

# *Procrustomachia*

Occasional Papers of the Uncensored Scientists Group

2, 1: 1-10

Milanówek

28 II 2017

ISSN 2543-7747

---

## **Index of curtailment – an interesting aspect of wing formula**

Roman B. HOŁYŃSKI

PL-05822 Milanówek, ul. Graniczna 35, skr. poczt. 65, POLAND

Bird Migration Research Station, University of Gdańsk, PL-80308 Gdańsk, ul. Wita Stwosza 59, POLAND

e-mail: [rhozynski@o2.pl](mailto:rhozynski@o2.pl)

This paper is dedicated to those thousands of “nameless” enthusiasts who, themselves not being interested in scientific elaboration of the results, have nevertheless devoted their time to work on ringing camps and gather the material allowing others (like me) to discover and elucidate the fascinating mysteries of bird migrations.

### **Introduction**

In my previous publications (HOŁYŃSKI 2015, 2016) I have reviewed those wing-formula indices routinely used in Baltic Operation and its “clones” and “personally” familiar to me from the time (1960-1988) of my active participation in the ringing and measuring of migrating birds. Wing-formula was introduced as a standard measurement in BO in 1962-1963, and already in the first years of its application it struck me that, while in most species (at least among European **Passeriformes**) the line connecting the tips of primaries makes a fairly regular curve, in some – esp. **Ploceidae**, **Fringillidae** and **Motacillidae** (according to traditional classifications) – the apex of wing looks like cut off: the length of three or four longest primaries is almost equal. Throughout my ringing activity, and for the next quarter of century, I had not gone beyond this general impression, but it remained stuck in my mind and now some irregularities observed in the distribution of traditional indices (“*the most interesting directions of later studies will certainly be the departures from the general rules*” – HOŁYŃSKI 2016) prompted me to have a closer look at the underlying phenomenon.

### Symbols (written in red) used for the analysed indices:

- w** – wing length
- a** – qualitative index of wing-pointedness (HOLYŃSKI 1965)
- L** – index of elongation (“index of pointness” of BUSSE 1967) “normalized” as % of **w**
- l** – sum of distances from tips of four longest primaries to the wing-tip
- s** – sum of distances from tips of three shortest (among those – 2. to 8. – measured for the “classic” wing-formula) primaries to the wing-tip
- C** – index of total curtailment [ $C = \Sigma s / \Sigma l$ ]
- d** – sum of distances from tips of four distal (2.-5.) primaries to the wing-tip
- p** – sum of distances from tips of three proximal (6.-8.) primaries to the wing-tip
- Q** – index of distal curtailment [ $Q = \Sigma p / \Sigma d$ ]
- D** – estimated distance of (one way) seasonal migration

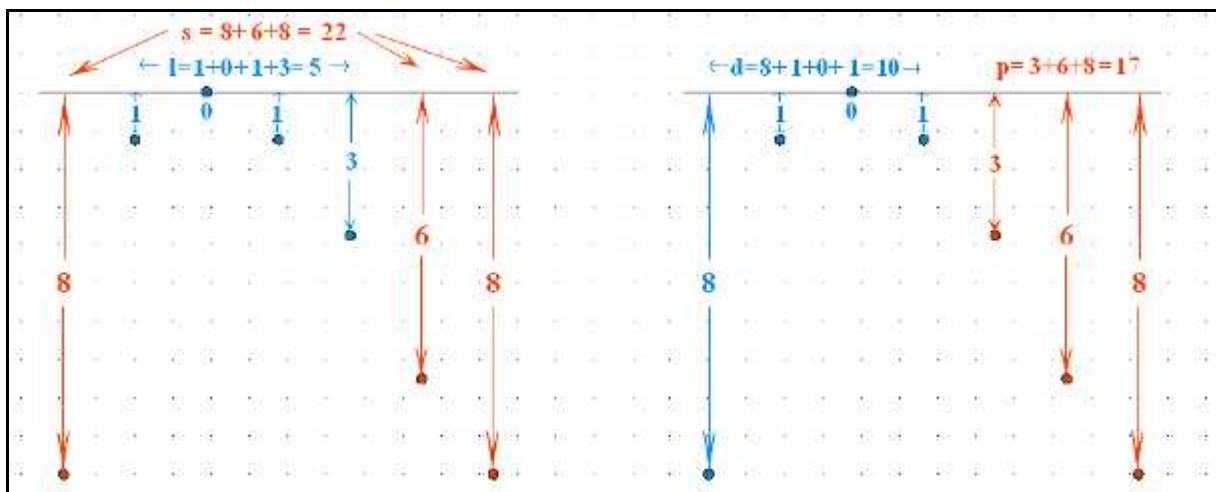
Indices on diagrams are represented by species averages, and each primary on **figs. 2, 3** and **8** by the average of individual measurements expressed as percent of wing-length ( $100x/w$ , where **x** is the distance from the tip of particular primary to the apex of wing)

