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Avian wing/tail morphology: interspecific relations of various indices to each other and to the distance of seasonal migration – preliminary assessment

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: rholynski@o2.pl

Attempts to correlate morphological traits of animals with their flight performances have been undertaken "from time immemorial", concerning not only recent birds but also their ancestors (ZHOU *&* FARLOW 2001, WANG *& al.* 2011, CHAN *& al.* 2013, DYKE *& al.* 2013), other recent (NORBERG 1986) or fossil (TOKITA 2015) vertebrates, or even insects (YOUNG *& al.* 2009, JOHANSSON *& al.* 2013), and not only external features but also – as well for palaeontological material (OLSON *&* FEDUCCIA 1979) as for recent birds (KALMÁR 1935) – *e.g.* skeletal elements. In particular, as regards the role of flight apparatus of birds very much has already been said and written, and many indices of shape (KIPP 1959; HOŁYŃSKI 1965; BUSSE 1967, 1986; MLÍKOVSKÝ 1978; TIAINEN 1982; HEDENSTRÖM *&* PETTERSON 1986; ЛЕВИН *& al.* 1991; LOCKWOOD *& al.* 1998) or their substitutes like "absolute" length of particular primaries (BERTHOLD *&* FRIEDRICH 1979; JENNI *&* WINKLER 1989; PILASTRO *& al.* 1995); *contra* GOSLER *& al.* 1995] were proposed – some of them have never been applied in practice, some had been used by their inventors in original publications and then sank into (usually deserved) oblivion, but quite a large series survived and makes an essential element of the argumentation concerning the functional aspects of birds' flight. A medley of preferences is, however, strongly marked; various scientists, or even various groups ("schools") of scientists, apply different indices, while the justification of the particular choice consists usually in the belief that "*it is a matter of taste*" (HEDENSTRÖM 1989) or that this one is "generally" better and the other is worse – differences in "specialization", the need to find out what purpose is properly served by this and when the other would be preferable, in which situation this will be the adequate solution and in which we should rather apply the other, is being usually neglected; here I will try to present some of my preliminary ideas on these matters. I will address (with one exception) only those indices I am "personally" acquainted with (from the times when I myself ringed and measured birds in frames of the Baltic Operation and its offshoots: Dukla Pass 1964-1965 and Akció Hungaria between 1973 and 1988), focusing on their interrelations and trying to assess the (mutual?) dependence between each of them and one aspect of the species' life history: the distance of seasonal migration; the most interesting directions of later studies will certainly be the ***departures*** from the general rules, but to ponder on departures we must previously clarify the rules. Another restriction is the fact that my remarks concern only **Passeriformes** and those groups traditionally considered (even if "molecules" often disagree...) their relatives – woodpeckers, rollers, kingfishers, hoopoos, nightjars, swifts, cuckoos – *i.e.* relatively small birds of "flapping" flight: soaring vultures, storks or albatrosses make certainly a different story, whereas to what degree the "passerimorph" rules apply to rather (in this respect) monotonous (all, except lapwings, with pointed wings) limicolae, to much heavier gallinaceans, to falcons, ducks, rails *&c.*, is a very interesting question which, however, could become seriously analysable only when at least the relations within the here discussed "reference morphotype" will be known in reasonable detail. With my negligible knowledge of Reynolds numbers, vortex distributions *&c.* I restrict the discussion to actually observed relationships, referring to aerodynamical factors only as far as I (hopefully…) can understand the conclusions of the competent students (Гладков 1949; Шестакова 1971; Rayner 1985, 1988, 1995; Thomas 1993, 1995a-d; Thomas & Balmford 1995; Balmford *& al.* 1995a-c; Maybury & Rayner 2001; Maybury *& al.* 2001;; Matyjasiak & Jabłoński 2001; Matyjasiak *& al.* 2004) and interprete them in here relevant terms.

This study – aimed at ***preliminary*** estimation of ***interspecific*** relations – has been based on rather heterogeneous material, the bulk of which made by the biometric data from the Autumn 2014 season of the Baltic Operation, but including also those from Dukla Pass 1964-1965 and various Hungarian camps of between 1974 and 1988, as well as (when appropriate) South Africa 2014/2015. Each species has been characterized by mean values of available measurements and indices, without discrimination between ages, sexes, populations or anything else. The migratory routes were assessed from maps of distribution, 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 – unless some additional information suggested more restricted or otherwise different region (the "operational definitions" of wintering grounds have, naturally, been treated with similar flexibility) – represented by *ca.* mid-point of that part of the breeding area lying within the 90^0 sector (between 315^0 and 45^0 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.

The interrelations between various indices [for the sake of simplicity, I use this term indiscriminately as well for "artificial" constructs (W_{exp}, W, a, e, l) as for relative ratios (T, E, L, IP, IT, K) and direct measurements (w, t, 1p, 1t, k, h)] have been presented below in form of correlation coefficients and scatter-diagrams, and tentatively all, even very slight and poorly supported, "taken at their face value" – of course it is not as if I would wish to convince anybody (or believe myself) that *e.g.* r≈-0,04 is a proof or even serious evidence of negative correlation between body weight and E, but the main aim of the present paper (and my accidental, mostly intuitive comments) is not to directly prove or disprove anything but to provide ***material*** for reflexions, to show what kind of relationships ***can*** be ***expected***, to ***provoke*** detailed studies based on more comprehensive material: for that purpose even the least substantiated ***suggestion*** may prove a fruitful source of ideas.

Symbols (written in red) used for the analysed indices (see also explanations in the text):

D – estimated distance of (one way) seasonal migration
h – weight of body
w – wing length (as actually measured)
$\mathbf{W_{exp}}$ – wing length expected from the relation to body weight
W – "theoretical" wing length, according to the formula $W \approx (30\sqrt[3]{h}+0.11h)[0.006(K-29)+1]$
t – tail length
a – qualitative index of pointedness
e – quantitative index of pointedness
l – index of elongation (Busse's index)
k – length of wing-tip (Kipp's index)
1p – relative length of remicle (as measured from tip of greater coverts)
1t – distance from tip of remicle to wing tip
[symbols in minuscules (t, e, 1p *&c.*) denote averages of actual measurements; those in capital letters (T, E, IP *&c.*– except D, $\mathbf{W_{exp}}$, and W) – normalized as % of w]

Interrelations among indices

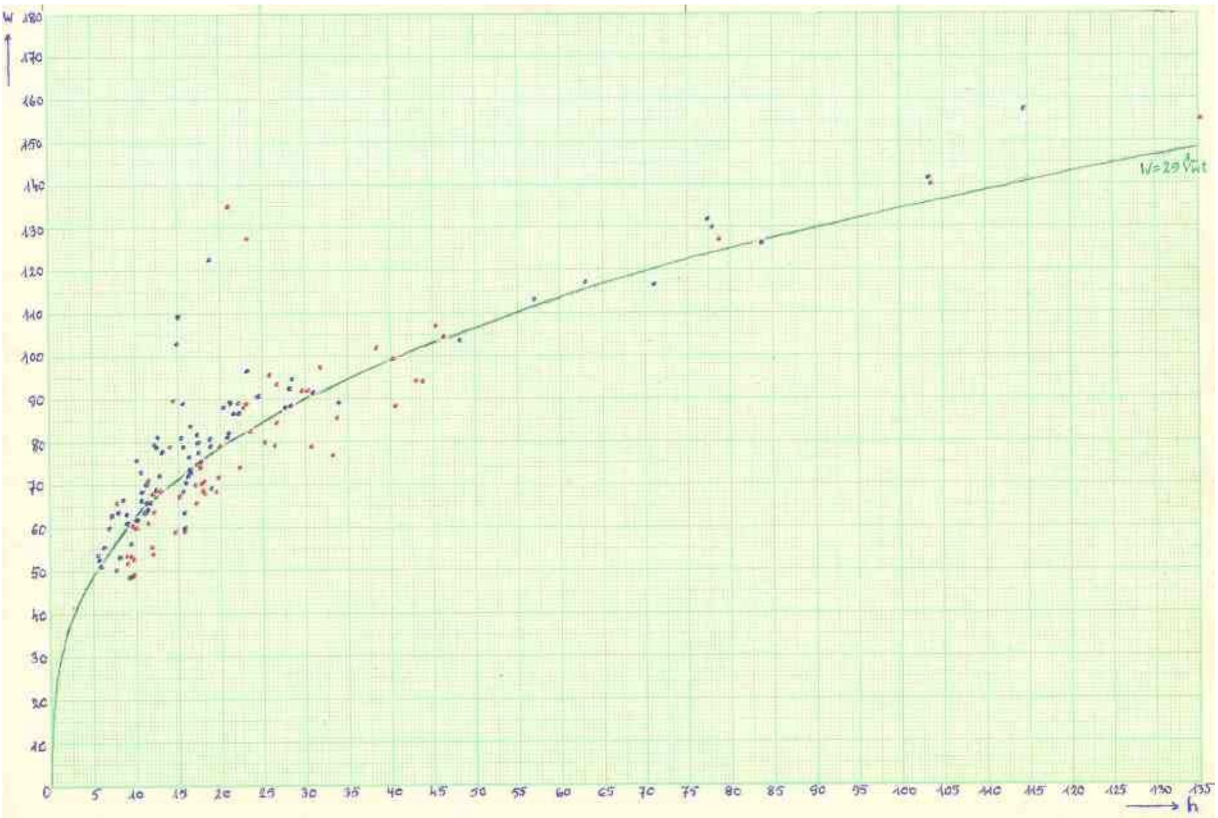
1. Wing length. The most popular measurement, used both as a gauge of the size of bird and as an index serviceable in migrational comparisons. Being conditioned by two rather not intercorrelated factors raises the evident problem: to interpret the length of wing from the viewpoint of one of them the elimination of the other's influence is necessary, and to be able to perform such correction we must not only ***be aware of*** the double dependence, but also ***know the details*** of its expression.

To evaluate the dependence of wing length on the size of the bird we must previously select the measure for that size. In this role often just the wing length appears, but naturally we cannot use it so. Also all the other proposed linear dimensions – tarsus or sternum length, overall length of body – are (for various reasons) unapplicable, the only appropriate "candidate" seems to be the weight of the bird. On the diagram (fig.1) of correlation between weight of body (h) and length of wing (w) the points related to particular bird species lie along a curve: the dependence is not linear but exponential, what naturally had to be expected in view of the fact that weight of the bird body is a function of its volume, and consequently must vary with the cube of linear dimensions. And indeed, the relationship seems best matched by the formula $W_{exp}\approx 29\sqrt[3]{h}$.

Fig. 1

Relation between wing length (w) and weight of body (h) – overall

● – Europe; ● – S-Africa



Strictly speaking, the formula derived above refers to the concatenated data for European and South African birds together; closer examination of Fig. 1 shows that red circles (Africa) tend to concentrate below the $W_{exp}=29\sqrt[3]{h}$ line, while the majority of blue marks (Europe) lie above it, suggesting some difference between the two groups. And indeed, for European species alone (Fig. 2) the line of best fit seems to agree rather with the formula

$W_{exp} \approx 30\sqrt[3]{h}$ [indicated by red points on the diagram], whereas African species (fig. 3) show relatively somewhat shorter wings: $W_{exp} \approx 28\sqrt[3]{h}$.

Fig. 2

Relation between wing length (w) and weight of body (h) – European birds

[red points ● mark the $W_{exp} \approx 30\sqrt[3]{h}$ line]

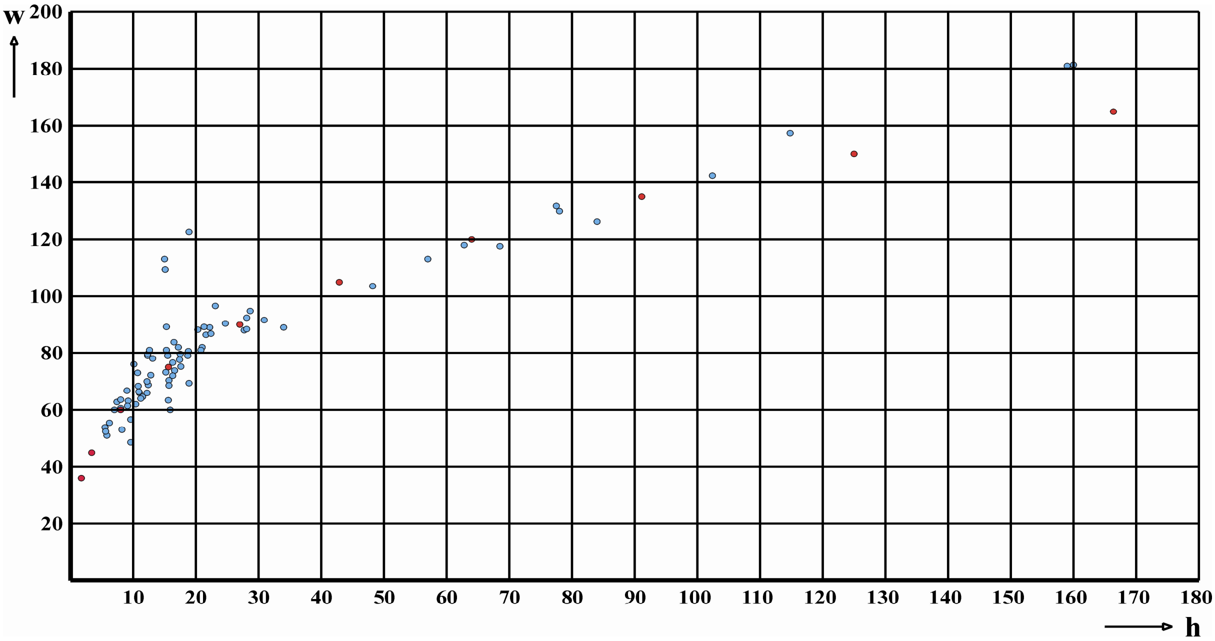
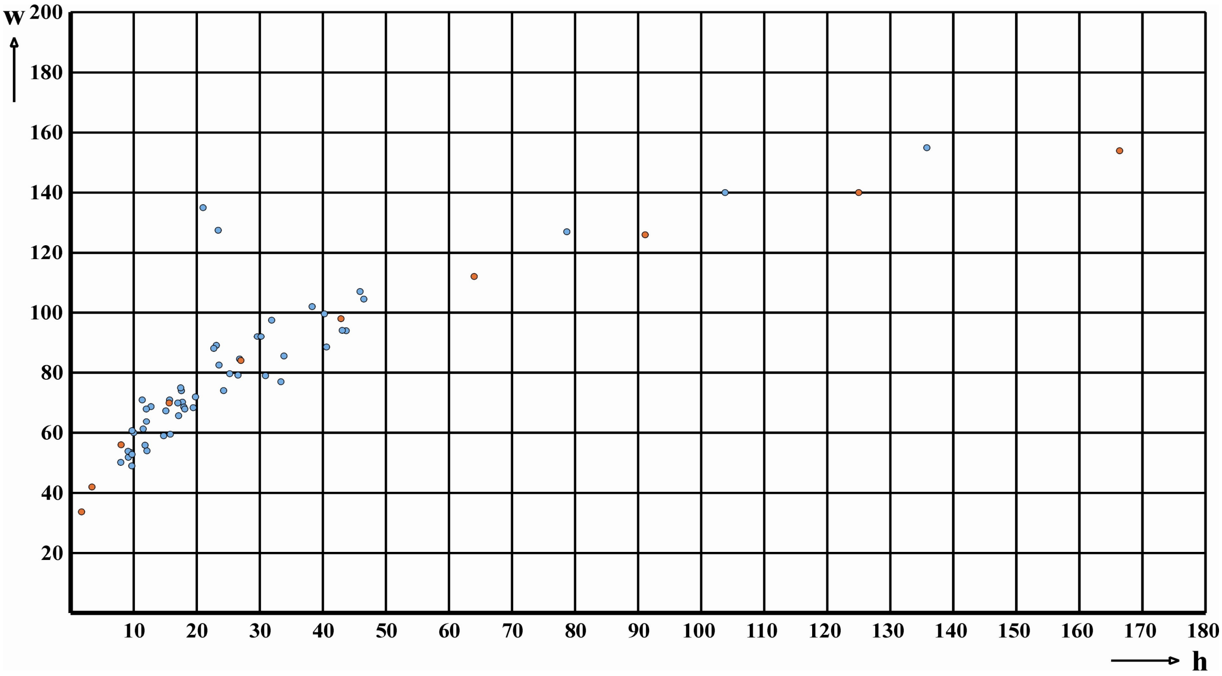


