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# More rounded wings in migratory swallows: anomalous adaptation or incomparable metrics? 

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,,The danger of statistical (and general of mathematical) methods in ecology is that their application gives a stamp of extreme exactitude and reliability to conclusions even if derived from faulty, though sufficiently numerous, data" Uvarov 1931
It is a long established fact (e.g. Kipp 1936, 1958, 1959; Rensch 1938; Stegmann 1962; HOŁYŃSKI 1965, 2016; \&c.) that migratory birds [at least "passerimorphs": "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" - HoŁYŃski 2016] have more pointed wings than their sedentary relatives. However, recently HUBER \& al. (2017) published the results of their study purported to show that swallows (Hirundinidae) make the exception to that rule: migrants having more rounded wingtips! With no material to verify the somewhat surprising but, on reflection, not improbable (swallows spent anyway most of their life on flight, so migration may not be the decisive factor in shaping their flight apparatus) conclusion, I would have it accepted at the face value, were it not for the, in my opinion rather strange, methodology based on measurements of absolute lengths of primaries (BERTHOLD \& Friedrich 1979; Jenni \& Winkler 1989) rather than the traditionally used distances between their tips and the tip of the wing. I must admit, I do not really understand the details of that method, in particular the assumed (Pilastro \& al. 1995; Lockwood \& al. 1998) relationship between absolute lengths of individual feathers and the shape of the wing, but it is a priori quite evident - and unmistakably confirmed by e.g. fig. 2 in PILASTRO \& al. (1995) - that the "wingtip pointedness" measured in that way is a quite different quality than that represented by traditionally calculated indices. HUBER \& al. (2017) do not compare their $C_{2}$ ["second component of size-constrained components analysis (SCCA)" - Lоскwood \& al. (1998)] in the studied species to any index used by other authors, so their conclusion that 1)
the relations in swallows differ from those in other "passerimorphs" remains, in my opinion, unsubstantiated: at least two other hypotheses seem conceivable: 2) if measured by traditional method, wings of migratory hirundines would (in agreement with the general rule) prove more pointed than in sedentary relatives; or 3) if $C_{2}$ 's are compared, at least some of the nonhirundines would also show the "anomaly".

## Terminology and abbreviations

In considerations concerning shape of wing the "longest" primary traditionally means that making the apex of the wing, and the "lengths" of the remaining ones are defined by the distances of their tips from that of the wing-tip (longer distance $=$ shorter primary). Such terminology served perfectly well until some authors started to base their conclusions on "primary lengths" of completely different sense (distance to the tip of the feather from the point of its insertion in skin). This is closer [though still not identical: primaries are attached not to the edge of patagium but to the (bones of) metacarpus and 2.-3. fingers!)] to the "normal" (colloquial) understanding of the word, but its application has introduced dangerous uncertainty: now qualifiers "long" vs. "short" or "longer" vs. "shorter" without additional descriptors have become either meaningless or misleading. To remove the confusion, it seems warranted to replace the adjectives "long" and "short" when used in traditional sense with other terms; for lack of something better ("apical"/"basal" would be misleading, "distal"/"proximal" have been widely used in yet another sense) I propose the neologisms "outstretched" vs. "retracted"). So:
Outstretched = primaries whose tips are close to the tip of wing ("long" in traditional terminology)
Retracted = primaries whose tips are closer to tips of secondaries ("short" in traditional terminology)
Symbols (written in red) used for the analysed indices (see also explanations in the text):
Normalized = presented as \% of w
$\mathbf{N}=\quad$ number of examined birds
D $\quad=\quad$ migration distance
w $\quad=\quad$ wing length
$\mathbf{T}=$ normalized tail length
a $\quad=$ qualitative index of pointedness (HOŁYŃSKI 1965)
$\mathbf{E} \quad=$ normalized quantitative index of pointedness: $100\left(\Sigma_{\Delta \mathrm{p}}-\Sigma_{\Delta \mathrm{d}}\right) / \mathrm{w}$ (HOŁYŃSKI 1965)
$\mathbf{L}=\quad$ normalized index of longation: $100\left(\Sigma_{\Delta \mathrm{p}}+\Sigma_{\Delta \mathrm{d}}\right) / \mathrm{w}$ (BUSSE 1967)
$\mathbf{K}=$ normalized length of wing-tip (KIPP's index): $100 \Delta \mathrm{~s} / \mathrm{w}$ (KIPP 1959)
$C_{2}=$ second component of "size-constrained components analysis" (LOCKWOOD \& al. 1998)
$\Delta \quad=$ distance between the tip of a feather and wing-tip ("primary distance")
$\lambda=$ length
B $\quad=\quad$ base retraction (distance between the base - insertion point to skin - of $p_{x}$ and that of P
P $\quad=\quad$ the most outstretched primary
d $\quad=$ distal (placed outwards of P) primary
p $\quad=\quad$ proximal (placed between secondaries and $P$ ) primary
$p_{x} \quad=\quad$ primary no. $x$
$\mathbf{p}_{2} \rightarrow \mathbf{p}_{9}=$ primaries 2 to 9 (numbered from the distalmost inwards)
$\mathbf{s} \quad=\quad$ distalmost secondary
$\Sigma=$ sum
"Primary lengths" vs. "primary distances"
Having neither access to the primary data (actual measurements made and used by HUBER \& al. 2017) nor possibility to measure the respective species myself, I am unable to check directly which of the three (mentiond above) hypotheses reflects the reality, but it seems reasonable to approach the general question indirectly, by "theoretical" evaluation of the properties of the method used by them, in particular the relationship between absolute lengths of primaries on the one hand and wing formula, especially wingtip pointedness, on the other.