### Indices of curtailment

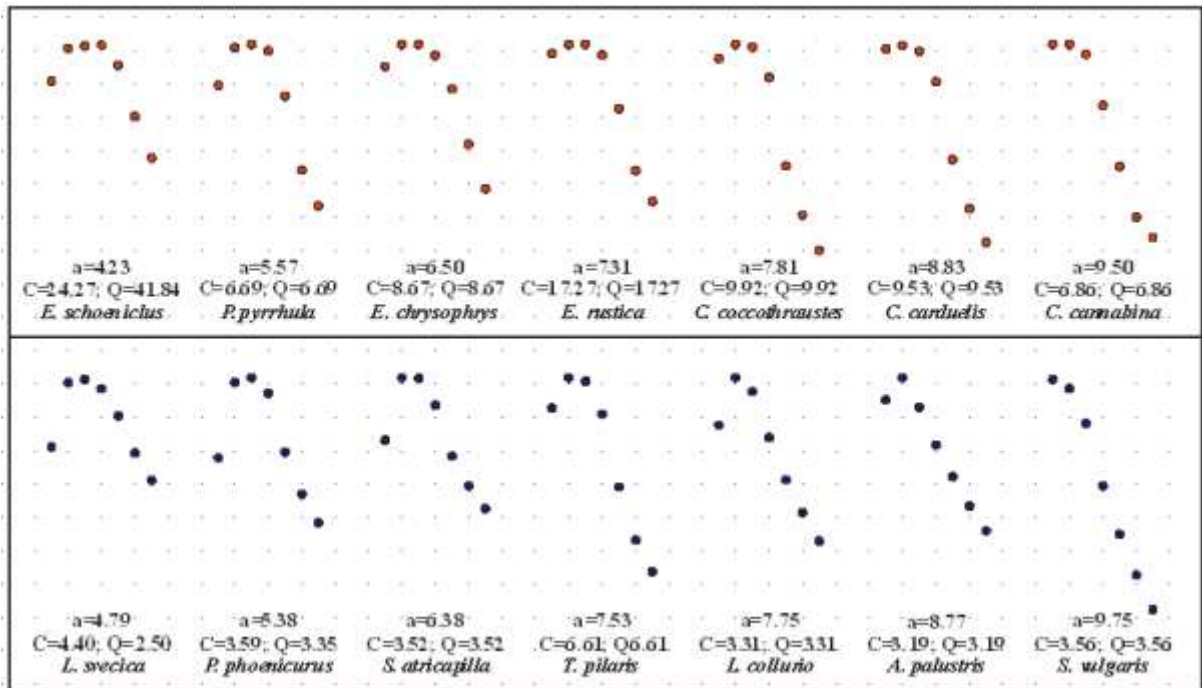
The difference between the wing-formulae of **Ploceidae**, **Fringillidae** (*sensu lato*) and **Motacillidae** (later on “PFM-group”) and the “typical” majority (“TM”) of at least **Passeriformes** is evident from **figs. 2** (Central Europe) and **3** (South Africa); these figures also clearly show that the difference increases with increasing pointedness (**a**) [unfortunately, the formulae of  $a > 7$  for African TM-group have not been available]. However, it was necessary to find an appropriate measure to quantitatively distinguish between “typical” and “truncated” wings and analyse the range of variability in this character (for which I propose the term “curtailment”). The obvious analogy to what in mathematics is termed “kurtosis” suggested to apply the respective formula, but the calculations are rather cumbersome and interpretation of results (at least to me) not sufficiently clear, so I decided to choose a more straightforward coefficient. The simplest seemed to be the proportion of the sum of distances (as measured for each wing-formula) between the apex of wing and the tips of four longest primaries to the respective sum for the shortest three [fig. 1 - left].

**Fig. 1**

Explanation of **C** and **Q**, on the example of the wing-formula  $4 > 3 = 5(1) > 5(3) > 6(6) > 2 = 8(8)$  (*P. collybita*):  
 $C = \Sigma s / \Sigma l = 22 / 5 = 4.40$ ;  $Q = \Sigma p / \Sigma d = 17 / 10 = 1.70$



**Fig. 2**  
 Examples of wing-formulae of various **a** values – C-Europe  
 Above (red markings) PFM-group, below (black) others



**Fig. 3**  
 Examples of wing-formulae of various **a** values – S-Africa  
 Above (red markings) seed-eaters, below (black) others