Fig. 3

Relation between wing length (w) and weight of body (h) – S-African birds

[red points ● mark the $W_{exp} \approx 28\sqrt[3]{h}$ line]

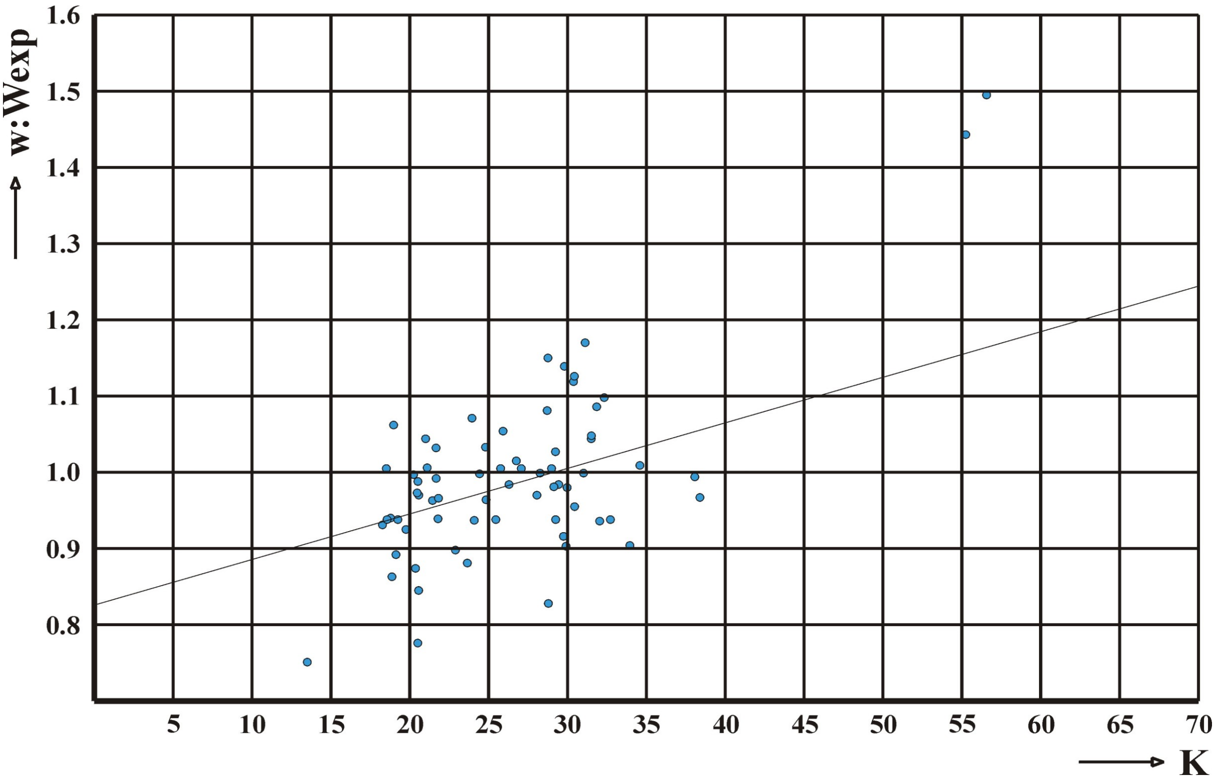


In both cases some allometric “deviation” can be ascertained: the formulas tend to underestimate the wing lengths of larger species; this (well known – RAYNER 1988) effect may be a manifestation of the need to maintain the near-optimal ratio of wing area to body weight with minimum deterioration of wing shape; inclusion of the allometric factor modifies the formula as $W_{exp} \approx 30\sqrt[3]{h}+0.11h$. Morover, the three included European and two African swallows do not comply to the predictions whatsoever: their wings (marks well above the others at $h \approx 15$-25) are by *ca.* 50% longer than expected.

My main aim is to evaluate the relations between wing/tail morphology and parameters of migration, but I have almost no reliable quantitative data on migration of African species, so further analysis of the factors influencing wing length are based on European birds only (and correlation coefficients, regression lines *&c*. are calculated – unless explicitly stated otherwise – with exclusion of swallows). As the diagrams clearly show, the correlation between actually measured and calculated length of wing ($r_{w:Wexp}=0.974$) is quite good but not perfect – on the one hand it follows from the very nature of biological objects [in the poet's, Stanisław BARAŃCZAK, aphoristic formulation: "*w świecie żyjątków nic prócz wyjątków*" (*in the living world* [there is] *nothing but exceptions*)]: biology is not mathematics, here not only every species but every individual and, indeed, the same individual in various phases of its life is different, behaves differently, differently reacts to the environmental stimuli; however, I cannot resist the temptation to check whether, beyond this "stochastic" variability and dependence on weight, regular relation of wing length to some other measurable morphological trait can be discernible? The known correlation with migration parameters suggests that such trait should be looked for among the indices of wing shape, and the obvious way to disclose the interrelation is to check if the extent and direction of the deviations from the line $W_{exp}=30\sqrt[3]{h}+0.11h$, *i.e.* of the differences between the expected (based on this formula) and true length of wing, varies in parallel with changes of the given index. As might be expected, that of wing pointedness has shown weak correlation (r=0.247), the index of elongation performs better (r=0.352), but – in full agreement with expectations – it is the length of wing-tip (Kipp's index, K – fig. 4) that proved most informative (r=0.396).

Fig. 4

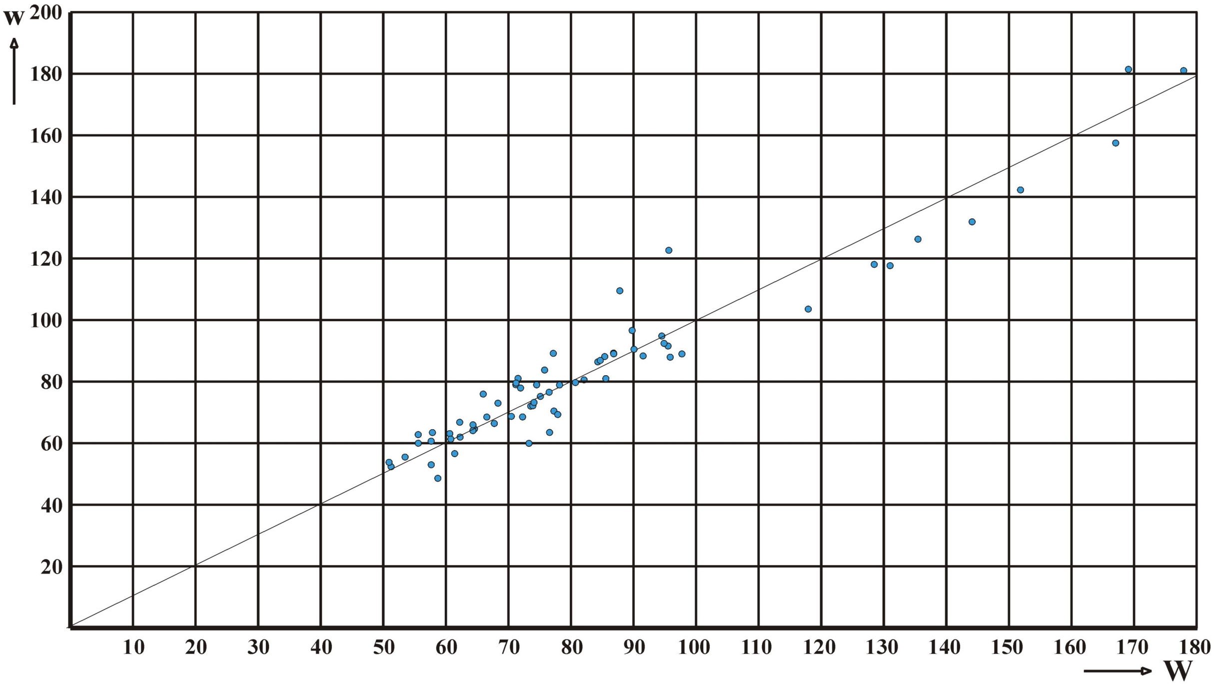
Departures from "expected" wing length (W_{exp}) as function of wing-tip length (K)



The line of regression fitted to this diagram (swallows disregarded) crosses the horizontal [$w:W_{exp}=1.00$, marking no deviation of empirical (w) from the calculated (W_{exp}) wing lengths] at $K\approx29$; from this point the proportion $w:W_{exp}$ decreases or increases by 0.006 for each unit of K. Now the accordingly modified formula for the "theoretical" length of wing assumes the form of $W\approx(30\sqrt[3]{h}+0.11h)[0.006(K-29)+1]$. The diagram of correlation between so calculated W and actually measured (w) lengths (fig. 5) shows a reasonably good fit ($r_{w:W}=0.963$ for all birds, 0.975 without swallows).

Fig. 5

Relation between empirical (actually measured – w) and "theoretical" (W) wing length



This is only a preliminary study based on somewhat accidental material: for many of the included species the measurements of but very few or even single specimen were available, weights have not been standardized for subcutaneous fat, larger birds (of wing-lengths above *ca*. 100 mm.) have been heavily underrepresented, *&c*. – the correlation would have certainly been still better if these shortcomings are corrected. But even cursory look at the Tab. 1 immediately shows that the most conspicuous departures from theoretical prediction are not randomly distributed: *e.g*. swallows and, to somewhat lesser degree, flycatchers have wings markedly longer than expected, while wren, dunnock, bearded tit, star and all European thrushes are definitely short-winged. The functional interpretation of these patterns would need more detailed considerations (out of the scope of the present study), but two main "targets" of selection pressure – weight of body (h) and length of wing-tip (K) seem evidently involved: *e.g*. for aerial hunters (flycatchers and – especially – swallows) manoeuvrability in open air is critical and relatively heavy body would obviously make swift turns difficult; on the other hand, inhabitants of dense reeds (*Panurus*) or bushes (*Troglodytes, Prunella*) may benefit from shortening of distal portion of wings, while massive body (like in case of – feeding often on the ground – *Sturnus* or *Turdus*) does not seem so disturbing (or even may – *e.g*. if resulting from development of more powerful musculature – prove advantageous).

Tab. 1

Ratio of “theoretical” (W) to really measured (w) wing length

Colours mark cases of distinct and slight underestimation *vs.* slight and distinct overestimation

Species	w	W	W:w	Species	w	W	W:w
H. rustica	122.65	95.64	0.7798	*P. major*	75,21	75,12	0,9989
R. riparia	109,50	87,81	0,8019	*P. palustris*	64,62	64,58	0,9994
M. striata	89,18	77,18	0,8655	*S. rubetra*	76,56	76,52	0,9996
P. sibilatrix	75,96	65,98	0,8685	*P. cristatus*	64,08	64,33	1,0039
F. albicollis	81,07	71,54	0,8824	*Parus montanus*	61,98	62,28	1,0049
C. familiaris	62,80	55,59	0,8852	*S. communis*	73,24	74,10	1,0117
F. hypoleuca	79,54	71,23	0,8955	*C. carduelis*	79,70	80,72	1,0127
C. flavirostris	79,00	71,19	0,9011	*S. curruca*	66,07	67,30	1,0187
P. ochruros	83,75	75,79	0,9050	*S. borin*	80,57	82,10	1,0190
A. caudatus	63,46	57,86	0,9118	*A. schoenobaenus*	66,42	67,75	1,0199
H. icterina	77,92	71,95	0,9234	*E. rubecula*	72,04	73,57	1,0214
P. bonellii	60,00	55,60	0,9266	*C. spinus*	72,15	73,91	1,0244
O. oenanthe	96,62	89,78	0,9293	*A. palustris*	68,71	70,47	1,0256
P. trochilus	66,79	62,22	0,9316	*L. collurio*	92,41	94,88	1,0267
G. glandarius	181,42	169,11	0,9322	*E. citrinella*	88,33	91,53	1,0362
C. flammea	73,00	68,34	0,9362	*P. pyrrhula*	91,56	95,52	1,0433
P. phoenicurus	78,97	74,52	0,9437	*S. torquata*	68,53	72,27	1,0546
R. regulus	53,79	50,93	0,9467	*C. erythrinus*	81,00	85,58	1,0565
P. collybita	60,66	57,66	0,9505	*T. viscivorus*	157,50	167,07	1,0608
C. brachydactyla	63,12	60,63	0,9606	*T. pilaris*	142,27	151,86	1,0674
P. inornatus	55,50	53,49	0,9638	*T. merula*	126,26	135,47	1,0730
M. alba	88,15	85,40	0,9688	*R. pendulinus*	56,63	61,42	1,0847
F. parva	68,50	66,55	0,9715	*P. fuscatus*	53,00	57,67	1,0880
F. montifringilla	89,28	86,82	0,9724	*T. iliacus*	118,06	128,47	1,0882
S. europaea	86,88	84,69	0,9749	*C. chloris*	87,94	95,86	1,0900
A. trivialis	89,03	86,83	0,9753	*S. vulgaris*	131,90	144,12	1,0926
P. caeruleus	65,97	64,34	0,9753	*L. luscinioides*	70,44	77,28	1,0970
F. coelebs	86,41	84,29	0,9754	*J. torquilla*	89,00	97,74	1,0982
R. ignicapillus	52,38	51,25	0,9784	*T. philomelos*	117,66	131,01	1,1135
N. caryocatactes	181,00	177,93	0,9831	*P. modularis*	69,32	77,89	1,1236
E. schoeniclus	78,93	78,18	0,9904	*C. coccothraustes*	103,56	117,93	1,1388
P. ater	61,35	60,80	0,9911	*L. naevia*	63,50	76,58	1,2060
L. luscinia	90,50	90,08	0,9954	*T. troglodytes*	48,60	58,73	1,2084
A. arundinaceus	94,83	94,52	0,9968	*P. biarmicus*	59,96	73,29	1,2223

2. Tail. Relative (in proportion to wing length) total (measured to the tip of the longest rectrix) length of tail (T) is weakly negatively correlated with the actual ($r_{T:w}$=-0.270 – fig. 6) or "theoretical" ($r_{T:W}$=-0.267) length of wing; however – as shown by more prominent relation to pointedness ($r_{T:E}$=-0.559 – fig. 7) and elongation ($r_{T:L}$=-0.538), as well as to the length of wing-tip ($r_{T:K}$=-0.500) and even to remicle ($r_{T:IP}$=-0.301) – the essential factor is shape, not size: the more pointed the wing, the proportionally shorter the tail.