Absolute length of primaries (termed simply "primary length" by the authors including HUBER \& al. 2017 - using them as basic data) is defined as the distance from the insertion in skin to the tip of the feather. The Authors prefer "primary lengths" over traditionally used "primary distances" (from the tip of wing to tips of particular feathers) for two reasons: measurements of the former being allegedly more exactly repeatable, and their distribution more closely approximating normality. The question of normality seems a trivial
hairsplitting: I cannot imagine how it could have influenced the results of any actual study to a degree even remotely comparable with the impact of other sources of error. As to the exactitude (and, consequently, repeatability) of measurements, the length of feather measured from skin might indeed seem likely to be relatively exact in case of museum specimens, whose skin is dry and stiff, but soft flexible tissue of living bird does not offer comparably fixed point of reference. On the other hand, primaries are not inserted perpendicularly to the skin but at a very acute angle, and in small birds like passerines the interstices between bases of neighbour feathers are very narrow, what makes pushing of relatively thick ( 1.4 mm . Jenni \& Winkler 1989) pin (marking the zero-point on the ruler) exactly to the very insertion point of the measured feather problematic especially just in museum specimens; moreover, it is hardly imaginable how post mortem shrinking (variable both between and within species!) of soft tissues including skin could have left that insertion point unaffected! I do not know - and I wonder if anybody knows... - how all these circumstances (not always "acting" in the same direction) actually influence the result of the measurement, but anyway these "theoretical" considerations (confirmed with practical experiments - BUSSE 2000) raise serious doubts (expressed already e.g. by Gosler \& al. 1995) as to the alleged superior exactitude of "primary lengths" as well in case of museum material as with living birds!


Fig. 1
Elements of wing-formula (Hirundo rustica)
Red - primaries 2.-8.; brown - primaries 9.-10. (not counted in Baltic Operation version of wing-formula); green - secondaries Black arrowed line $\downarrow$ on the left (marked as w) - wing length; Red arrowed lines $\downarrow$ numbered 2-8-absolute lengths of primaries 2.-8. Blue arrowed lines $\mathfrak{\downarrow}$ on the right: $\mathbf{L P}$ - length of most outstretched primary; $\mathrm{B}_{8}, \mathrm{~L}_{8}, \mathrm{D}_{8}-$ base retraction, absolute length and distance of p 8

But the most suspicious aspect of the procedure applied by HUBER \& al. (2017) is the transmogrification of absolute feather-lengths into the index of wing pointedness! If - as in MARCHETTI \& al. (1995) - "primary lengths ... were measured from the wrist bend" [boldface mine - RBH] (or from any other fixed, the same for all primaries, point), then the calculation is straightforward: length of the most outstretched (making the wing tip) primary (P) minus that of $p_{x}$ equals the "primary distance" of $p_{x}: \Delta p_{x}=\lambda P-\lambda p_{x}$. However, "primary lengths" used by HUBER \& al. (2017) were measured from skin, and points of insertion into skin, as well as their distances from the wing-tip, are different for each feather, i.e. now - as shown for $\mathrm{p}_{8}$ on Fig. 1 (blue lines on the right) $-\Delta \mathrm{p}_{\mathrm{x}}=\left(\lambda \mathrm{P}+B p_{x}\right)-\lambda \mathrm{p}_{\mathrm{x}}$ [so, e.g., in the wing presented on Fig. 1, the longest is $p_{3}$ but nevertheless it is $p_{2}$ which makes the wing-tip (i.e. is the most outstretched, P)]! Neither Huber \& al. (2017), nor LOckwood \& al. (1998) who had invented the procedure, seem to have taken these different additional distances into consideration (at least I have not found any reference to them), so it is evident that if their $C_{2}$ has any relation to what has generally been termed "pointedness", anyway it is not the same: it measures quite a different aspect of wing shape than any of the traditionally used indices [see e.g. fig. 2 in Pilastro \& al. 1995].

