than biological roles. E6 depicts the interdependence of skull and beak height, E7 that of leg diameters, in E8.Only units E1 and E8 where measures of the flying apparatus (carpometacarpus (41) and ulna lengths (39)) respectively bill tip are tied together (length of pars symphysialis (1) with dentary length of the mandible (2)) allow for an interpretation of biological roles: The first unit comprises the feather-carrying bones of the wing, responsible for manoevrability in flight per se. Unit E8 represents "the bill tip grasp", a feeding tool well developed in carduelid finches (NEMESCHKAL et al. 1992).

S4 with the lengths of femur (24), tibiotarsus (26) and tarsometatarsus (28) obviously reflects a character pattern of concerting limb dimensions as guided by developmental processes during ontogeny (NEMESCHKAL 1999).

Comparison of interspecific correlation patterns (macroevolutionary pattern, this study Fig. 3) with infraspecific analyses of variable correlations (microevolutionary level, NEMESCHKAL & VAN DEN ELZEN 1994, fig. 7) reveal that six modules (E3, E4, E5, E7, E8 and E9 of this study) correspond to units also found within carduelid finches and three modules (E5, E7 and E9) even to units occurring within the phylogenetically distant pigeons. At the microevolutionary level NEMESCHKAL et al. (1992) provided evidence for clade specificity of variable units (modules) and their correspondence to expressions of developmental control genes (NEMESCHKAL 1999). Morphological modularity might generally be seen as product of developmental modularity, because morphological patterns of organization emerge in ontogeny (EBLE 2005). Consequently, each of the extracted variable complexes might additionally also correspond to developmental or body plan modules.

Table 2. Skeletal variables under study and their coefficients of determination. BO represent original data, BCM residuals for the body mass reduced variables.

Skeletal variables	Coeff. of determination
Skull measures	
01 mandible, pars symphysialis length	0,7014
02 mandible, dentary length	0,7641
03 mandible, pars caudalis length	0,7642
04 mandible, dentary depth	0,6924
05 mandible, pars caudalis depth	0,7883
06 skull width	0,8239
07 interorbital, maximal width	0,8353
08 interorbital, minimal width	0,6704
09 postorbital width	0,8048
10 internasal width	0,7856
11 premaxilla length	0,8240
12 postorbital length	0,86
13 quadratojugal length	0,7953
14 orbital width	0,7888
15 skull height	0,7280
16 skull length	0,8610
17 palatinum width	0,6176
18 pterygoid length	0,6932
19 processus orbitalis quadrati length	0,7988
20 premaxilla depth	0,7911
Pelvic girdle and hindlimbs	
21 synsacrum length	0,7748
22 synsacrum width	0,7076
23 synsacrum distal length	0,7464
24 femur length	0,8355
25 femur width	0,7781
26 tibiotarsus length	0,7675
27 tibiotarsus width	0,7562
28 tarsometatarsus length	0,6180
29 tarsometatarsus width	0,3034
Pectoral girdle and forelimbs	
30 sternum length	0,8413
31 keel depth	0,6897
32 keel length	0,7632
33 sternum, distal width	0,6617
34 sternum depth	0,7393
35 coracoid length	0,8401
36 scapula length	0,8114
37 humerus length	0,7644
38 humerus, proximal end width	0,6246
39 ulna length	0,3233
40 ulna width	0,6235
41 carpometacarpus length	0,2333
42 carpometacarpus width	0,6454

How genes and developmental pathways co-operate is best documented for the avian beak. It is constructed by multiple facial prominences (HELMS et al. 2005, HELMS & BRUGMANN 2007), where the frontal nasal mass (FNM), lateral nasal prominences (LNP), and maxillary prominences (MXP) comprise the upper beak and the mandibular prominence (MDP) forms the lower beak. The identities of facial prominences are specified early in the neural crest stage and may involve homeobox genes such as Hox (COULY et al. 1998) or MSX (BROWN et al. 1997, WU et al. 2006).

In metazoa, at least 17 signal transduction pathways operate to activate or repress different genes at distinct times and places in the embryo. Five predominate in early embryonic development: the Wnt, TGF-beta, Hedgehog, RTK, and Notch pathways. Five more are used in late development, and seven more in the functions of differentiated cells (GERHART 1999).