Fig. 6

Relation between "normalized" (T) tail length and empirical (w) wing length

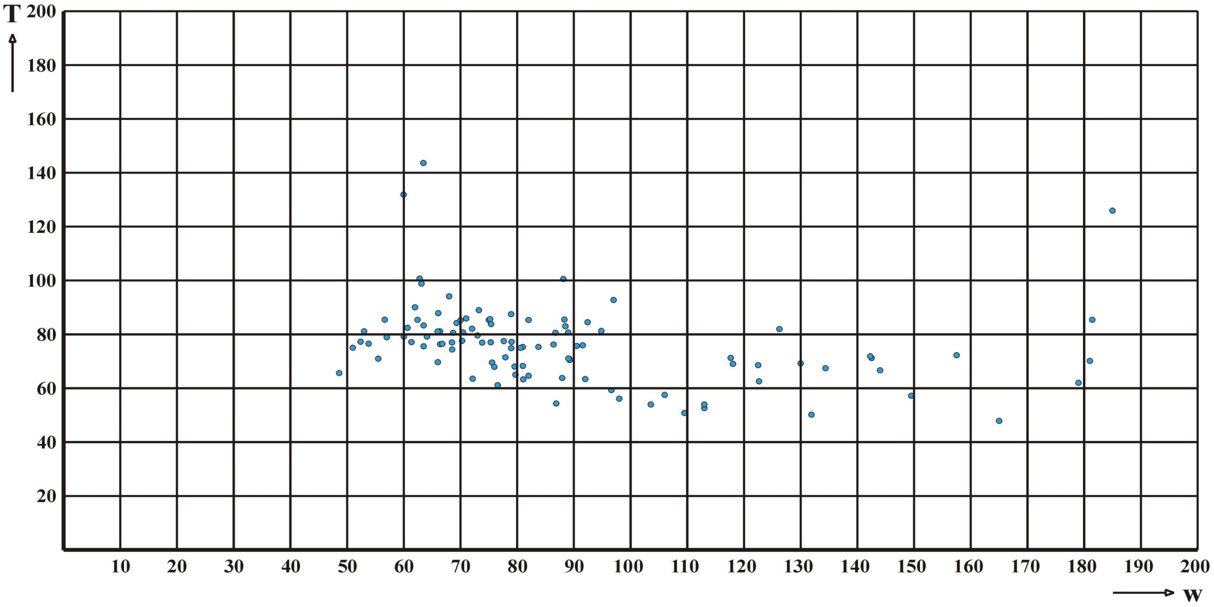
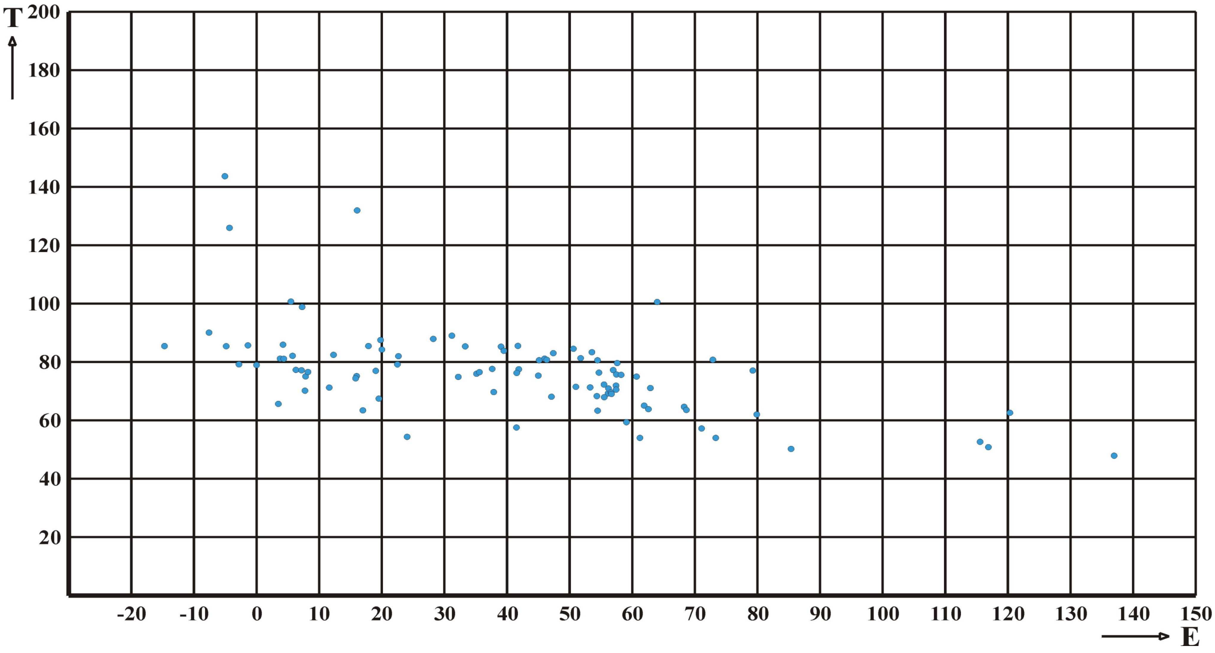


Fig. 7

Relation between tail length (T) and quantitative index of pointedness (E)



Since long I have intuitively supposed that closer relation to flight parameters (and so, consequently, to wing shape indices) would reveal the length of central (rather than each time the longest) pair of tail-feathers, and aerodynamical considerations (Thomas 1993; Rayner 1988; Maybury & Rayner 2001; Maybury *& al.* 2001) seem to (at east partly: for forked tails) justify such conjecture: additional (to that created by wings) lift is provided solely by the basal – to the line of maximum continuous span – part of the tail, while the portion extending behind that line increases only drag, and so hampers fast and persistent flight (contributing, however, to improved manoeuvrability, what for the rounded-winged birds is usually more important – but realized by elongation of ***central*** rectrices, less than the outer ones exposed to damage in the thick of bush or reeds).

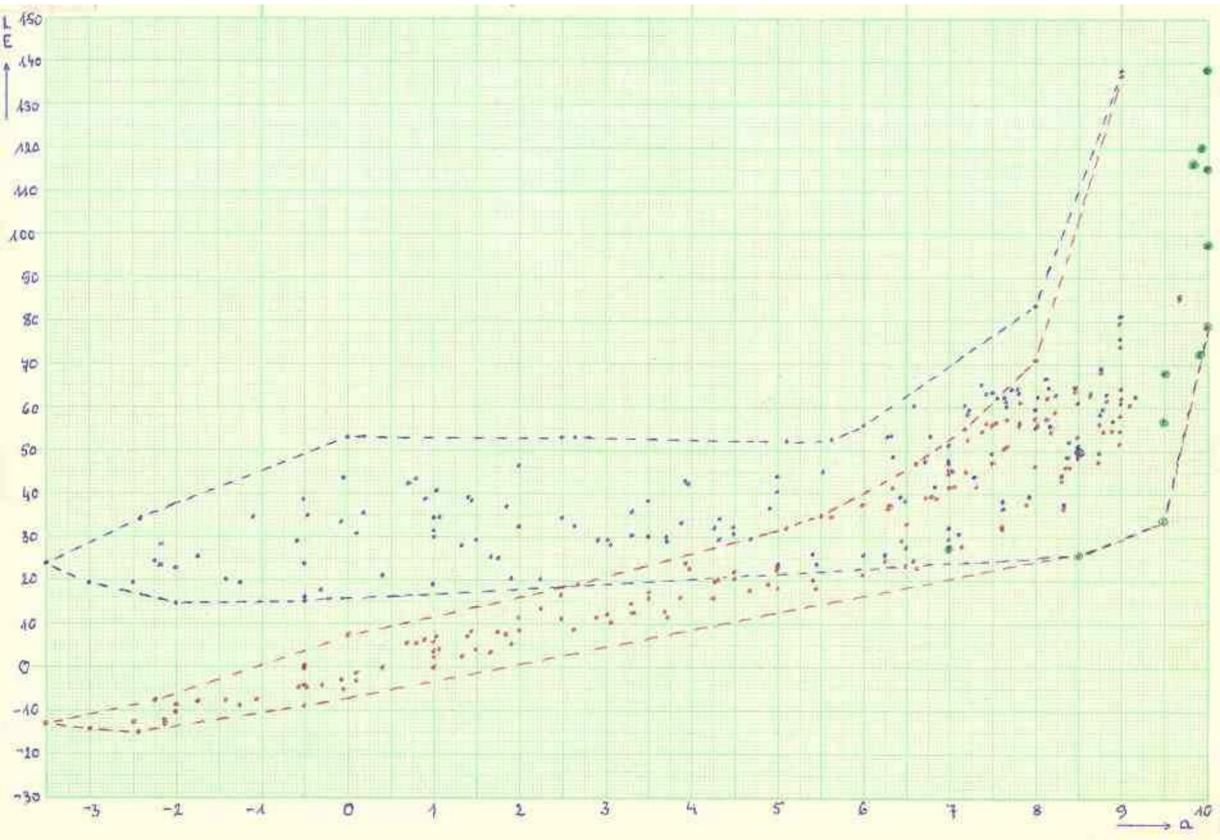
3. „Qualitative" index of wing-pointedness (a). So termed in the original publication (Hołyński 1965); later Busse (1967, 1986) renamed it (together with "qualitative" e and E) as "index of symmetry" what, however, does not seem to make much sense (symmetry has nothing to do here) and we should – not only by force of the "principle of priority"... – return to the original term. This (a) is the basic „reference-point" in analyses of the relations among indices, the only independent of either the size or general body proportions of the bird.

4. „Quantitative" index of wing-pointedness. A shortcoming of the „qualitative" index (a) is its relatively low precision, especially towards its upper limit – more exactly is the wing-pointedness represented by the "quantitative" version which, however, is in its basic form (e) dependent upon the size of the bird, and therefore in most cases, especially – but not only – in interspecific comparisons, becomes truly informative and directly interpretable only after normalization (E=100e:w). The correlation between a and E (fig. 8) is nearly linear and

Fig. 8

E and L as function of a

● – E; ● – L; ● – E=L

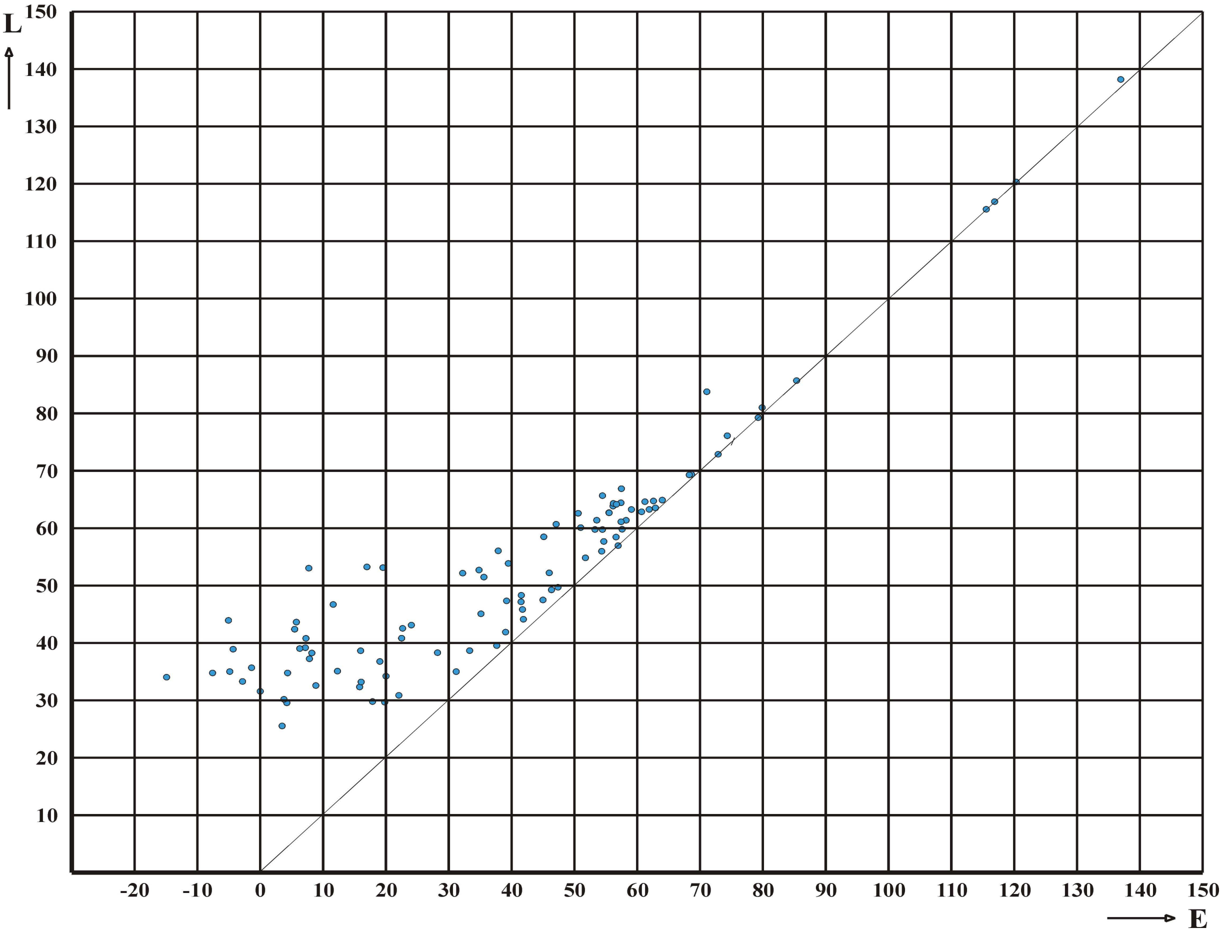


very strict at lower values, but for pointed wings assumes exponential character and scatter rapidly increases – the "wall effect": whereas there is no formal restriction for E, for a 10 makes the impassable limit. In most considerations relevant to bird migrations E is the most informative index.

5. Indices of elongation. Like in case of pointedness (and of course for the same reasons) in (especially interspecific) comparisons usually much more appropriate is the relative ("normalized") index L (=100l:w) than the, overwhelmed by the size of bird, "basic" l. Transfer of the term "index of pointedness" from e and E to l and L is a misconception also from the latter's perspective: as seen from fig. 8, with pointedness they have little in common, remaining practically unchanged (L≈30-40) from extremely rounded to rather pointed wings, and only above a≈6, pushed" (fig. 9) by increasing E (L „by definition" cannot be lower than E), begins also to grow (becoming simultaneously almost or quite identical) with it. In fact, L is the measure of elongation of the distal portion of wing: based on somewhat different principle (and in a sense more exact) equivalent of KIPP's index (K). Not inexpectably, L is somewhat better ($r_{w:L}$≈0,467) correlated with length of wing than E ($r_{w:E}$≈0,325).

Fig. 9

L as function of E



6. KIPP's indices. As expected from the above, in European birds (fig. 10) both absolute (k) and relative (K) length of wing-tip is strictly and linearly (K≈0.4L+6) correlated with L; the correlation with E is almost as strict but clearly non-linear ("concave": K≈0,017$E^{1.6}$+20). Oddly enough, in the case of African species (fig. 11) these relations look

Fig. 10

K as function of E (•) and L (•) – European birds

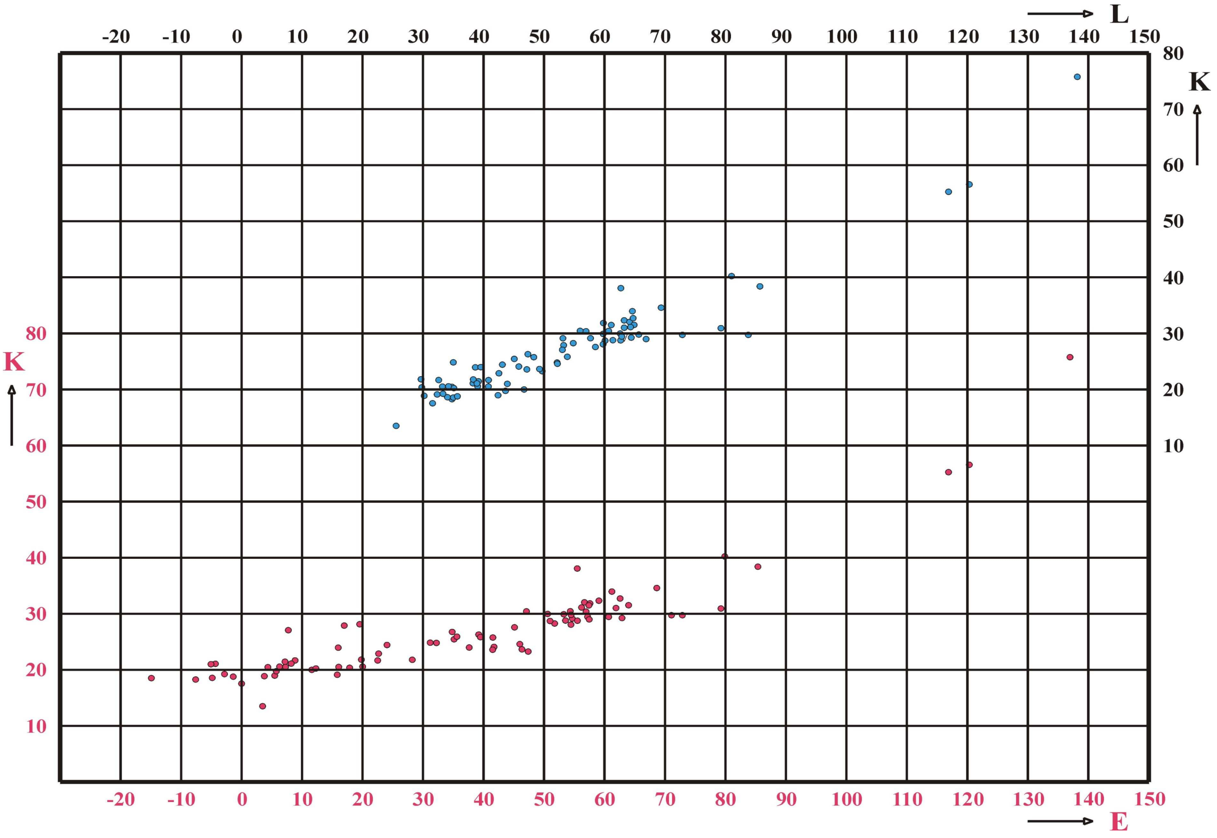
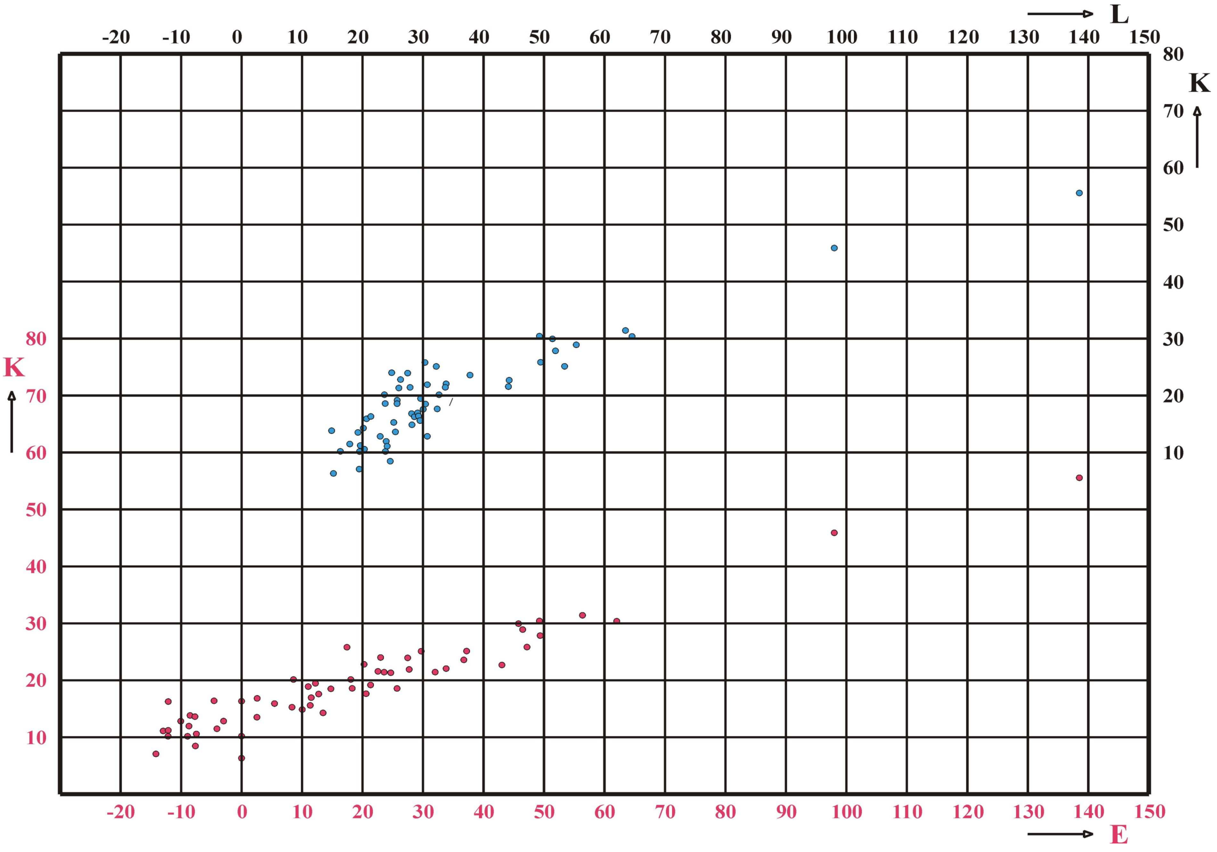