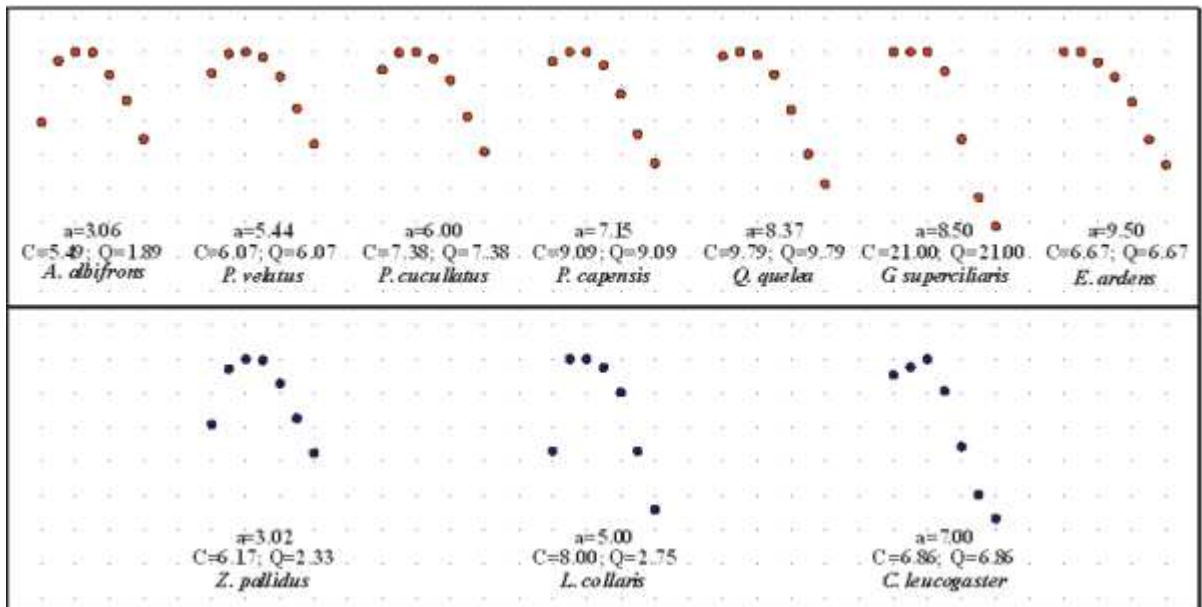


Fig. 4

Relation between index of total curtailment [C] and qualitative index of pointedness [a] in Central European birds

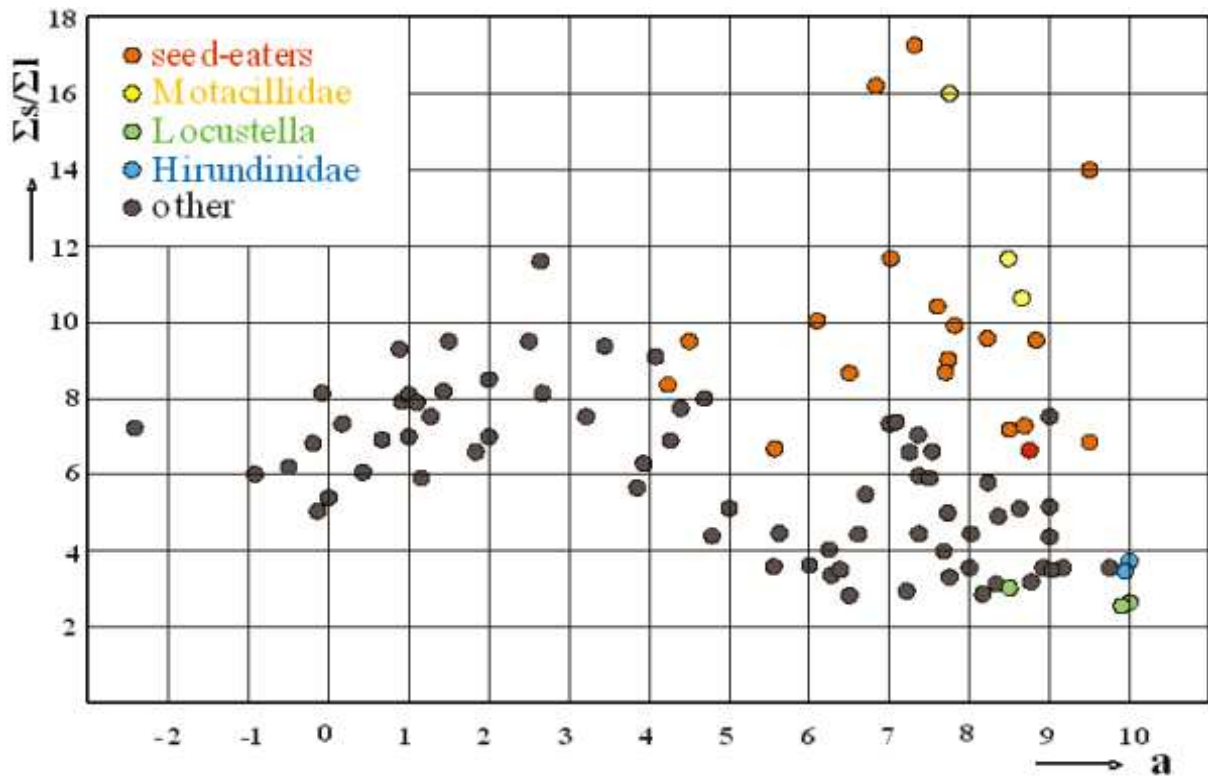
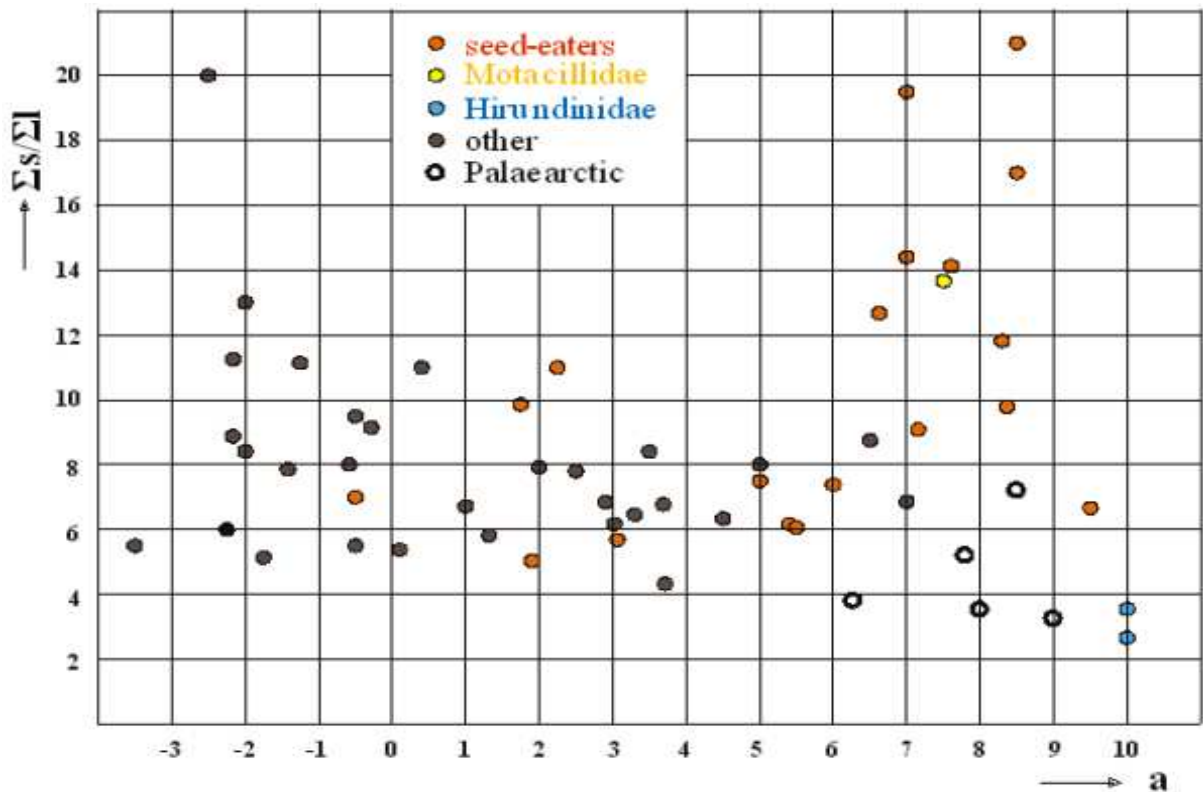