Diversity in beak shapes of Galapagos finches, e. g., is known to originate from the activity of a morphogenetic bone protein (BMP4 of the TGF-beta family; ABZHANOV et al. 2004) and calmodulin, a protein that binds and transports calcium ions (CaM; ABZHANOV et al. 2006). Whereas BMP4 stimulated growth of beaks along two dimensions, – it produced deeper and wider beaks and thus explained the linkage in the variation of these traits, – the authors found CaM as regulator of beak length. Thus in Galapagos finches, beak length develops independently from width and depth due to two different factors that lead to changes in growth along different dimensions (ABZHANOV et al. 2006). In ducks, chickens and cockatiels, BMP4 is also differently expressed (WU et al. 2004, WU et al. 2006). At late stages of development, chicken and duck embryos had two localized growth zones in the FNM, which melted in the chicken, but stayed separated in the duck. Ducks, moreover exhibited a wider FNM and more activity in another growth factor (fibroblast growth factor 8). In cockatiels a thicker FNM increased in a different direction and the mandibular prominence (MDP) was suppressed. BMP4 was involved in all species in mediating activity in all localized growth zones. Experimental overexpression in BMP4 altered beak shapes among all species and beak curvation was induced by asymmetric growth activity in a facial prominence. BMP4 was also found to be responsible for regulating a homeobox gene: As it increased the expression of MSX1, the authors suggested that MSX1 activity is regulated by the BMP pathway.

4.3. Conclusions

Under the assumption that BMP4 is a main regulator for the expression of developmental control genes in the avian skeleton, this protein, for instance, can be seen as a key growth factor accounting for size and shape variation in our skeletal variables. A developmental growth factor can also explain the strong size dependence of single variables, but cannot elucidate the interspecific correlation patterns of variable units. Thus in the light of current knowledge on gene expression variability and research in developmental genetics the classical view on morphological integration and genesis of modularity might be too one-sided.

WAGNER et al. (2007) offer a broader approach to modularity. Summarizing empirical evidence, they discern between two levels: The elements the modules consist of and their kinds of interaction. Elements vary from molecular level (nucleotides) to morphological traits and their connections from physical to dynamical and statistical. They define three kinds of modules: Variational, functional and developmental modules, but stress a duality, as modules may belong to several categories at the same time. Units observed in the present study on cardueline/fringilline skeletal variables fall in the category of variational modules, as their measure is statistical. For the interpretation of variational modules the authors offer several answers: identical developmental origin, similarity of covariation and gene expression territories, and pleiotropic effects. So our variable units (or character complexes; NEMESCHKAL et al. 1992) can be defined not only as a duality but a plurality: according to their operability they are functional modules, according to their mode of exploration they are variational modules, and according to their genesis developmental modules.

The open problem is, whether modules arise through the action of natural selection or because of biased mutational mechanisms (WAGNER 2007). Both neutral models and models based on natural selection are offered: e. g. LYNCH (2007) favors the neutral model and stated that "... emergent biological features such as complexity, modularity, and evolvability, all of which are current targets of considerable speculation, may be nothing more than indirect by-products of processes operating at lower levels of organization." We do not follow the author in refusing natural selection and external evolutionary forces, but assume, that selection via fitness promotes certain phenotypes derived from their genetic basis and processes in ontogeny. Under the viewpoint of developmental constraints as internal evolutionary forces, we like to generalize the findings of WU et al. (2004, 2006) on the origin of beak shape in birds. The authors offer a more reconciling conclusion, that morphological diversity may be achieved by modulating prototypical molecular and cellular modules. Transforming growth factors may mediate the range, level, and duration of locally enhanced growth, thus providing a spectrum of morphological designs for selection (WU

et al. 2006). Also WAGNER et al. (2007) arrive at the conclusion that mutational processes (internal processes) favor the origin of modularity and selection pressures (external processes) reinforce the mutational bias.

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Authors' addresses: Renate VAN DEN ELZEN (corresponding author), Section Ornithology, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany; E-Mail: r.elzen.zfmk@uni-bonn.de; Hans L. NEMESCHKAL, Department of Theoretical Biology, University of Vienna, Althanstrasse 14, A-1090 Wien, Austria; E-Mail: Hans.Leo.Nemeschkal@univie.ac.at

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