Fig. 11

K as function of E (•) and L (•) – S-African birds



somewhat different: rather strict and linear ($K \approx 0.3E+14$) between K i E, but much looser and slightly “convex” [$K \approx (17.5\sqrt[3]{L})-35$] between K i L – the interpretation of this disparity remains unclear to me!

7. First primary („remicle”). The relation between the length (more exactly: the distance between its tip and the tip of primary coverts) of first primary (1p for „basic” version, IP for „normalized”) and wing pointedness may seem almost shockingly illogical: as the outermost one it „should” be positively correlated with pointedness and elongation of wing, whereas in fact the interrelation is markedly ***negative***: the correlation is quite close (r = -0.764) in case of E (fig. 12), still somewhat better (-0,819) with a, looser but also undeniably negative (-0,552) with L. The apparent contradiction has been resolved by STEGMANN’s hypothesis: during the evolution from pointed to more rounded wing (fig. 13) the strongest shortening selection pressure is, indeed, exerted on the outermost primary; however, when an already markedly rounded wing evolves „back” into pointed (fig. 14), the aerodynamically most efficient strategy is elongation of – still fully functional – primary 2., while the 1., short and in fast straightforward flight practically useless, generating only disturbances, undergoes further reduction.

Fig. 12

IP as function of E

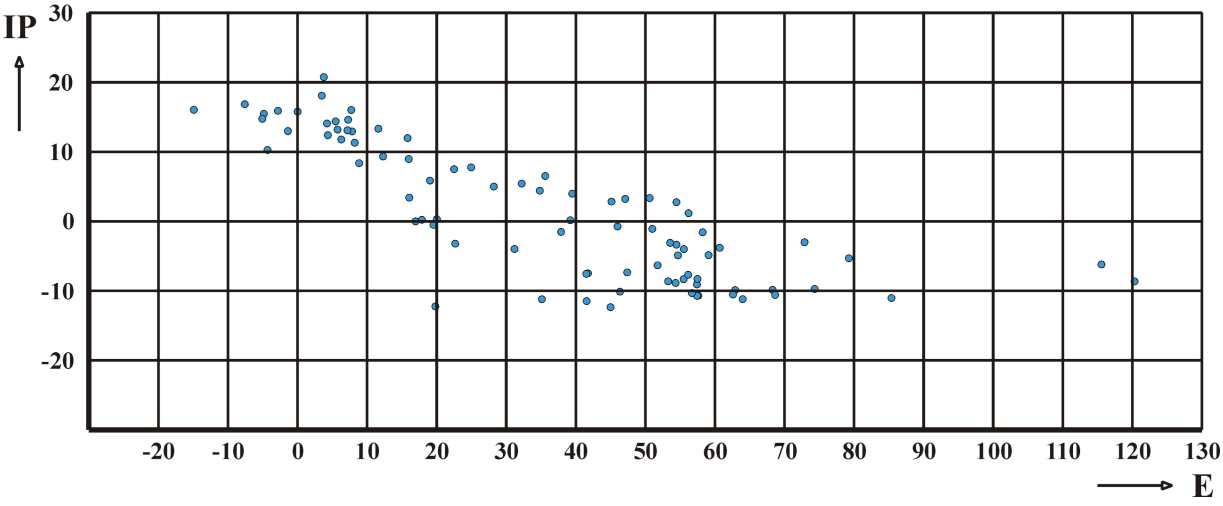


Fig. 13

Evolution from pointed to rounded wing

[from STEGMANN (1965)]

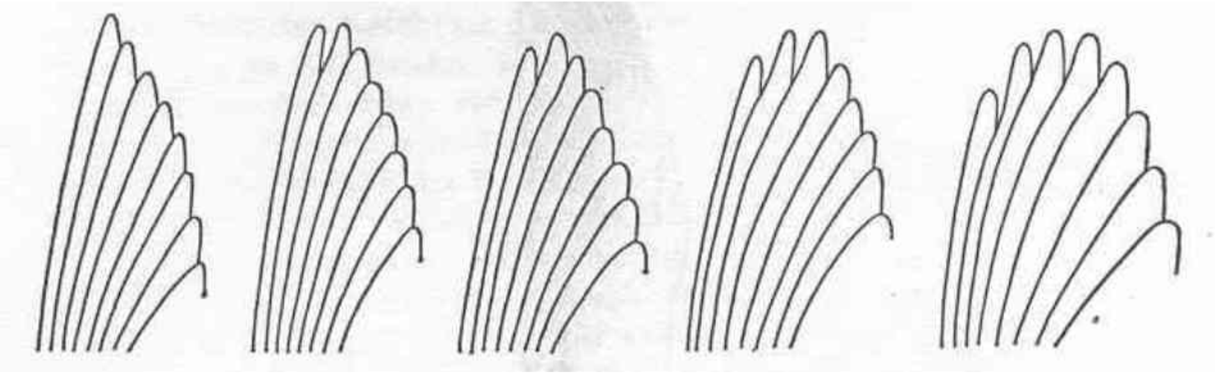
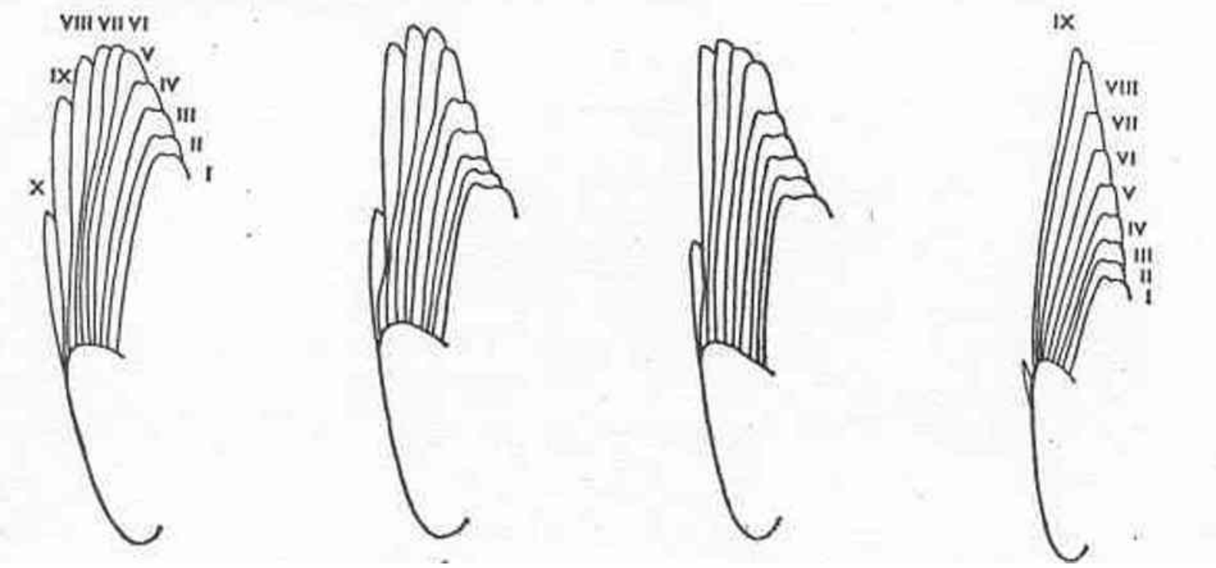


Fig. 14

Evolution from rounded to pointed wing in **Meropidae**

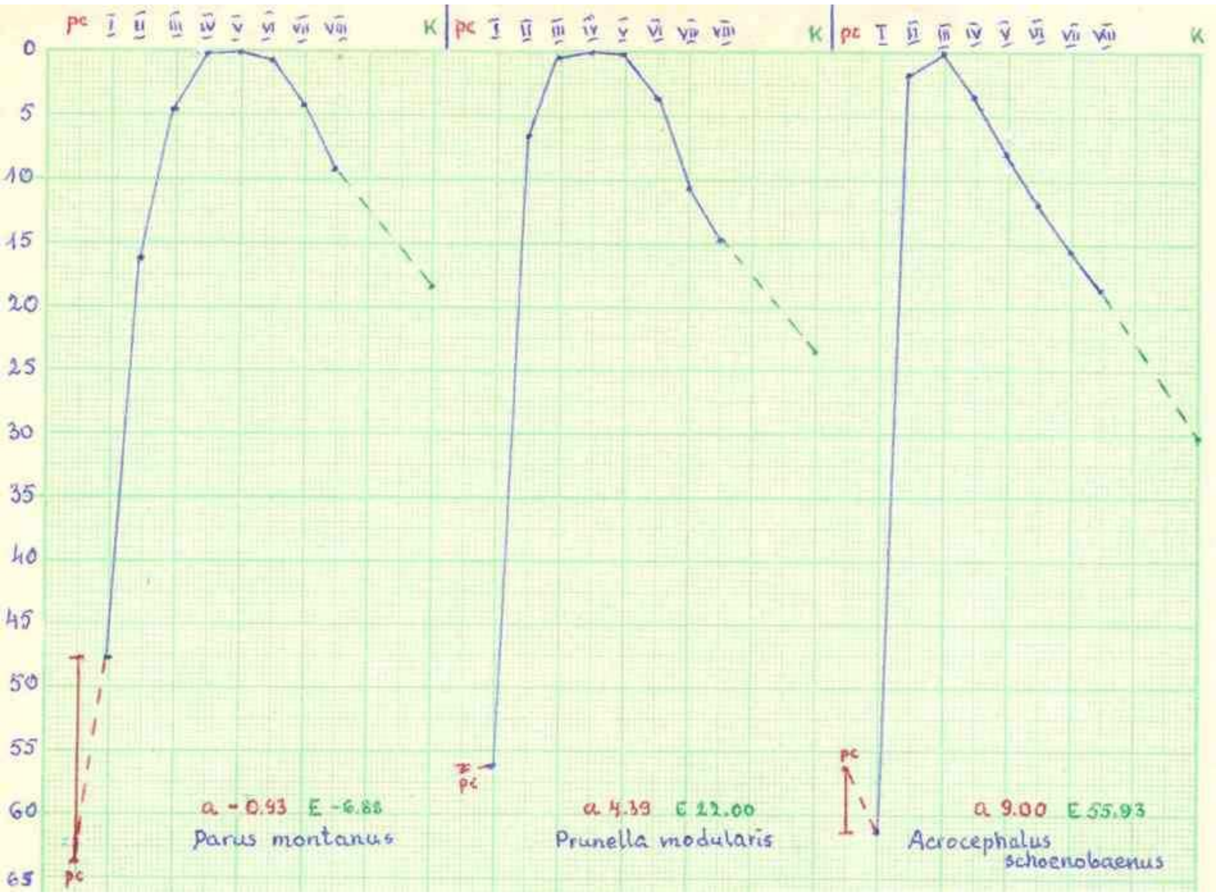
[after STEGMANN (1965)]



Recently Baltic Operation introduced a new measurement: the distance from the tip of 1. primary to the apex of ***wing*** [1t in empirical, IT (fig, 15) in normalized version] rather than

Fig. 15

Extended (showing IT) formulae in rounded, intermediate and pointed wing



to great coverts; initially I shrugged my shoulders „well, this is also possible, but what for?” – and yet I was apparently wrong with my skepticism: in the light of STEGMANN’s hypothesis it (evtl. in somewhat modified version, *e.g.* as the distance between 1. and 2. primary) may prove the most serviceable measure in evolutionary considerations.

Whereas K, expectably, shows marked positive relation to the length of wing (fig. 16), distinct [in European birds: in case of African species scatter is so great that even for normalized IP=100(1p/W) no significant trend is discernible] negative [very slight (r = -0.050) “overall”, but astonishingly pronounced (r = -0.695) after removal of the disturbing effect of few apparently aberrant species (**Corvidae**, *Oriolus* and *Upupa*)] correlation of ***non-*** normalized (traditionally measured: 1p) length of remicle (fig. 17) is intriguing: the latter is, indeed, influenced by pointedness, but the body size should, one might expect, overbalance.