Fig. 5

Relation between index of total curtailment [C] and qualitative index of pointedness [a] in South African birds *Sphenoeacus afer* ( $a=-3.00$ ,  $C=29.00$ ) and *Crithagra flaviventris* ( $a=6.25$ ,  $C=38.00$ ) out of the diagram



To assess the “information content” of so calculated “index of curtailment” (**C**), its relations to others – first of all to pointedness (**a**) – must be checked; **fig. 4** shows the results concerning European birds: the variability in **C** is low among species with rounded wings and becomes very high with increase of **a**, but this simple general pattern is in fact the resultant of two separate components: the PFM-group makes a rather well-defined cluster in the right upper area of the diagram, while representatives of the TM extend over the entire scale of **a** but show definitely negative (albeit somewhat irregular) correlation between **a** and **C**; **fig. 5** reveal rather similar, even if much less clear relations among South African birds.

As **Figs. 2-5** demonstrate, the degree of curtailment in the PFM-group markedly increases with increasing pointedness, the difference between PFM and TM becoming truly evident only at  $a \approx 4$ , and all European (like the majority of African) representatives of the former have at least moderately pointed wings. These facts immediately suggest that curtailment is really significant only as long as distal primaries are involved, and consequently more useful index may be obtained by replacement of **l** and **s** in the formula for **C** (“index of *total* curtailment”) by, respectively, **d** [sum of distances from apex of the wing to tips of four distalmost (2.-5.) primaries] and **p** [the same for the three proximal (6.-8.) elements of the wing-formula (**fig. 1** – right)]. The relation of the so obtained “index of *distal* curtailment” [ $Q = \Sigma p / \Sigma d$ ] to **a** is presented on **figs. 6** and **7**, and indeed now the distinctiveness of the “curtailed” group [above  $a \approx 4$ : **Q** by definition does not apply to rounded wings] became striking. Unexpected was only the shape of the borderline: neither horizontal (**Q** below some value in TM and above it in PFM), nor sloping regularly, but angular: increasing to  $a \approx 7$  (where, at that, both groups display strikingly enhanced variability in terms of **Q**!) but then suddenly turning down! Anyway, all the European representatives of the PFM-group are placed above the “demarcation line” and all TM **Passeriformes** (the apparent exception –  $a=9.00$ ;  $Q=7.53$  – being *non-Passeriform Streptopelia turtur*) below it; even in South Africa the pattern is disturbed only by *Acridotheres tristis* (**Sturnidae** –  $a=6.50$ ;  $Q=8.75$ ) and – at  $a=4.50$ ;  $Q=4.50$  – by *Cinnyris mariquensis* (**Nectariniidae**).

### Interpretation

Explanation of the role of the index of curtailment [as **C** seems much less informative than **Q**, my further considerations will refer only to the latter] in terms of aerodynamical factors is obviously far beyond my competence, but even the determination of biological coordinates has proven difficult and remains indecisive. Although some variability in **Q** among species or genera of the TM-group is also evident (*e.g.* the index assumes much higher values in *Turdus* than in *Luscinia* or *Acrocephalus*), only in two groups – granivores (**Ploceidae+Fringillidae s.l.**) and **Motacillidae** – the wing-tip curtailment has developed to the degree making it a truly distinctive peculiarity. I have not been able to find any common morphological or biological feature which could provide an explanation applicable to both groups, so probably the factors contributing to the similarity of their wings were in each case different; two (one Palaearctic and one S-African) species of *Motacilla* and two of *Anthus* do not allow for meaningful deliberations on the **Motacillidae**, so I can only suggest some vague ideas as regards granivores.