LOCKWOOD \& al. (1998) claim that "Only $I_{K}, I_{L a}, I_{L \beta}$ and our shape components $\left(C_{2}\right.$ and $C_{3}$ ) detected differences in wingtip shape between migratory and less-migratory species. Only these latter indices and our new measures are effective at discerning the morphological adaptations to migration" $\left[I_{K}\right.$ means KIPP's index ( K in the terminology used herein); $I_{L \alpha}$ and $I_{L \beta}$ are Lewin's indices (Левин \& al. 1991)] - so, in their opinion, e.g. E or L ( $I_{H}$ and $I_{B}$ in their notation) do not show differences connected with migration and are not "effective at discerning the morphological adaptations to migration". This astounding conclusion is not only theoretically questionable but glaringly contradicted by the experience accumulated during more than half a century of the Baltic Operation work! Having no access to their primary (or even "secondary": neither the four categories of migration, nor the criteria used in the "phylogenetical and ecological control" or other relevant aspects of the procedure have been exactly defined...) data I am unable to demonstrate the concrete misleading element, but there are several suspects: extremely imprecise migration-variable (four "categories", two of them - "partially migratory" and "dispersive" - practically uninformative or at least incongruent with the remaining two); inclusion of almost certainly incomparable groups of birds ("to what degree the "passerimorph" rules apply to rather (in this respect) monotonous (all, except lapwings, with pointed wings) limicolae, to much heavier ... 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" - HoŁYŃsKI 2016); different statistics (ANOVA vs. correlation coefficient); \&c.

Whatever the source of misconception, also a comparison of the T, a, E, L and K indices in some (unfortunately, I do not have the relevant data for all of them) species-pairs used in "phylogenetically and ecologically controlled analysis" (their Table 5) by LOCKwOOD \& al. (1998) persuasively shows that their conclusion is glaringly erroneous. As seen from the Tab. 1, although only one of the 16 species involved is a really long-distance (transsaharan) migrant, in almost all cases (with but two rather controversial exceptions) the relations are as expected: values of T are lower, while those of a , $\mathrm{E}, \mathrm{L}$ and K much higher in "more migratory" birds. One of the apparent exceptions is the pair Regulus ignicapillus/R. regulus, where only L is (minimally) greater in the former, the proportions of all the remaining indices seem anomalous - but the "anomaly" appeared only as a result of Regulus ignicapillus having been assumed by LOCKWOOD \& al. (1998) to be "more migratory" of the two, while according to my (here accepted from HoŁyŃski 2016) evaluation they do not significantly differ in this respect, while a look on the maps of distribution (more northern in R. regulus)
suggests rather the latter having on the average longer distance to cover, in which case the apparent anomaly disappears! So Turdus philomelos vs. T. viscivorus remains the only real exception from the general pattern, but even here the "anomalous" differences in E and L (as well as in $\mathrm{D}!$ ) are very small, while T and a follow (albeit also slightly) the rule!

## Tab. 1

Comparison of various traditional indices in some of the species-pairs used by Lockwood \& al. (1998)
(blue - more migratory; red - less migratory; yellow background - anomalous relation)