Fig. 16

K as function of wing length (w)

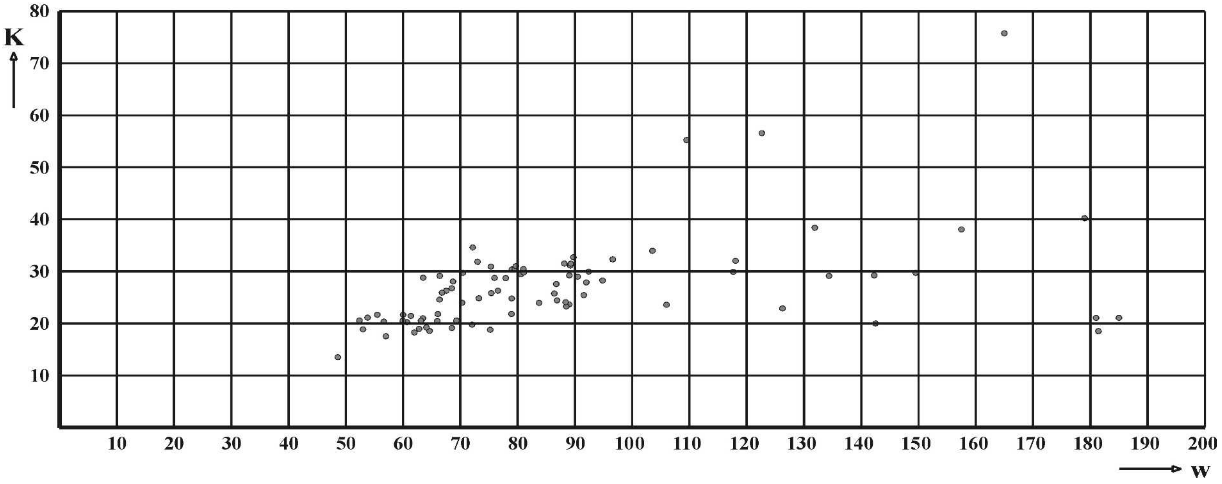
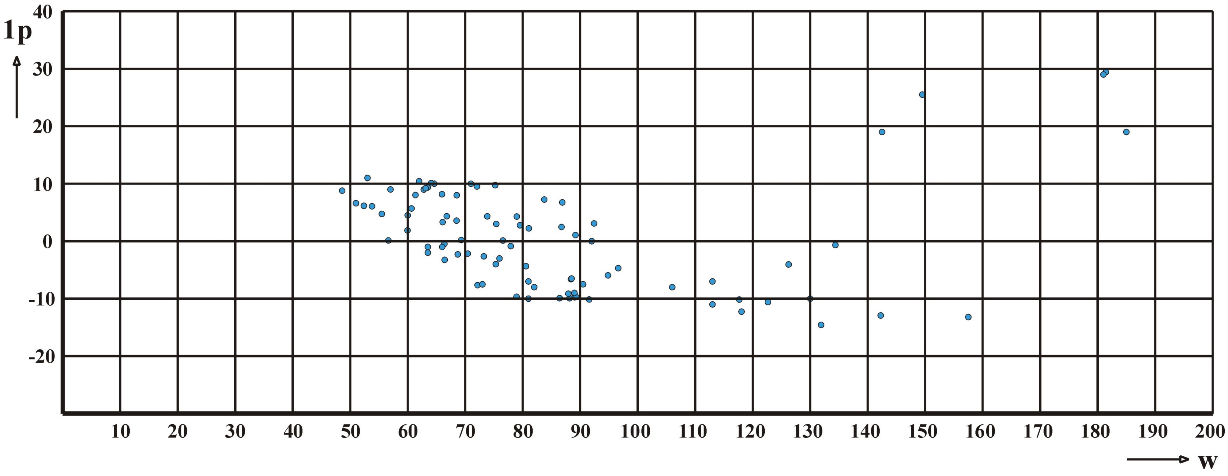


Fig. 17

1p as function of wing length (w)



It would be interesting to analyze the reasons making hoopoe, pirol, magpie, jay, nutcracker (and probably also their relatives) to so sharply diverge from the general trend – perhaps it is the effect of the aerodynamical requirements of "undulating" flight, prevalently replacing in their size category the "bounding" type dominant among smaller **Passeriformes** (RAYNER 1985).

To sum up all the above, Tab. 2. presents the coefficients of correlation between various indices.

Tab. 2

Coefficients of correlation between indices

Positive values marked 🟩green, negatives 🟦blue; related to distance of migration (D) written in red; those in right upper half of the table (above grey rectangles) calculated with exclusion of swallows

	w	w:Wexp	W	T	a	E	L	IP	IT*	K	h	D
w		0.0904	0.9750	-0.2457	0.0841	0.2881	0.4648	-0.1714	0.0059	0.4552	0.9569	-0.1127
w:Wexp	0.2354		-0.0857	-0.1460	0.2025	0.2475	0,3518	-0.1172	0.0656	0.3960	-0.0939	0.3756
W	0.9632	-0.0226		-0.2651	0.1600	0.2788	0.3844	-0.3391	0.0663	0.4409	0.9550	-0.1150
T	-0.2697	-0.3158	-0.2667		-0.4224	-0.5167	-0.4978	0.2823	-0.1078	-0.4705	-0.1954	-0.1046
a	0.1164	0.3260	0.1671	-0.4541		0.9612	0.6774	-0.8157	0.7112	0.6173	-0.0318	0.4706
E	0.3254	0.5603	0.2659	-0.5587	0.8943		0.8995	-0.7948	0.6732	0.8576	0.0935	0.4310
L	0.4669	0.7036	0.3227	-0.5382	0.6716	0.9204		-0.5877	0.4117	0.9270	0.2478	0.3662
IP	-0.0742	-0.1850	-0.3428	0.3012	-0.8190	-0.7642	-0.5521		-0.9074	-0.7138	-0.1457	-0.2192
IT	0.0059	0.0656	0.0663	-0.1078	0.7112	0.6732	0.4117	-0.9074		0.5667	-0.1265	0.1918
K	0.4556	0.6962	0.3524	-0.5001	0.6233	0.8845	0.9464	-0.6527	0.5667		0.2445	0.3165
h	0.9141	-0.1087	0.9499	-0.1659	-0.0477	0.0418	0.1312	-0.1364	-0.1265	0.1406		-0.1991
D	-0.0705	0.4553	-0.0972	-0.1578	0.5008	0.4873	0.4358	-0.2441	0.1918	0.3787	-0.2085	

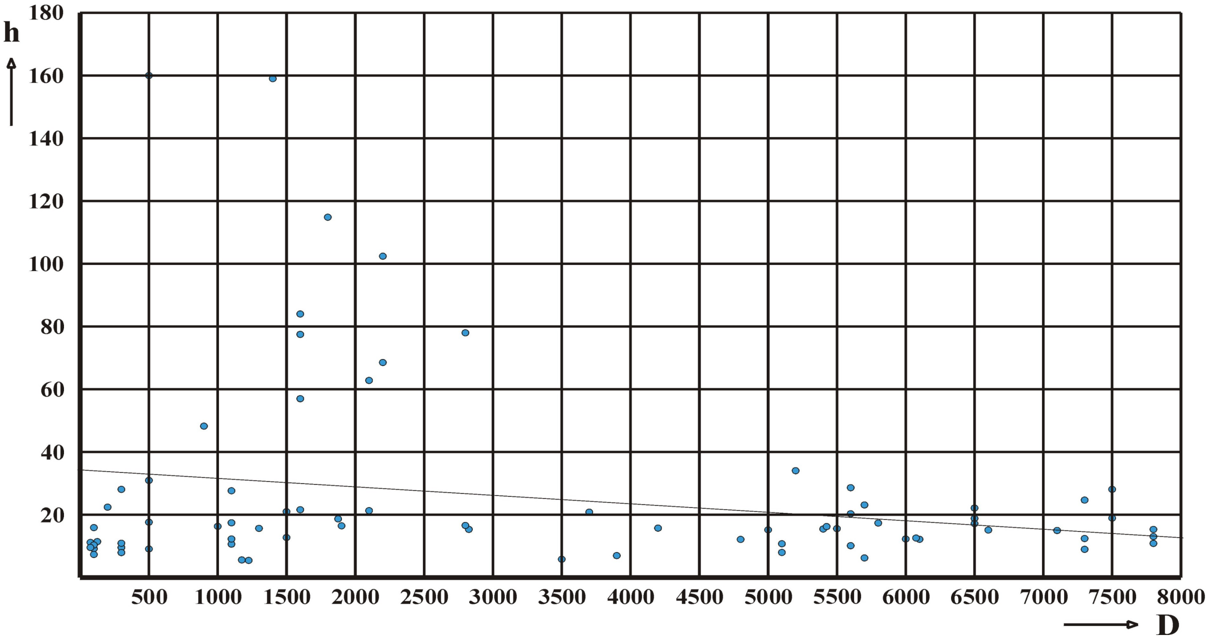
* Identical values of IT with and without swallows result from lack of data: the distance between tips of first (remicle) and longest primary has not been measured for any swallow in the material currently available to me.

Relations to the distance of seasonal migration

As the diagram (fig. 18) shows, weight appears as slightly but distinctly (r = -0.209)

Fig. 18

Relation between body weight (h) and distance of seasonal migration (D)

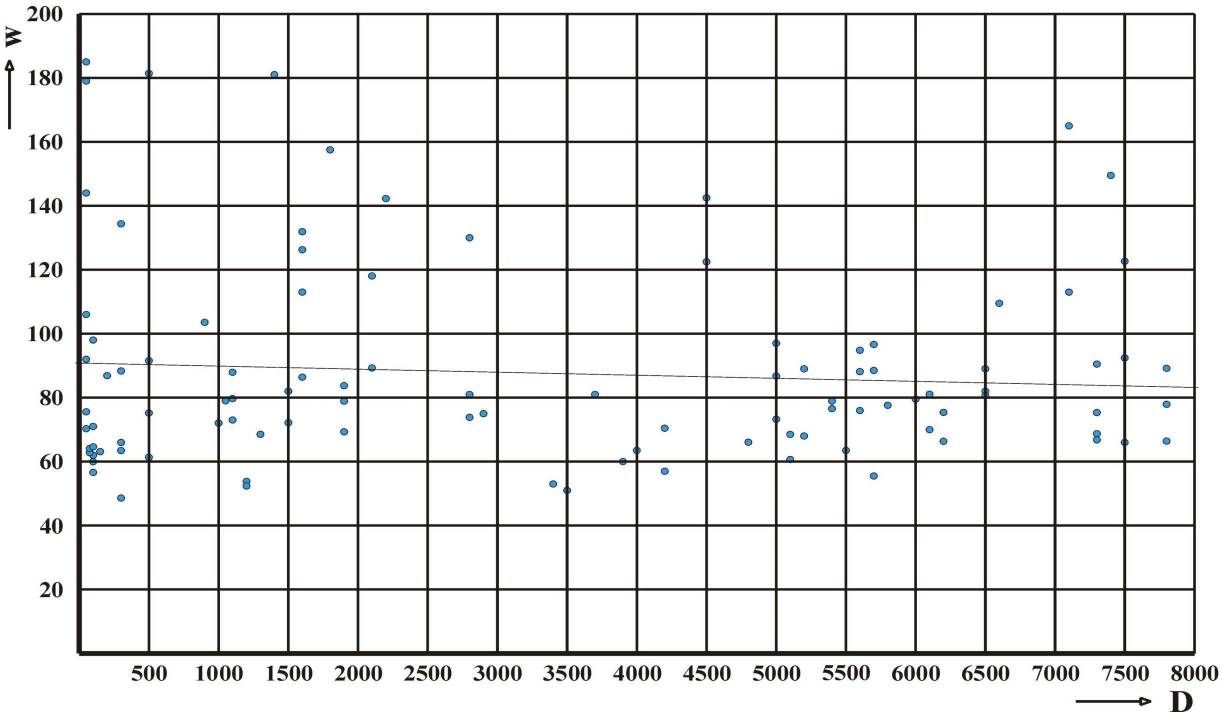


negatively correlated with migration distance; in fact, small birds show practically no correlation at all, but all those above 45g. winter less than 3000 km. from the breeding grounds. This, at least in part, is an artifact of taxon sampling: several long-distance migrants of larger size (*e.g. Oriolus*, *Coracias*, *Upupa*, *Cuculus*, *Caprimulgus*) have not been included because of lack of data; however, with the sole exception of *Oriolus*, all of them represent non-passeriform groups, and it would be interesting to ask ***why*** none (with the only apparent exceptions of the above-mentioned *Oriolus* and *ca*. 60 g. *Lanius minor*) of the larger mid-northern European passeriforms – *Turdus*, *Sturnus*, **Corvidae** – is a true long-distance migrant: does their larger body enable them to better tolerate winter temperatures? does their more generalized food preferences make easier to survive close to breeding area? would they be exposed to stronger competition from tropical (not necessarily passeriform) groups? is crossing Sahara more dangerous to them due to increased susceptibility to dehydration (HAAS & BECK 1979)? had their evolutionary history (earlier colonization of northern Palaearctis?) offered them more time to accommodate to the local conditions? or are they still too small to soar but already too close to upper size-limits enabling energetically efficient long-distance flapping flight?

Length of wing (w), as expected from its dependence upon size of body, shows slightly negative (fig. 19) relation to the migration distance, but the correlation is so slight (r = -0.071) that for practical purposes may be considered as zero; minimally better correlated (r = -0.097) seems “theoretical” wing length (W), but even this “improvement’ is only apparent, based on the same artifact as in the case of weight: missing data for larger long-distance migrants (somewhat higher – similar to those for weight: r = -0.174 – value for Wexp is a simple effect of its having been calculated entirely from h). Only after elimination of the noise introduced by body-weight the relation to migratory distance may be expected to become “visible”; indeed, it is made so with replacement of w or W by the proportion w:Wexp (fig. 20): even though the correlation coefficient (r = 0.455) is somewhat inflated by the evidently

Fig. 19

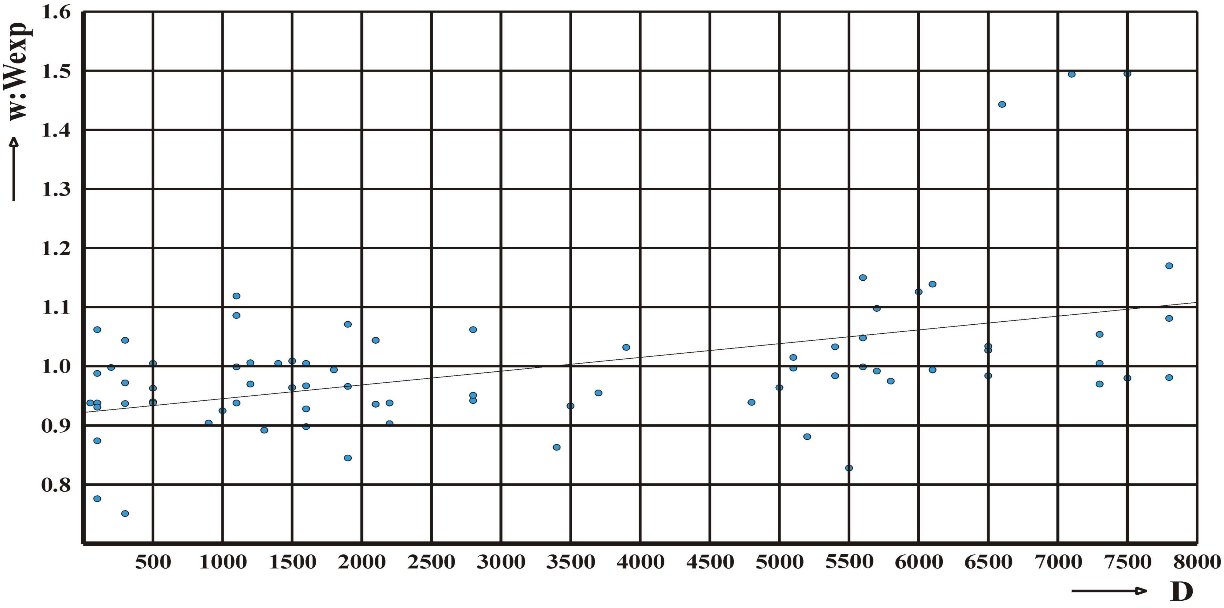
Relation between wing length (w) and distance of seasonal migration (D)



aberrant swallows (three uppermost points on the right), it remains moderately high (0.376) also without **Hirundinidae** [theoretically, still somewhat better predictor of migration distance should be the ratio W:Wexp; I have not used it here because the potential improvement is anyway very slight, hardly ever expectable to exceed the lowest limit of statistical significance – so *e.g.* in my material it is marginally "confirmed" ($r \approx 0.380$) only after exclusion of swallows: in case of all species included the correlation with migration distance appears even ***worse*** (0.444) than for w:Wexp – while dependence upon K makes it unapplicable to those species (in my material *ca.* 20%) for which KIPP's index has not been measured].