One of the conceivable explanations may be a compromise between two different and partly contradictory selective demands. Many granivore species form large (sometimes – especially on savannahs – enormous) flocks to fly over large distances in search of food; this was probably the original habitat (savannah) and ancestral behaviour of the group, the main factor of their evolutionary divergence. Persistent, energetically efficient flight seems to demand pointed (long distal primaries) wings, but excessive elongation (**L**) and narrowness may impair the ability to perform instantly coordinated manoeuvres in dense, quickly moving

Fig. 6

Relation between index of distal curtailment [Q] and qualitative index of pointedness [a] in C-European birds

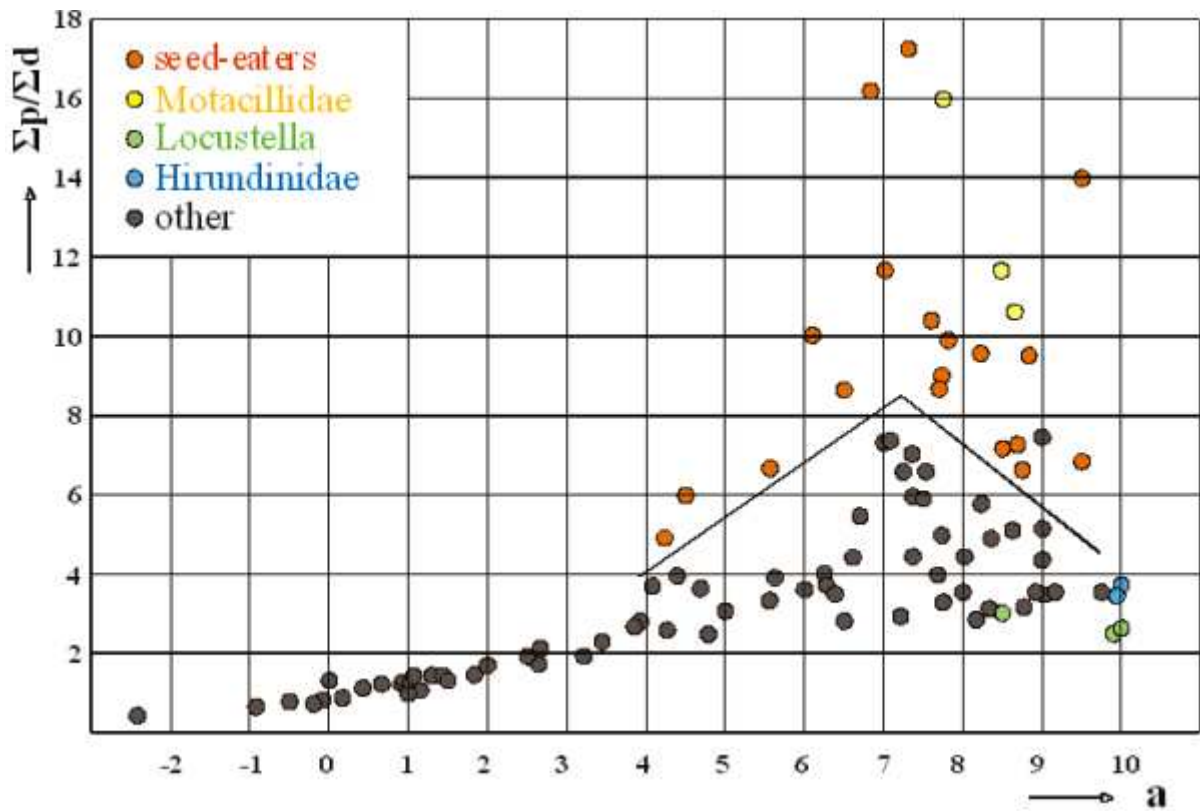
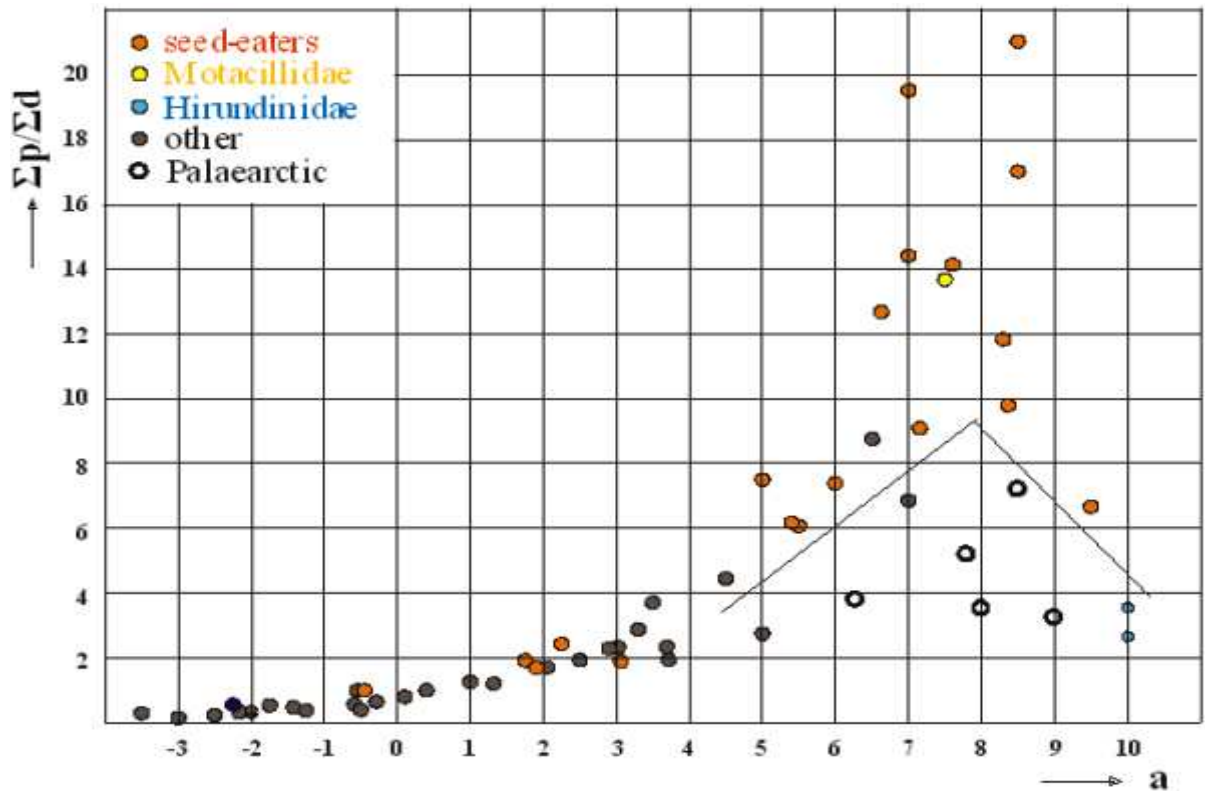