|  | N | D | W | T | a | E | L | K |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| Saxicola rubetra | 9 | 5400 | 77.10 | 61.36 | 6.70 | 38.94 | 46.99 | 26.59 |
| Saxicola torquata | 15 | 1300 | 68.53 | 74.39 | 4.27 | 15.82 | 32.34 | 19.12 |
| Turdus iliacus | 33 | 2100 | 119.50 | 70.02 | 7.37 | 58.11 | 66.59 | 33.34 |
| Turdus merula | 58 | 1600 | 129.70 | 82.96 | 3.85 | 21.25 | 44.26 | 22.79 |
| Turdus philomelos | 312 | 2200 | 117.67 | 71.27 | 7.25 | 53.24 | 59.77 | 29.88 |
| Turdus viscivorus | 6 | 1800 | 157.29 | 72.56 | 7.08 | 55.81 | 63.63 | 37.60 |
| Regulus ignicapillus | 26 | 1200 | 52.38 | 77.20 | 0.91 | 6.28 | 38.98 | 20.47 |
| Regulus regulus | 116 | 1200 | 53.80 | 76.61 | 1.30 | 7.54 | 38.76 | 21.19 |
| Parus ater | 149 | 500 | 61.43 | 77.57 | 1.43 | 7.46 | 39.88 | 21.76 |
| Parus palustris | 60 | 100 | 64.06 | 85.64 | -0.20 | -4.43 | 34.76 | 18.70 |
| Fringilla montifringilla | 46 | 2100 | 89.56 | 70.91 | 7.73 | 58.39 | 62.30 | 32.77 |
| Fringilla coelebs | 109 | 1600 | 85.78 | 77.08 | 6.10 | 41.61 | 48.34 | 27.94 |
| Carduelis spinus | 60 | 1500 | 72.23 | 63.68 | 8.69 | 68.30 | 69.36 | 34.74 |
| Carduelis chloris | 18 | 1100 | 87.94 | 63.85 | 8.22 | 63.55 | 65.57 | 32.72 |
| Carduelis cannabina | 1 | 1500 | 82.00 | 64.63 | 9.50 | 68.29 | 68.29 | ------ |
| Carduelis flavirostris | 1 | 1100 | 79.00 | 77.22 | 9.50 | 56.96 | 56.96 | 30.38 |

The relations are clearly visualized on Fig. 2


Fig. 2
Relation between wing pointedness and distance of migration in species-pairs from Tab. 2

## Are Hirundinidae anomalous?

Thus, contrary to the allegations of LOCKWOOD \& al. (1998) but in full accordance with traditional "uncontrolled" analyses of e.g. KIPP (1936, 1958, 1959), RENSCH 1938, StEGMANN (1962) or HOॄYŃSKI (2016) and with theoretical considerations, also in "phylogenetically and ecologically controlled" comparisons indices based directly on "primary distances" prove perfectly "effective at discerning the morphological adaptations to migration". As they are also - unlike cumbersome, counter-intuitive $C_{2}$ - simple in calculation and very close to (in fact, direct representation of) the basic ideas of the respective
qualities [wing pointedness (a, E), elongation (L), wing-tip length (K)] and, consequently, incomparably easier to interpret as well as to disclose eventual mistakes, errors or misconceptions, it is hard to imagine a reasonable justification for replacing them with logically flawed (see also BUSSE 2000) "primary lengths" and computationally complicated component analyses. Last not least, evaluation of different features is, of course, likely to lead to different conclusions, so the comparison between Hirundinidae and other birds, to be meaningful, should also be done with directly comparable metrics, what would need either calculation of $C_{2}$ values also for non-hirundine passeriforms, or presentation of hirundine data in form of traditional indices on which the general rule of "longer migration-distance, more pointed wings" has been based!

Unfortunately, I do not have data to perform my own calculations on the speciespairs used by HUBER \& al. (2017), so am unable to test whether a, E, L or K would also show the "anomaly"; indeed I cannot reliably do this even on other swallows, as measurements of only two appropriate (one long- one short-distance migrant, the latter in both cases represented by single individual...) congeneric hirundine pairs are currently available for me (Tab. 2). The result of these two comparisons are contradictory: Riparia riparia has, like other migratory passeriforms, all indices correlated with wing pointedness ( $\mathrm{E}, \mathrm{L}, \mathrm{K}$ ) much higher than its near-sedentary relative R. cincta, while trans-saharan migrant Hirundo rustica fits the anomaly suggested by HUBER \& al. (2017): only the length of wing-tip (K) being (minimally!) greater, but wing-pointedness ( E ) and elongation ( L ) markedly less pronounced that in African H. albigularis (T measured on outer rectrices, as well as a with upper limit at 10 and accuracy of 0.5 , are in this case uninterpretable).