Fig. 20

Relation between the ratio of w to Wexp and distance of seasonal migration (D) – my data

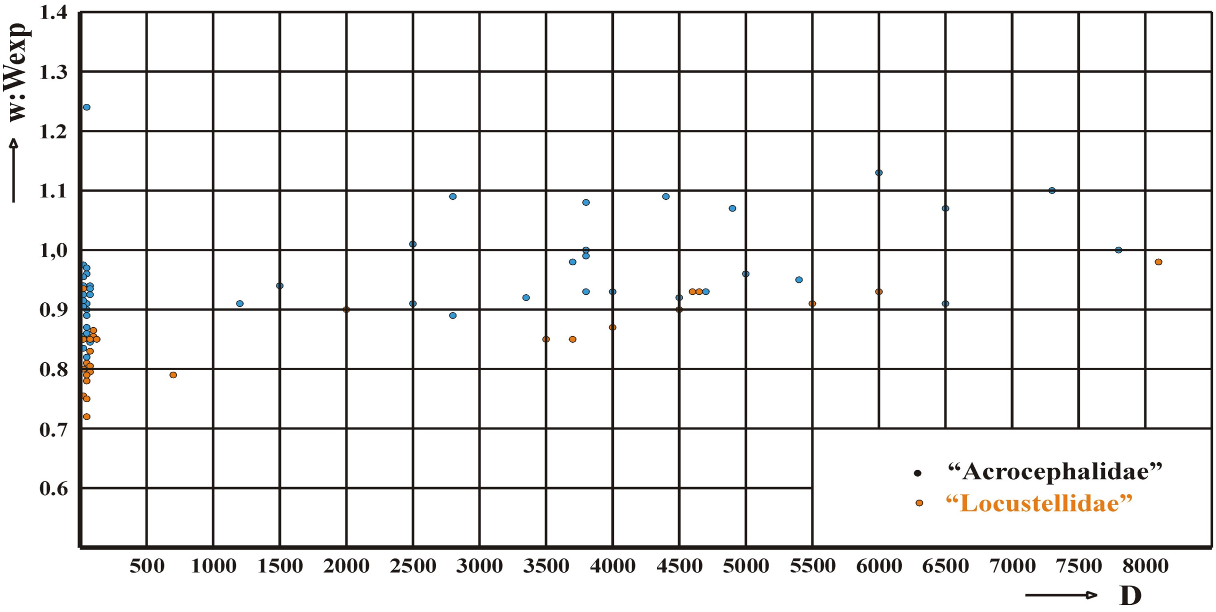


Recently NOWAKOWSKI *& al.* (2014) published a paper on the relations between wing length and migration distance in what they (aparently after cladistic interpretation of some recent molecular phylogenetic reconstruction) term "**Acrocephalidae**" and "**Locustellidae**"; different taxon sampling [*e.g.* the groups studied by NOWAKOWSKI *& al.* (2014) contain much larger proportion of non-migrants, and these are mainly tropical/subtropical species which generally tend to have somewhat shorter wings than their palaearctic counterparts, while among relatively short-distance migrants (sedentary or near-sedentary birds are very few) in my analyses well represented are gregarious, open area granivores of typically high values of w:Wexp], and applied statistical elaboration make our results not strictly comparable, but anyway they do not seem incongruent. Judging from their Fig. 1, the scatter of wing lengths in relation to migration distances, as calculated by them, looks greater than in my data for **Passeriformes** *& al.* presented on figs. 19 and 20, what would seem rather astonishing; however, having recalculated (fig. 21) their basic data (weight and wing-length) according to formula $Wexp=w/29\sqrt[3]{h}$ [intermediate between those derived herein for European and South African birds; having (in most species included in their study) no data for K I cannot calculate "theoretical" W] the scatter apparently decreased and the correlation coefficients – as expected: for two closely related taxa of birds they should naturally be higher than those for the heterogeneous sample of much more inclusive and morphologically, ecologically *&c.* highly variable group – reached much higher values ($r = 0.734$ for "**Locustellidae**", 0.459 for "**Acrocephalidae**", and 0.499 for both together); also the slopes (assessed by the Authors as

Fig. 21

Relation between the ratio of w to Wexp and distance of seasonal migration (D)

[recalculated from NOWAKOWSKI *& al.* (2014)]

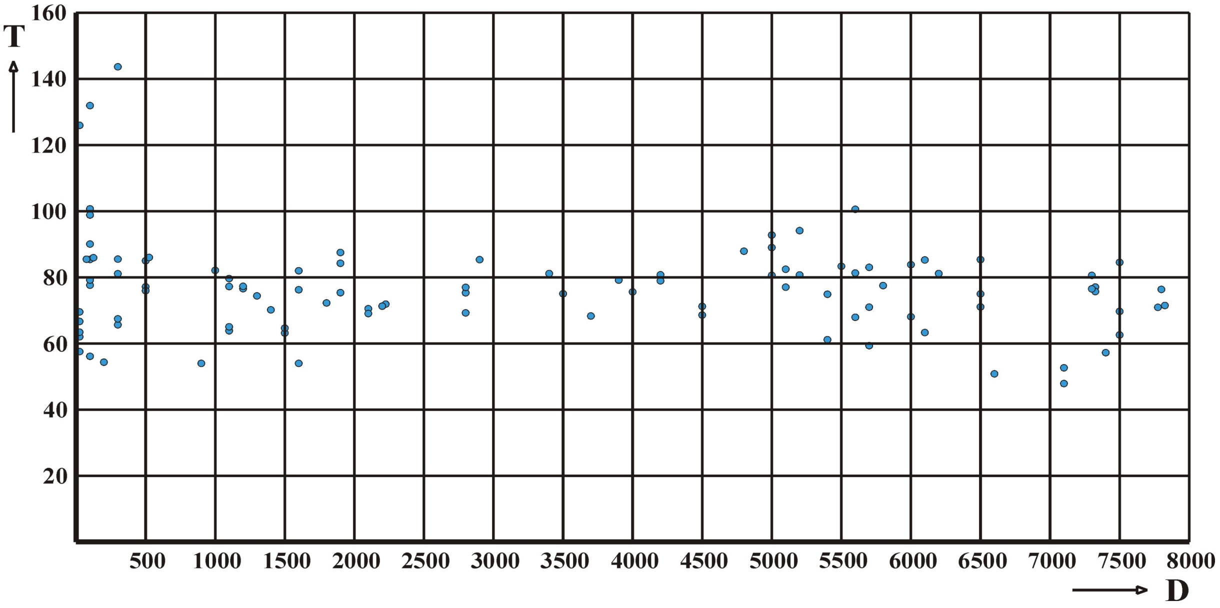


ca. 2.7% increase of wing length for each 1000 km. distance of migration) become closer to mine [*ca*. 1.6% ("**Acrocephalidae**"), 1.9% ("**Locustellidae**"), or 2.0% (together), compared to *ca*. 2.0% in my material]. As to the differences between the "**Locustellidae**" and "**Acrocephalidae**" (relatively shorter wings in the former) reported by NOWAKOWSKI *& al.* (2014) I would look for the explanation among different ecological specializations rather than phylogenetic "heritage".

Not surprisingly the interdependence between the migration distances and tail lengths is (very slightly) negative as well for actually measured (t) as for relative (T=100t:w – fig. 22)

Fig. 22

Relation between length of tail (T) and distance of seasonal migration (D)



values; astonishing is only their being so unbelievably identical (r = -0.1584 and -0.1578).

Contrary to my expectations, the qualitative index of pointedness (a – fig 23) shows stronger (r = +0.501) correlation with migration distance than either “basic” (e) or “normalized (E=100e/w – fig. 24) quantitative indices (r = +0.354 and +0.487, respectively); the values for indices of elongation (0.234 for l and 0.436 for L – fig 25) being still lower.

Fig. 23

Relation between qualitative index of pointedness (a) and distance of migration (D)

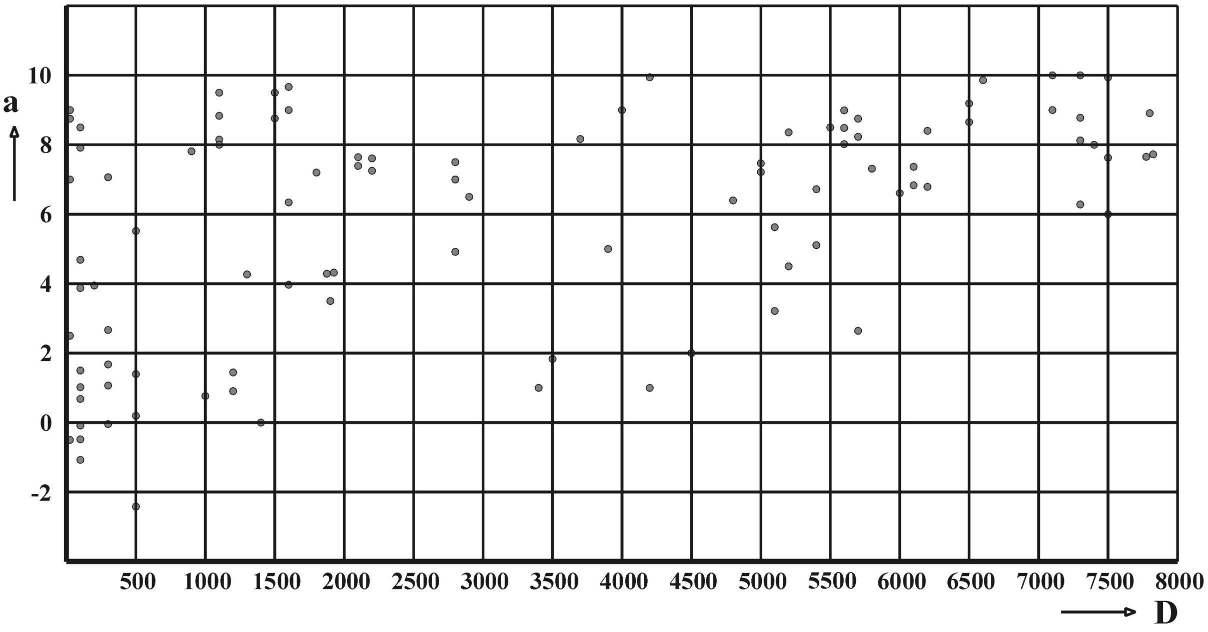


Fig. 24

Relation between quantitative index of pointedness (E) and distance of migration (D)

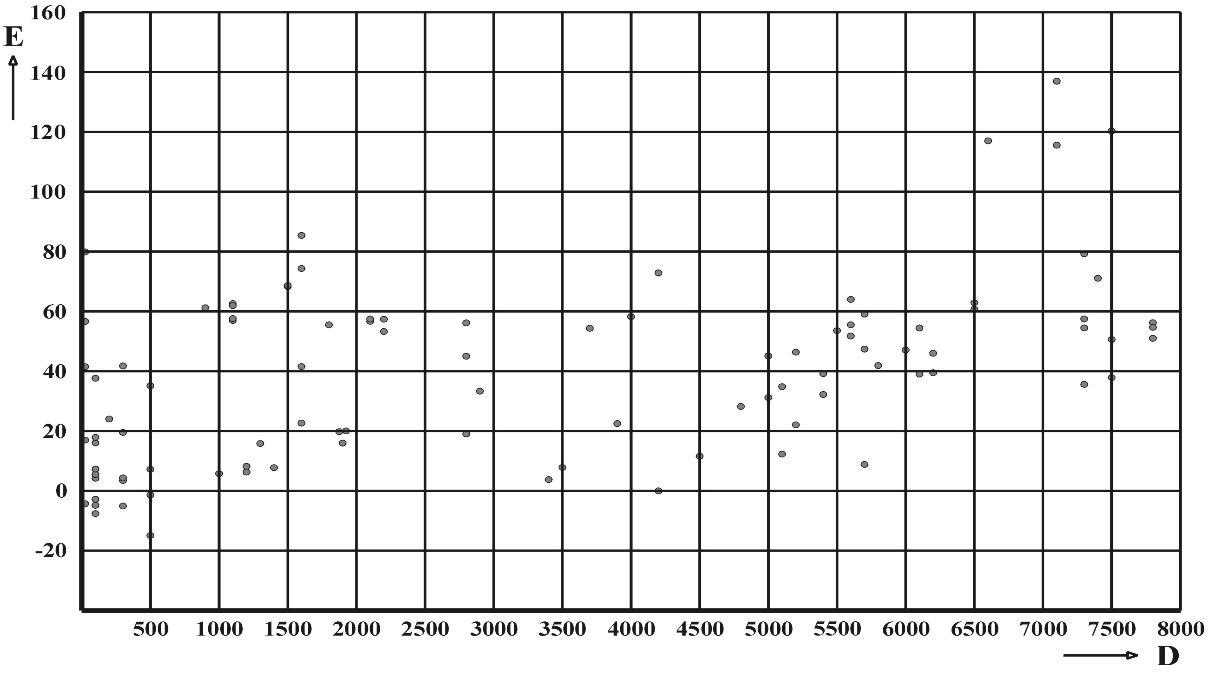
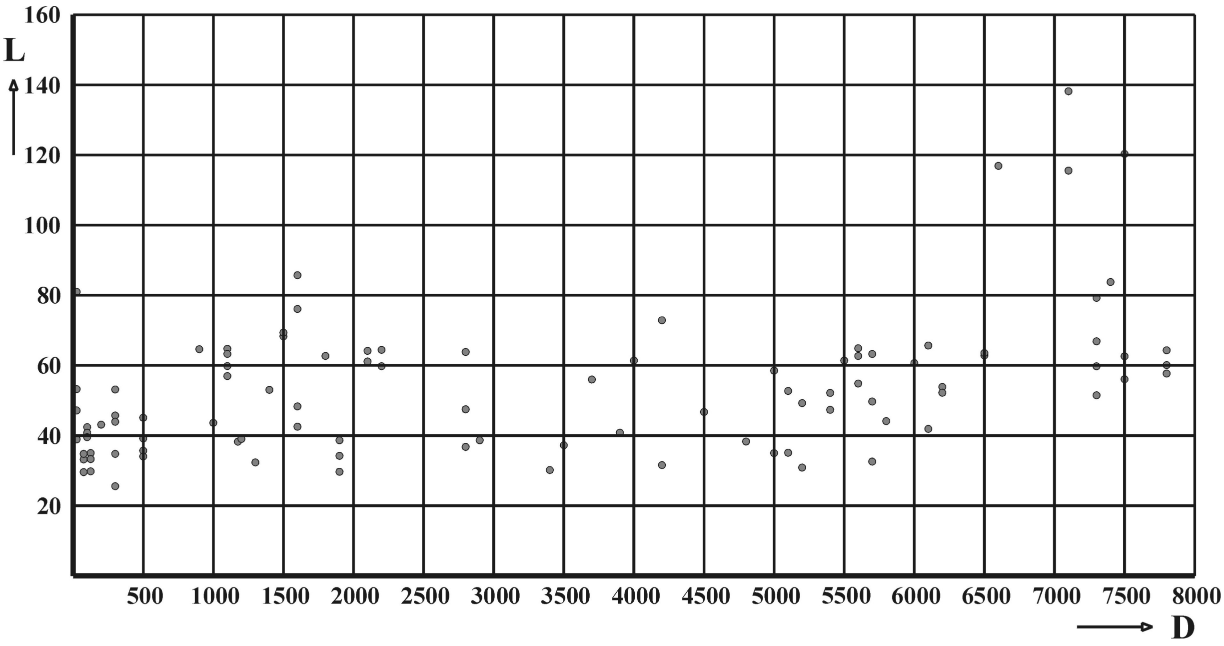


Fig. 25

Relation between index of elongation (L) and distance of migration (D)

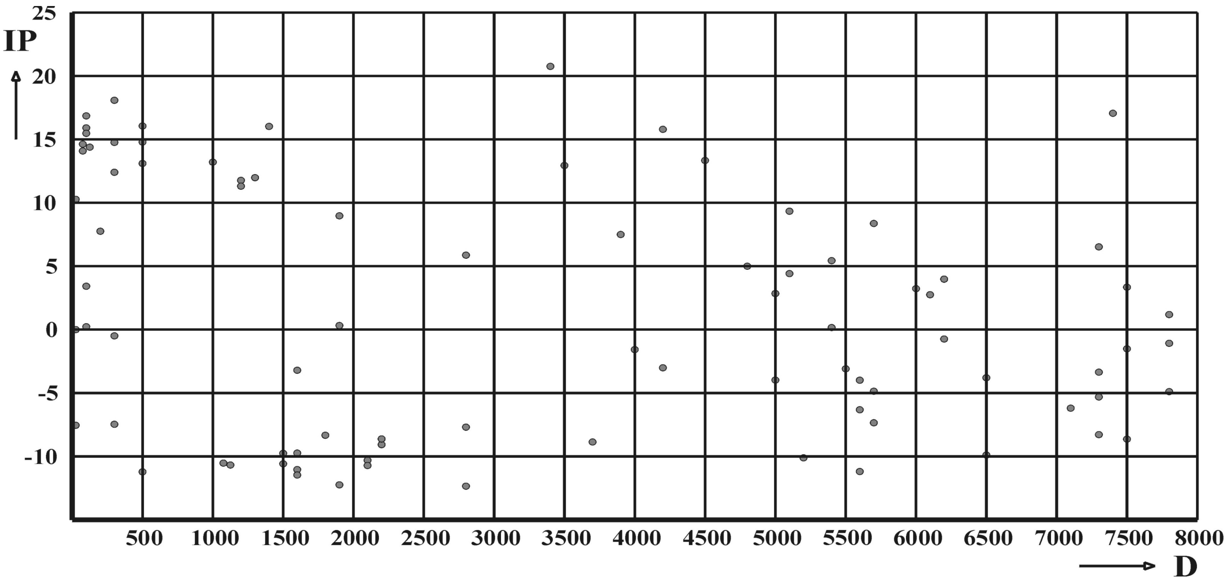


As the diagrams (especially in case of a) show, it is apparently only lower limit of a, E and L variability that is really correlated with migration distance: while values of the indices are high in all long-distance migrants, the [near-]sedentary species fill the entire range from very low to very high; evidently many thousand km. long flight is rigorous but not the only selective factor responsible for the evolution of pointed wings.