Fig. 7

Relation between index of distal curtailment [Q] and qualitative index of pointedness [a] in South African birds *Crithagra flaviventris* (a=6.25, C=38.00) out of the diagram

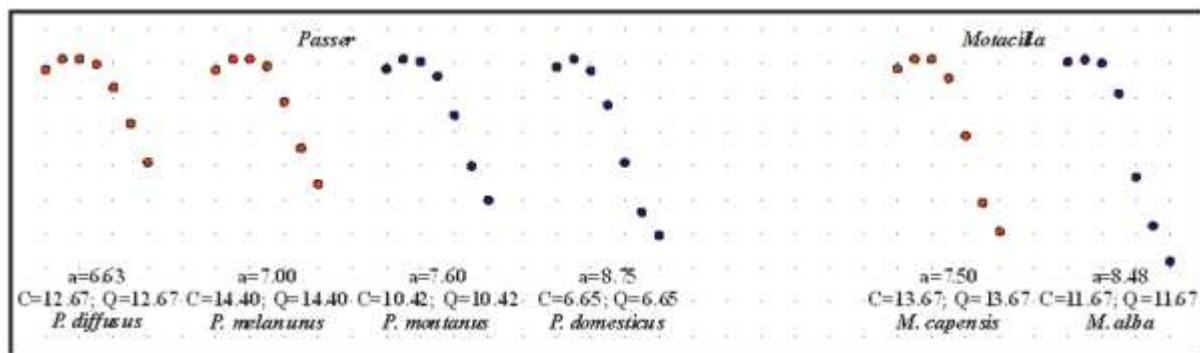


flocks; optimal compromise may be just “curtailed” wing: pointed but moderately long and relatively wide also in apical part.

If this conception is true, *i.e.* if wing-tip curtailment is the ancestral adaptation of granivores to feed on seeds and live in savannahs, then it should perhaps be maximally developed in Africa and partly compromised in (especially northern) Palaearctis where extensive grass-plains have been replaced by forests, swamps and (further north) tundra, and some fringillids adapted to live in forested habitats, not forming flocks and becoming increasingly insect- (*e.g.* *Fringilla*) or fruit- (*Pyrrhula*) rather than seed-eaters. Generalized diagrams (figs. 2-7) seem, indeed, congruent with such expectation, and the relevant characters of African and European representatives of the only granivore genus (*Passer*, Fig. 8) available to intercontinental comparisons does apparently also support it (*Motacilla* seems to conform to the same trend, what might suggest that it has nothing to do with either granivory or gregariousness, but here only two not closely related species have been compared, and anyway the factors involved in case of each group need not necessarily be the same).

Fig. 8

Comparison of wing-formulae of African (red markings) and European (black) species of *Passer* and *Motacilla*



The particular, somewhat contra-intuitive pattern of **Q** (consistent increase to  $a \approx 7$  and decrease thereafter) might perhaps have evolutionary explanation: in the course of transformation of rounded into pointed wing (*cf. e.g.* figs. 2-3) the selection-pressure, and consequently the rate of increase in length, is highest in case of 2. primary and decreases inwards, so – especially in the presence of additional selection promoting curtailment – 2. and 3. primaries rather quickly, at the stage of moderate pointedness, “catch up” and become near-equal with 4. and 5; here those species for whom the curtailed shape is optimal “stop” the evolution of pointedness (evtl. further increasing **Q** but with already “fixed” **a** – likely explanation of the observed enhanced variability at  $a \approx 7$ ), and only if the advantages of pointedness prevail over those of (perhaps in the new environment less important) curtailment, the distalmost (2.-3.) primaries grow (relative to more proximal ones) further to produce higher values of **a** but decreasing **Q**.