Tab. 2
Comparison of various traditional indices in two hirundine species-pairs

|  | (blue - more migratory; red - less migratory) |  |  |  |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
|  | N | D | W | T | a | E | L | K |
| Riparia riparia | 14 | 4500 | 109.50 | 50.81 | 9.86 | 116.89 | 116.89 | 55.25 |
| Riparia cincta | 1 | 500 | 127.50 | 49.42 | 10.00 | 98.00 | 98.00 | 45.90 |
| Hirundo rustica | 17 | 4800 | 122.65 | 62.58 | 9.94 | 120.32 | 120.32 | 56.57 |
| Hirundo albigularis | 1 | 2000 | 135.00 | 57.78 | 10.00 | 127.41 | 127.41 | 55.56 |

Thus, I am not able to decide whether Hirundinidae are really anomalous as regards the relation between wing-pointedness and distance of seasonal migration or not. HUBER \& al. (2017) are right: for swallows (and perhaps swifts), as typical "aerial hunters" spending most of the time on flight and, consequently, having wings anyway almost extremely pointed, migration may not offer sufficient selective motivation to further increase of this aspect of wing-shape and improvement of some other abilities (precision of movements, manoeuvrability) may prevail. And indeed, e.g., both factors (necessity to occasionally forage low about the ground, and crowd-roosting habit) suggested by the authors as conceivable explanation of the hirundine anomaly, can promote more "curtailed" and, consequently, less pointed wings: indices of curtailment C and Q - apparently roughly equivalent to "convexity" $\left(C_{3}\right)$ of LOCKWOOD \& al. (1998) - are in pointed (a>7.5) wings negatively correlated with pointedness (HoŁYŃski 2017). So, Huber \& al. (2017) have presented good arguments to show that wings of migratory swallows may conceivably be less pointed that those of their sedentary relatives, but their results, based on inappropriate and incomparable methods, do not convincingly demonstrate that it is really so!

## Closing remark: if it ain't broke, don't fix it

The requirement not to multiply entities beyond necessity („entia non sunt multiplicanda praeter necessitatem"), known as Oскнам's Razor, widely considered the basic principle of scientific reasoning, has usually been applied to explanation of results but is equally valid for earlier steps of elaboration of the accumulated data. So, until a simple, more
intuitive procedure proves sufficient to arrive at the correct conclusion, there is no need to introduce more complex, indirect ones: proverbial using a cannon to kill a mosquito, or sophisticated statistics to demonstrate that elephants are bigger than mice, is not only superfluous but often counter-effective or even misleading [see e.g. BuSSE's (1986) remarks on the indices $S$ and $P$ proposed by MLíкovsKÝ (1978)]! And nevertheless the currently dominating fashion, obstinately enforced (on the - usually false and/or irrelevant... - pretexts of "modernness", "objectivity", or philosophical purity) by publishers, editors, grant distributors \&c., is just to use possibly most complicated, counter-intuitive, often incomprehensible even to users (let alone readers...), methods, computer programs, "models" (usually "multi-storeyed": a model selected by a program based on another model, corrected by still another and evaluated by yet another...), \&c., each introducing its own a priori assumptions, its own inherent errors, its own ambiguities ("... a particular model can be chosen as 'optimal', but might simply represent the best of several extremely poor choices, none of which fit the empirical data well. ..." - Gatesy (2007), so that the reliability of the end result becomes less and less obvious ("numbers are increasingly used as a substitute for real explanation" - FRYER 1987). And, at that, a very destructive effect of this trend is that almost any study is being performed using a different method, with different set of metrics, formulae, indices, making - like in this case - the reliable comparison impossible not only between the results of e.g. Baldwin \& al. 2010, Marchetti \& al. 1995, Pilastro \& al. 1995, LOCKWOOD \& al. 1998, \&c. and those accumulated by earlier authors but even among themselves!

To sum up, indices like a, E, L, or K, based on logically straightforward evaluation of obviously relevant "primary distances", exactly and unambiguously describe the respective aspects of wing shape, so they are - as long as applicable - so to say "inherently" the best possible: any transformation, adaptation to this or that philosophical tenet or statistical model, or other modification, can only spoil the adequacy of final conclusions and should be avoided! Although "Multivariate techniques (such as "factor analysis") perform the illusion of taking all measurements simultaneously" (ELDREDGE 1989) and "a misperception that you are not doing real science unless you are doing it on computers" (Kelly 2008) is almost universal nowadays, but scientists ought to be immune to misleading lures of illusions and misperceptions...

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