Slight but evident interdependence between distance and "traditionally" (with the tip of longest covert as reference-point) measured first primary (r = -0.177 for 1p and -0.244 for IP – fig 26) had to be expected, like positive (although very slight: respectively +0.035 and

Fig. 26

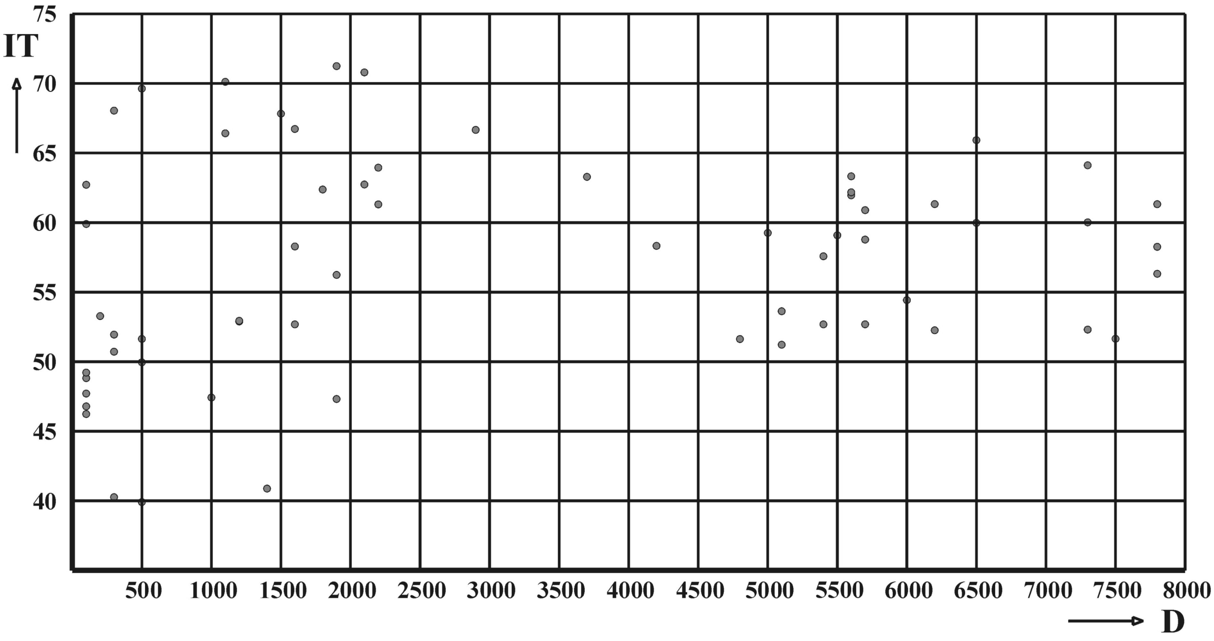
Relation between relative length of first primary (IP) and distance of migration (D)



+0.192) relation in case of measurement done to the apex of wing (actual 1t and adjusted IT – fig. 27), but the best effect (r = -374) can be obtained by considering the combination of both

Fig. 27

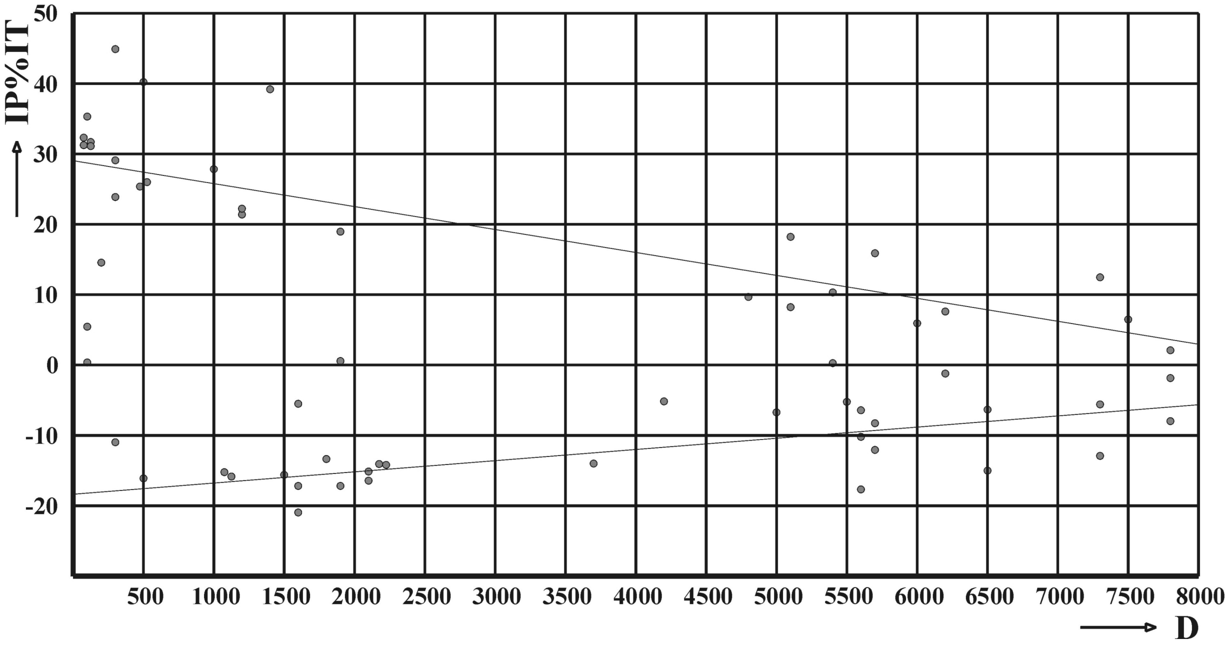
Relation between IT and distance of migration (D)



(100IP:IT – fig. 28). However – as was already perceptible in case of IP (fig. 26) and (even if much less clearly) IT (fig. 27) themselves – the "overall" correlation is, in fact, the resultant of two different tendencies: both the highest (>*ca.* 20) and lowest (<*ca.* -12) values of IP:IT

Fig. 28

Relation between ratio of IP to IT and distance of migration (D)

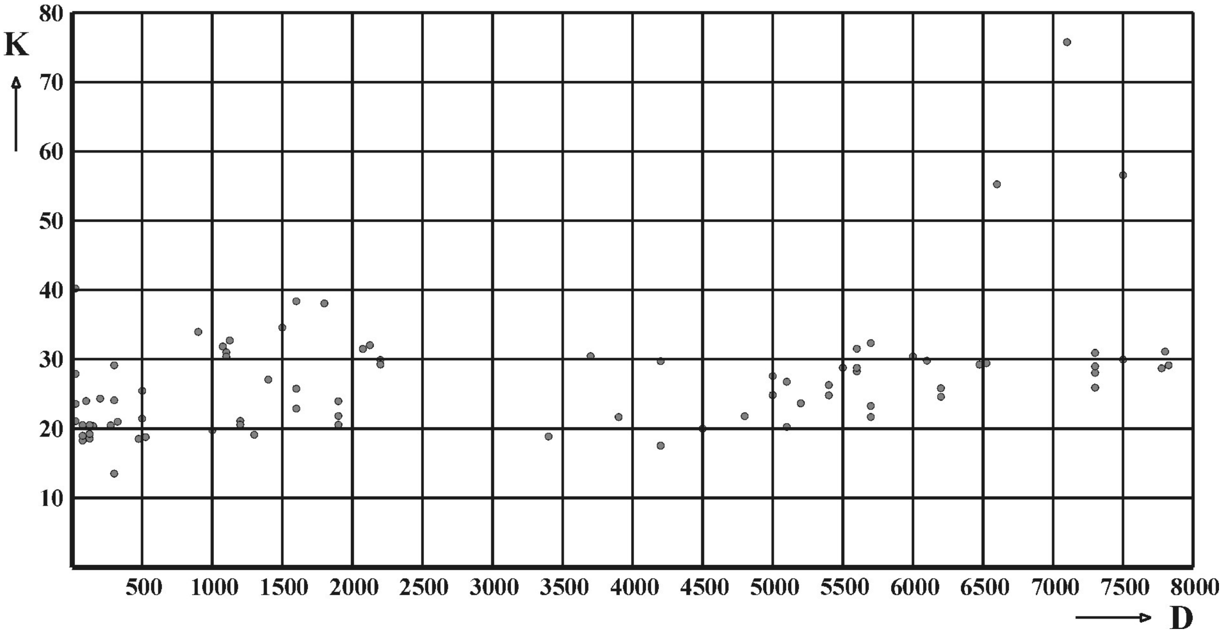


characterize only (or almost so) near-sedentary birds or short-distance migrants, with two separate lines of regression starting on the left side at values of approximately +30 and -20 to converge at near zero at the right end of the diagram. The "lower" trend, ***increase*** of the size of remicle with length of seasonal migration, seems paradoxical; its interpretation (and even robust confirmation) must wait for more abundant, representative material and special study, but one hypothesis suggests itself already now: perhaps the sedentaries and short-distance migrants with rudimental 1. primaries represent the descendants of species that have, in course of their evolutionary development, passed a stage of long-distance migration (with – according to STEGMANN's scenario – abbreviation of remicle) and only secondarily became less mobile?

On the other hand, higher positive values for wing-tip length (+0.186 for k and +0.379 for K – fig. 29) agree well with the fact that the relatively high coefficient (r =0.428) for w:Wexp (see above) is mainly just the effect of the latter's being dependent upon, and thence highly (r = 0.730) correlated to, K.

Fig. 29

Relation between KIPP'S index (K) and distance of seasonal migration (D)



To conclude, the best "predictor" of migration distance among the indices analysed herein seems to be the qualitative index of pointedness, a (r = +0.501) [to be sure, still higher (0.635) correlation coefficient has been obtained for the shape of tail (distance between tips of outer and central pair of rectrices), but this is based on glaringly insufficient material: I have data for very few (usually single) individuals of but 6 species, only one of them (*Apus apus*, 1 ex.) with forked tail (see also **Appendix**!)]. Somewhat less close relation shows the quantitative index of pointedness E (r = +0.487), followed by that of elongation L (+0.436), ratio of actually measured and expected wing length (W:Wexp: +0.428), length of wing-tip (Kipp's index, K: +0.379), and "traditionally" (to coverts) measured lenth of 1. primary in proportion of the distance between its apex and wing-tip (IP:IT, r = -0.374); correlation between IP itself (-0.244), weight of body (h: -0.209) or length of tail (T: -0.158) with migration distance seems very slight, and that of either actual (w: -0.071) or "theoretical" (W: +0.015) wing length practically none.

As pointed out in the introduction (and what anyway stands glaringly out), the above is nothing like a well substantiated monograph, nor even a solid “first draft”, but only something like a snapshot from the start of a long-distance race. I have nevertheless decided to publish it, and to suggest some promising applications of the indices, in the hope to persuade some Colleagues that the race is worth joining: that various aspects of wing/tail formulae provide a fruitful source of ideas for special studies.

Appendix

“In the last moment”, when the paper was almost ready for publication, I received the results of measurements of “tail-formulas”, performed on my request during the autumn season of Operation Carpathica [ringing camp in Myscowa, $49^0$31’N-$21^0$33’E]. It was already too late to integrate them in the “main body” of the paper, and anyway these data, based on different material, would not readily fit into it, so I decided to include their summary presentation (Tab. 3) and some preliminary remarks separately.

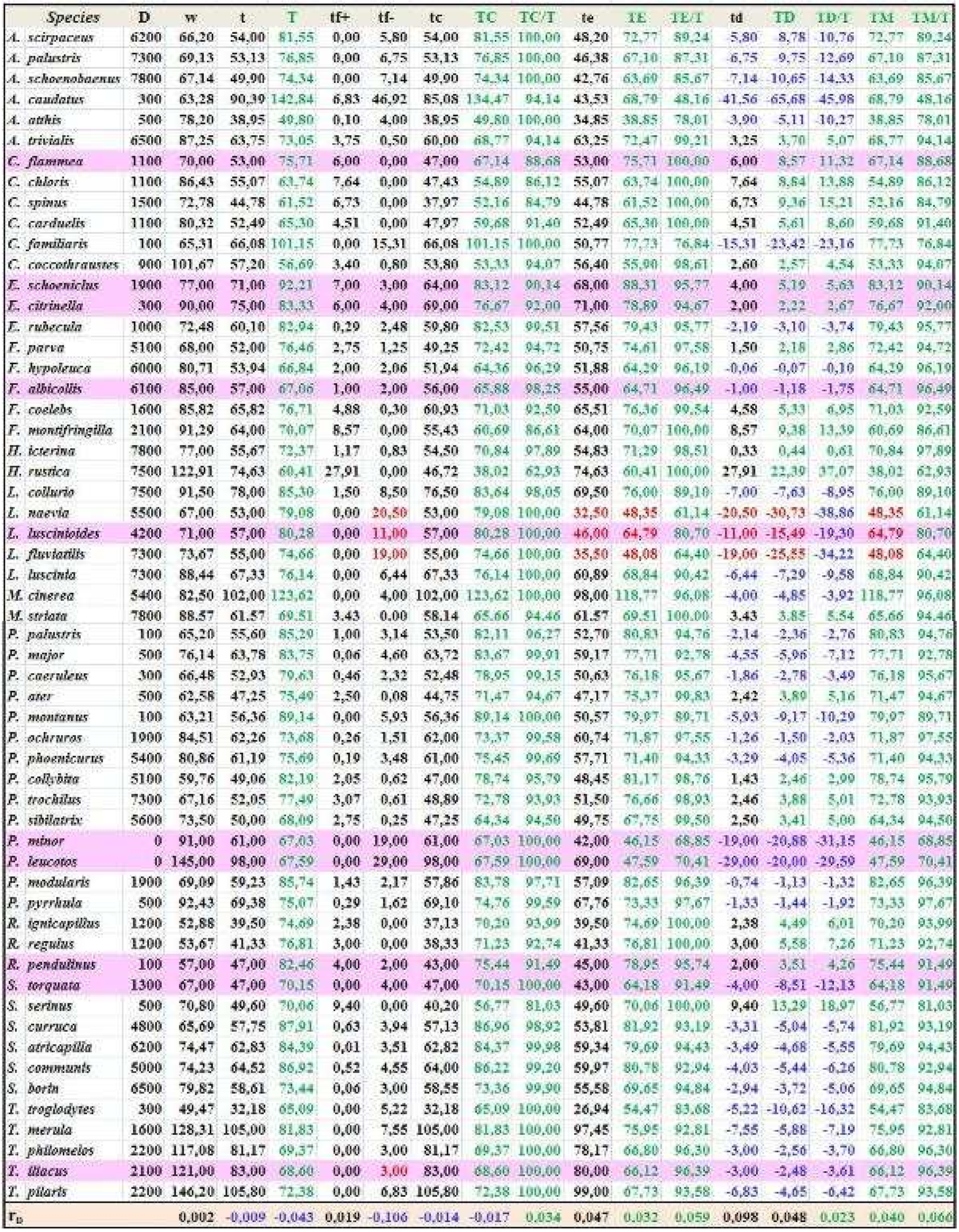
Groping completely in the dark (as far as I am aware, hitherto nobody had ever attempted this kind of analysis) in search for “migrationally” informative aspects of tail shape, I have contrived several indices and tried various versions of each by calculating the coefficients of their correlation with estimated distance between the nesting area and winter quarters. The “overall” results are rather unconvincing – none of the r_D values does reliably differ from zero – what, however, could be expected: 1840 “records” may seem fairly abundant material, but in fact it is deficient in many ways. Some species (*Erithacus rubecula*, *Hirundo rustica*, *Parus major*, *Phylloscopus collybita*, *Sylvia atricapilla*) are represented by hundreds of individuals, but for many others (including some of the potentially most “desirable” in the context of this study, *e.g.* all three grasshopper warblers) we have information on but very few or even single one; there are (perfectly understandable in case of a newly introduced, not yet “routinized” measurement) many (again including the *Locustella*s) evidently (and much more numerous – but also much more dangerous – not evidently) erroneous data (*e.g.* plus sign instead of minus or opposite); but most important is virtual lack of reliable material concerning regular migrants with markedly forked (the only exception being barn swallow) or markedly rounded tails: in the majority of the included taxa it is almost straightly truncated or but slightly rounded, the difference between inner and outer rectrices not much (if at all) exceeding the range of individual variability and remaining apparently deep within the limits of drowning effect of the “noise” caused by allometric or especially ecological (*e.g*. type of habitat, behavioural factors *&c*.) interspecific disparities of no relevance to seasonal migrations. If we add the extremely inexact estimation (in partial migrants practically guess-work) of migration distances, then more convincing correlations could only be a kind of miracle…