Naturally, one of the immediately emerging questions is the impact of curtailment on seasonal migration (or the opposite). Fig. 9 (a modified version of fig. 23 in HOŁYŃSKI 2016) seems to suggest that, whereas in the majority of birds the distance of migration is positively correlated with wing pointedness, at least among granivores the relation between **a** and **D** is (even if but slightly) negative. As this exceptional trend is characteristic just of the group distinguishable by its high degree of curtailment, which generally increases with increasing **a** (at least up to  $a \approx 7$ ), we could attribute the negative correlation with **D** to the influence of **Q**. Indeed, as seen on fig. 10, the general tendency among granivores (“seed-eaters” on the

diagram) is, as expected, “higher degree of curtailment – shorter seasonal migration”. The only – but strongly confusing... – exceptions are two bunting “rarities” (in Central Europe): *Emberiza pusilla* and *E. rustica*, joining highest **Q** with greatest distance between the breeding and wintering grounds. This, however, may be a methodological artifact: “*The migratory routes were assessed ... as the distance between the assumed breeding and wintering range of the populations likely represented in my samples; in case of the former, it was usually ... represented by ca. mid-point of that part of the breeding area lying within the 90° sector (between 315° and 45° compass direction) north of the Polish seashore (where the majority of analysed measurements were taken), i.e. including Scandinavia, NW parts of the Baltic Countries, and northwesternmost fringes of European Russia*” (HOŁYŃSKI 2016), but both *Emberiza pusilla* and *E. rustica* are only recent immigrants in Europe from the (probably far) East, their “morpho-migrational” characteristics had been shaped by the (perhaps mainly eastern-) Siberian circumstances, with much shorter distances of seasonal movements. Moreover, also their expansion to the North, away from the wintering areas, was probably also a fairly recent (post-glacial) event.

Negative correlation between **Q** and **D** seems to be a reflection of the contradictory foundations – conflicting demands of energetical efficiency of flight on the one hand and manoeuvrability on the other – of the curtailment itself: what is advantageous in breeding (and/or wintering) grounds may be harmful on migration. However, conceivable is also an evolutionary explanation: perhaps those species having, in the expansion from their ancestral savannah areas, reached further northwards, found themselves in the increasingly different environment, and consequently experienced weaker or no selection pressure in favour of maintaining high degree of curtailment, being at the same time compelled to perform longer seasonal migrations.

Incidentally, perhaps somewhat similar in principle (although differing – in some aspects opposite – in details) factors might have led to the phenomenon recently described by HUBER & al. (2016) for quite different group of birds: “*migratory swallows (Hirundinidae) have less pointed wings than residents*” [unfortunately I have not seen the paper itself – I asked the corresponding author for a reprint/pdf but received no answer – so I do not know the material that conclusion had been based on, nor even what exactly does the term “*pointed*” in their interpretation mean]. For aerial hunters like swallows, individually chasing small insects on flight, manoeuvrability is evidently of critical importance, and this importance must drastically increase when and where the abundance of prey is low and/or the prey species and their behaviour less familiar. In the warm, tropical environment (the breeding ground of most sedentary swallows) to which the bird is optimally adapted and where reactions of native insects are well known and easily predictable, the selection pressure promoting the ability to exactly follow all the sudden turns of the pursued “game” seems less stringent: the missed fly or mosquito can be immediately substituted by another one. But during migration over less familiar and mostly inhospitable areas collection of sufficient food to supply the energetical demands may be challenging, so the requirement of successful capture of every hunted insect becomes imperative. If, as it seems, somewhat “truncated” wing-tips increase manoeuvrability, relative shortening of the 2. (or lengthening of 3.) primary in the (generally characteristic of swallows) extremely pointed wing – *i.e.* transformation of the formula  $2>3>4$  into  $2=3>4$ , making the wing somewhat “curtailed” and less pointed ( $a=10.0\rightarrow 9.5$ ) – may be advantageous.

All these divagations do not, naturally, pretend to the role of well substantiated hypotheses: I present them only as loose ideas to be, I hope, evaluated and further developed – or rejected and replaced with more fitting interpretations – by specialists of aerodynamics and/or field ornithologists better than me acquainted with details of bionomy and behaviour of the relevant groups of birds.



Fig. 9

Relation between qualitative index of pointedness (**a**) and distance of migration (**D**) in C-European birds  
● – Ploceidae & Fringillidae (*s. l.*); ● - Motacillidae; ● – other

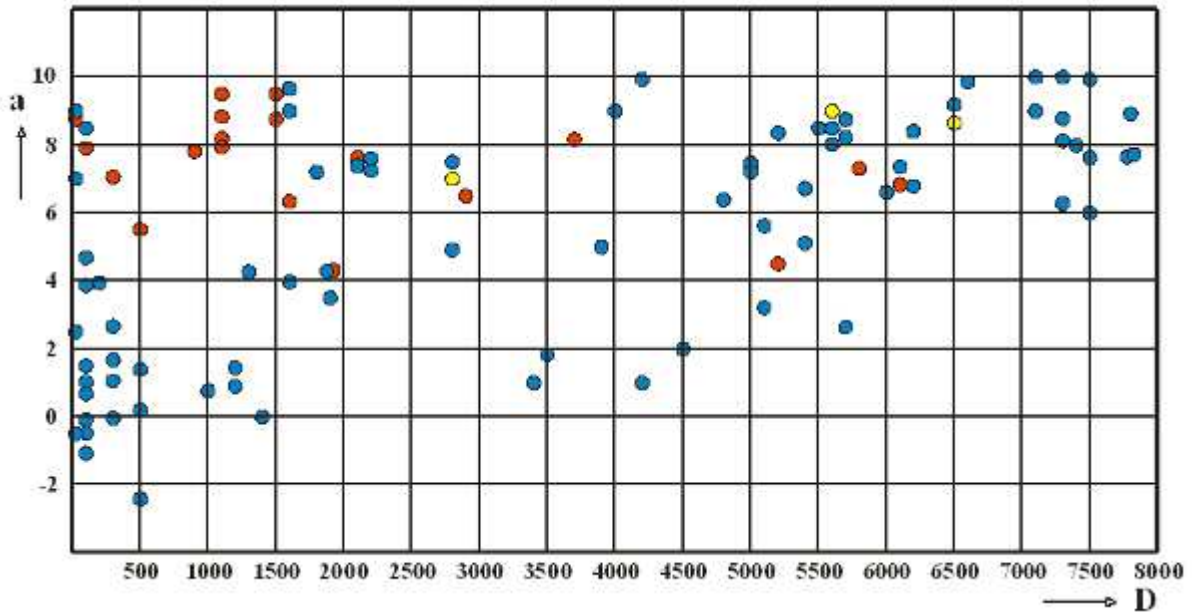
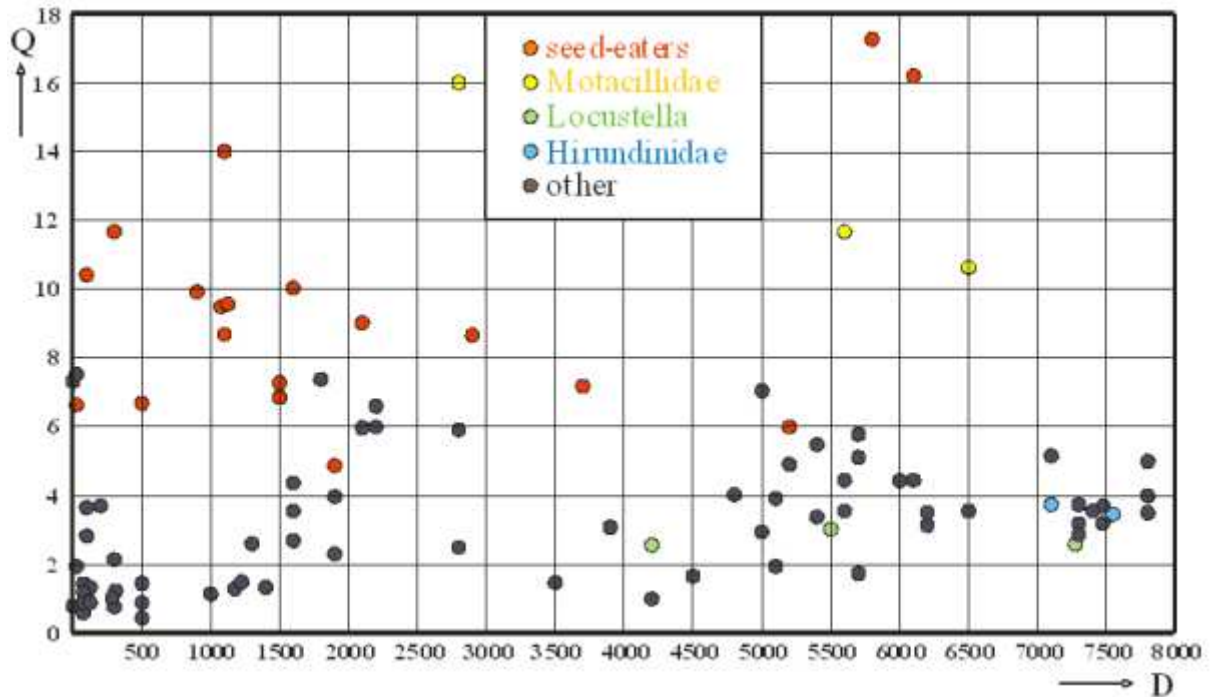


Fig. 10

Relation between index of distal curtailment (**Q**) and distance of migration (**D**) in C-European birds



### Acknowledgements

Like in my earlier papers on wing formulae, the bulk of the material for the main part of this study has been provided by Dr. Jarosław NOWAKOWSKI, and I am greatly indebted to him and the team of Baltic Operation for making it accessible to me!

### **Literature:**

- BUSSE P. 1967. Zastosowanie liczbowych współczynników kształtu skrzydła [Application of the numerical indexes of the wing-shape]. *Not. Orn.* **8**, 1: 1-8
- HOLEŃSKI R.B. 1965. Metody analizy zmienności formuły skrzydła ptaków [The methods of analysis of wing-formula variability]. *Not. Orn.* **6**, 2: 21-25
- HOLEŃSKI R.B. 2015. Alfabet formułkowy: co mówią a czego nie mówią wskaźniki kształtu skrzydła i ogona (uwagi przedwstępne) [Wing/tail formula ABC: what do shape-indices say and what they do not (pre-preliminary remarks)]. *Abstr. Konf. „Współczesne obrózkowanie ptaków: aspekt naukowy i etyczny” – Górkki Wsch. 28-29 XI 2015*
- HOLEŃSKI R.B. 2016. Avian wing/tail morphology: interspecific relations of various indices to each other and to the distance of seasonal migration – preliminary assessment. *Procrustomachia* **1**, 3: 24-52
- HUBER G.H., S.P. TURBEK, K.S. BOSTWICK, R.J. SAFRAN. 2016. Comparative analysis reveals migratory swallows (Hirundinidae) have less pointed wings than residents. *Biol. J. Linn. Soc.* [2016], 8: ???-???

### **Open access**

Edited, published and distributed by:  
Informal *Uncensored Scientists Group*  
c/o Roman B. HOŁYŃSKI  
PL-05822 Milanówek, ul. Graniczna 35, skr. poczt. 65, POLAND  
e-mail: [rhoynski@o2.pl](mailto:rhoynski@o2.pl)