To reduce the influence of the above-mentioned “noice” I have analysed some (traditionally, broadly understood) genera separately (tab. 4). Having no more than 4 species available in any of these groups I could not expect truly convincing results, but some preliminary conclusions are nevertheless possible. The first impression is the colour mosaic: almost all aspects of tail shape show marked inter-group variability in relation to migration distance: negative values (blue background) alternate with positive (white) ones, strong correlation in one genus may appear as negligible in another; these differences are partly a stochastic effect of inadequate “taxon sampling”, but mainly (I believe) reflect (and probably could in future be exploited in the study of) morphological adaptations to various (non-migratory) ecological factors (two of those apparent already now are the contrasting influence of open habitats *vs*. dense vegetation and aerial hunting – swifts, swallows, or even flycatchers – *vs*. “surface-picking”). However, four characters (T, TC, TE and TM: tail lengths as measured to the tip of, respectively, longest, central, outermost, and shortest rectrix, all “normalized” as percent of wing-length) behave (at least in the sense of showing always negative – and, except in *Phylloscopus*, relatively strong – correlation with the length of seasonal passage) rather coherently, with TM appearing as the best “predictor” of migration distance (average r_D=0.685), followed by TC (0.640), while T (0.619) and TE (0.615) seem somewhat less indicative. The differences between them – albeit admittedly slight and so not truly convincing – suggest that (among possible “tail lengths”), it is neither the traditionally accepted longest, nor (as intuitively expected by me) central, but the shortest rectrix that may

Tab. 3

Tail-formula indices

Negative values written in blue; doubtful or probably erroneous ones in red;
those on pink background based on but single specimen; *P. montanus* = ***Passer*** *montanus*
lowermost row (r_D) – coefficients of correlation with migration distance; for explanation of indices see tab.4



Species	D	w	t	T	tf+	tf-	tc	TC	TC/T	te	TE	TE/T	td	TD	TD/T	TM	TM/T
A. scirpaceus	6200	66,20	54,00	81,55	0,00	5,80	54,00	81,55	100,00	48,20	72,77	89,24	-5,80	-8,78	-10,76	72,77	89,24
A. palustris	7300	69,13	53,13	76,85	0,00	6,75	53,13	76,85	100,00	46,38	67,10	87,31	-6,75	-9,75	-12,69	67,10	87,31
A. schoenobaenus	7800	67,14	49,90	74,34	0,00	7,14	49,90	74,34	100,00	42,76	63,69	85,67	-7,14	-10,65	-14,33	63,69	85,67
A. caudatus	300	63,28	90,39	142,84	6,83	46,92	85,08	134,47	94,14	43,53	68,79	48,16	-41,56	-65,68	-45,98	68,79	48,16
A. atthis	500	78,20	38,95	49,80	0,10	4,00	38,95	49,80	100,00	34,85	38,85	78,01	-3,90	-5,11	-10,27	38,85	78,01
A. trivialis	6500	87,25	63,75	73,05	3,75	0,50	60,00	68,77	94,14	63,25	72,47	99,21	3,25	3,70	5,07	68,77	94,14
C. flammea	1100	70,00	53,00	75,71	6,00	0,00	47,00	67,14	88,68	53,00	75,71	100,00	6,00	8,57	11,32	67,14	88,68
C. chloris	1100	86,43	55,07	63,74	7,64	0,00	47,43	54,89	86,12	55,07	63,74	100,00	7,64	8,84	13,88	54,89	86,12
C. spinus	1500	72,78	44,78	61,52	6,73	0,00	37,97	52,16	84,79	44,78	61,52	100,00	6,73	9,36	15,21	52,16	84,79
C. carduelis	1100	80,32	52,49	65,30	4,51	0,00	47,97	59,68	91,40	52,49	65,30	100,00	4,51	5,61	8,60	59,68	91,40
C. familiaris	100	65,31	66,08	101,15	0,00	15,31	66,08	101,15	100,00	50,77	77,73	76,84	-15,31	-23,42	-23,16	77,73	76,84
C. coccothraustes	900	101,67	57,20	56,69	3,40	0,80	53,80	53,33	94,07	56,40	55,90	98,61	2,60	2,57	4,54	53,33	94,07
E. schoeniclus	1900	77,00	71,00	92,21	7,00	3,00	64,00	83,12	90,14	68,00	88,31	95,77	4,00	5,19	5,63	83,12	90,14
E. citrinella	300	90,00	75,00	83,33	6,00	4,00	69,00	76,67	92,00	71,00	78,89	94,67	2,00	2,22	2,67	76,67	92,00
E. rubecula	1000	72,48	60,10	82,94	0,29	2,48	59,80	82,53	99,51	57,56	79,43	95,77	-2,19	-3,10	-3,74	79,43	95,77
F. parva	5100	68,00	52,00	76,46	2,75	1,25	49,25	72,42	94,72	50,75	74,61	97,58	1,50	2,18	2,86	72,42	94,72
F. hypoleuca	6000	80,71	53,94	66,84	2,00	2,06	51,94	64,36	96,29	51,88	64,29	96,19	-0,06	-0,07	-0,10	64,29	96,19
F. albicollis	6100	85,00	57,00	67,06	1,00	2,00	56,00	65,88	98,25	55,00	64,71	96,49	-1,00	-1,18	-1,75	64,71	96,49
F. coelebs	1600	85,82	65,82	76,71	4,88	0,30	60,93	71,03	92,59	65,51	76,36	99,54	4,58	5,33	6,95	71,03	92,59
F. montifringilla	2100	91,29	64,00	70,07	8,57	0,00	55,43	60,69	86,61	64,00	70,07	100,00	8,57	9,38	13,39	60,69	86,61
H. icterina	7800	77,00	55,67	72,37	1,17	0,83	54,50	70,84	97,89	54,83	71,29	98,51	0,33	0,44	0,61	70,84	97,89
H. rustica	7500	122,91	74,63	60,41	27,91	0,00	46,72	38,02	62,93	74,63	60,41	100,00	27,91	22,39	37,07	38,02	62,93
L. collurio	7500	91,50	78,00	85,30	1,50	8,50	76,50	83,64	98,05	69,50	76,00	89,10	-7,00	-7,63	-8,95	76,00	89,10
L. naevia	5500	67,00	53,00	79,08	0,00	20,50	53,00	79,08	100,00	32,50	48,35	61,14	-20,50	-30,73	-38,86	48,35	61,14
L. luscinioides	4200	71,00	57,00	80,28	0,00	11,00	57,00	80,28	100,00	46,00	64,79	80,70	-11,00	-15,49	-19,30	64,79	80,70
L. fluviatilis	7300	73,67	55,00	74,66	0,00	19,00	55,00	74,66	100,00	35,50	48,08	64,40	-19,00	-25,55	-34,22	48,08	64,40
L. luscinia	7300	88,44	67,33	76,14	0,00	6,44	67,33	76,14	100,00	60,89	68,84	90,42	-6,44	-7,29	-9,58	68,84	90,42
M. cinerea	5400	82,50	102,00	123,62	0,00	4,00	102,00	123,62	100,00	98,00	118,77	96,08	-4,00	-4,85	-3,92	118,77	96,08
M. striata	7800	88.57	61.57	69,51	3.43	0.00	58.14	65,66	94,46	61,57	69,51	100,00	3,43	3,85	5,54	65,66	94,46
P. palustris	100	65,20	55,60	85,29	1,00	3,14	53,50	82,11	96,27	52,70	80,83	94,76	-2,14	-2,36	-2,76	80,83	94,76
P. major	500	76,14	63,78	83,75	0,06	4,60	63,72	83,67	99,91	59,17	77,71	92,78	-4,55	-5,96	-7,12	77,71	92,78
P. caeruleus	300	66,48	52,93	79,63	0,46	2,32	52,48	78,95	99,15	50,63	76,18	95,67	-1,86	-2,78	-3,49	76,18	95,67
P. ater	500	62,58	47,25	75,49	2,50	0,08	44,75	71,47	94,67	47,17	75,37	99,83	2,42	3,89	5,16	71,47	94,67
P. montanus	100	63,21	56,36	89,14	0,00	5,93	56,36	89,14	100,00	50,57	79,97	89,71	-5,93	-9,17	-10,29	79,97	89,71
P. ochruros	1900	84,51	62,26	73,68	0,26	1,51	62,00	73,37	99,58	60,74	71,87	97,55	-1,26	-1,50	-2,03	71,87	97,55
P. phoenicurus	5400	80,86	61,19	75,69	0,19	3,48	61,00	75,45	99,69	57,71	71,40	94,33	-3,29	-4,05	-5,36	71,40	94,33
P. collybita	5100	59,76	49,06	82,19	2,05	0,62	47,00	78,74	95,79	48,45	81,17	98,76	1,43	2,46	2,99	78,74	95,79
P. trochilus	7300	67,16	52,05	77,49	3,07	0,61	48,89	72,78	93,93	51,50	76,66	98,93	2,46	3,88	5,01	72,78	93,93
P. sibilatrix	5600	73,50	50,00	68,09	2,75	0,25	47,25	64,34	94,50	49,75	67,75	99,50	2,50	3,41	5,00	64,34	94,50
P. minor	0	91,00	61,00	67,03	0,00	19,00	61,00	67,03	100,00	42,00	46,15	68,85	-19,00	-20,88	-31,15	46,15	68,85
P. leucotos	0	145,00	98,00	67,59	0,00	29,00	98,00	67,59	100,00	69,00	47,59	70,41	-29,00	-20,00	-29,59	47,59	70,41
P. modularis	1900	69,09	59,23	85,74	1,43	2,17	57,86	83,78	97,71	57,09	82,65	96,39	-0,74	-1,13	-1,32	82,65	96,39
P. pyrrhula	500	92,43	69,38	75,07	0,29	1,62	69,10	74,76	99,59	67,76	73,33	97,67	-1,33	-1,44	-1,92	73,33	97,67
R. ignicapillus	1200	52,88	39,50	74,69	2,38	0,00	37,13	70,20	93,99	39,50	74,69	100,00	2,38	4,49	6,01	70,20	93,99
R. regulus	1200	53,67	41,33	76,81	3,00	0,00	38,33	71,23	92,74	41,33	76,81	100,00	3,00	5,58	7,26	71,23	92,74
R. pendulinus	100	57,00	47,00	82,46	4,00	2,00	43,00	75,44	91,49	45,00	78,95	95,74	2,00	3,51	4,26	75,44	91,49
S. torquata	1300	67,00	47,00	70,15	0,00	4,00	47,00	70,15	100,00	43,00	64,18	91,49	-4,00	-8,51	-12,13	64,18	91,49
S. serinus	500	70,80	49,60	70,06	9,40	0,00	40,20	56,77	81,03	49,60	70,06	100,00	9,40	13,29	18,97	56,77	81,03
S. curruca	4800	65,69	57,75	87,91	0,63	3,94	57,13	86,96	98,92	53,81	81,92	93,19	-3,31	-5,04	-5,74	81,92	93,19
S. atricapilla	6200	74,47	62,83	84,39	0,01	3,51	62,82	84,37	99,98	59,34	79,69	94,43	-3,49	-4,68	-5,55	79,69	94,43
S. communis	5000	74,23	64,52	86,92	0,52	4,55	64,00	86,22	99,20	59,97	80,78	92,94	-4,03	-5,44	-6,26	80,78	92,94
S. borin	6500	79,82	58,61	73,44	0,06	3,00	58,55	73,36	99,90	55,58	69,65	94,84	-2,94	-3,72	-5,06	69,65	94,84
T. troglodytes	300	49,47	32,18	65,09	0,00	5,22	32,18	65,09	100,00	26,94	54,47	83,68	-5,22	-10,62	-16,32	54,47	83,68
T. merula	1600	128,31	105,00	81,83	0,00	7,55	105,00	81,83	100,00	97,45	75,95	92,81	-7,55	-5,88	-7,19	75,95	92,81
T. philomelos	2200	117,08	81,17	69,37	0,00	3,00	81,17	69,37	100,00	78,17	66,80	96,30	-3,00	-2,56	-3,70	66,80	96,30
T. iliacus	2100	121,00	83,00	68,60	0,00	3,00	83,00	68,60	100,00	80,00	66,12	96,39	-3,00	-2,48	-3,61	66,12	96,39
T. pilaris	2200	146,20	105,80	72,38	0,00	6,83	105,80	72,38	100,00	99,00	67,73	93,58	-6,83	-4,65	-6,42	67,73	93,58
r_D		0,002	-0,009	-0,043	0,019	-0,106	-0,014	-0,017	0,034	0,047	0,032	0,059	0,098	0,048	0,023	0,040	0,066

prove the best correlate of migration distance. Anyway, “*the use of the tail appears to have a larger effect than often assumed in models used for* ***estimating*** *flight performance in birds*” (KleinHeerenbrink *& al.* 2016), but morpho-functional aspects of that effect remain largely unclear – hopefully the accumulation of more extensive and more representative (including more migrants with definitely forked and more with definitely rounded tails) data (both Baltic Operation and Operation Carpathica included tail-formula measurements in their schedules) will allow the elucidation of some here relevant questions.

Tab. 4

Correlation of tail-formula indices with migration distance in selected taxa

Empty pink cells pi – character invariable among included species, so correlation with distance indeterminable; negative values written in blue; other explanations below the table

Species	w	t	T	tf+	tf-	tc	TC	TC/T	te	TE	TE/T	td	TD	TD/T	TM	TM/T
Σ	0,076	0,052	-0,041	-0,019	0,026	0,055	0,000	0,079	0,040	-0,046	-0,067	-0,026	-0,046	-0,098	-0,018	-0,040
Sylvia	0,811	-0,067	-0,829	-0,978	-0,864	0,026	-0,800	0,970	0,115	-0,785	0,979	0,582	0,859	0,811	-0,785	0,979
Turdus	0,056	-0,489	-0,921		-0,601	-0,489	-0,921		-0,461	-0,957	0,637	0,601	0,735	0,637	-0,957	0,637
Parus	0,348	0,027	-0,560	0,180	-0,183	0,061	-0,387	0,115	0,084	-0,762	0,245	0,186	0,176	0,192	-0,732	-0,512
Phylloscopus	0,260	0,996	-0,029	0,867	0,282	0,995	-0,119	-0,865	0,976	-0,032	-0,081	0,649	0,879	0,676	-0,119	-0,865
Acrocephalus	0,509	-0,862	-0,999		1,000	-0,862	-0,999		-0,921	-0,997	-0,986	-1,000	-0,982	-0,986	-0,997	-0,986
Muscicapa s.l.	0,862	0,964	-0,458	0,426	-0,695	0,896	-0,611	-0,226	0,965	-0,235	0,729	0,573	0,479	0,513	-0,566	-0,302
Carduelis	-0,412	-0,969	-0,535	0,255		-0,996	-0,641	-0,675	-0,969	-0,535		0,255	0,498	0,675	-0,641	-0,675
M	0,348	-0,057	-0,619	0,150	-0,177	-0,053	-0,640	-0,136	-0,030	-0,615	0,254	0,264	0,378	0,360	-0,685	-0,246
σ	0,443	0,798	0,333	0,685	0,709	0,791	0,308	0,727	0,806	0,366	0,714	0,586	0,649	0,625	0,294	0,760
m	0,167	0,302	0,126	0,306	0,290	0,299	0,116	0,325	0,305	0,138	0,291	0,222	0,245	0,236	0,111	0,287
N	7	7	7	5	6	7	7	5	7	7	6	7	7	7	7	7

D – estimated distance of (one way) seasonal migration
w – wing length
t – tail length
tf+ – difference between the longest and the innermost pair of rectrices
tf- – difference between the longest and the outermost pair of rectrices
tc – tail length measured to the tips of innermost rectrices
te – tail length measured to the tips of outermost rectrices
td – difference between the inner- and outermost rectrices
tm – tail length measured to the tips of shortest (either inner- or outermost) rectrices
[symbols in minuscules (w, t, tc *&c.*) – averages of actual measurements; in capitals (T, TC, TE, TD, TM) standardized as % of w; TC/T, TE/T, TD/T, TM/T – standardized as % of T]
Σ – all species except *Certhia familiaris*, *Picoides minor* and *Picoides leucotos*
M – mean
σ – standard deviation
m – standard error of mean
N – number of elements

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