AN INDEX TO ESTIMATE THE WING AREA IN A SMALL PASSERINE, USING THE BLUE TIT (*Cyanistes caeruleus*) AS A CASE STUDY

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ABSTRACT

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In this paper we suggest two new indices that can be used to estimate passerines' wing area. The first is a simplified index that considers wing pointedness and the width of each primary, the second is an extended index that also considers the length of the forearm. Using the Blue Tit as an example, we show that the sum of the width of all remiges is correlated with the maximum length of the folded wing ($r_r = 0.42$, $p = 0.020$, $N = 30$). The length of the ulna is correlated with the maximum length of the folded wing ($r_r = 0.56$, $p = 0.005$, $N = 24$). The two indices were derived from measurements of the wing length and the wing formula of birds caught at ringing stations. The indices can be used to analyse materials the stations have collected over the past 50 years. We also discuss how these indices can be applied in intra- and interspecific comparisons and to data collected using different standard methods.

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INTRODUCTION

The ecomorphology of the bird wing has been widely studied to define differences between species' flight aerodynamics and their energetic costs of flight (Yong and Moore 1994, Chatterjee 1997), their tendency to migrate (Lockwood *et al.* 1998, Calmaestra and Moreno 2001, Perez-Tris *et al.* 2003, Fiedler 2005), how related species use different ecological niches (Norberg 1979, Moreno *et al.* 1997) and avoid predatory pressure (Marchetti *et al.* 1995, Swaddle and Lockwood 1998, Fernandez-Juricic *et al.* 2006). The wing loading, the ratio of the bird's weight to its wing surface, is one of the most important parameters used to describe birds' flight performance (Tenne-

kes 1996). Wing area seems to be a simple requirement, but until now there is no uncomplicated and precise method to measure the surface of the wing. The only direct method of taking this measurement is to trace the outline of the open wing (Pennycuick 1989). This measurement is time-consuming and therefore cannot be used as a standard at bird-ringing stations where hundreds of individuals are ringed and measured every day. An additional flaw in this method is the low repeatability of results caused by the subjective way of extending and flattening the wing while drawing the outline (Evered 1990, own experience). Evered (1990) therefore repeated his measurements and used the mean in his calculations, though experience has shown that the first and subsequent measurements taken by one person do correlate well (Evered 1990, Calmaestra and Moreno 2001). At present, measurements of the length of consecutive primaries and secondaries that are processed using Primary Component Analysis (*PCA*) are often used to estimate the flight parameters of wings (Senar *et al.* 1994, Mönkkönen 1995, Alonso and Arizaga 2006, Peiro *et al.* 2006). This technique usually provides two or three significant principal components (*PC1*, *PC2*, *PC3*). The first parameter (*PC1*) reflects the wing size, the second and the third components (*PC2*, *PC3*) describe wing shape. However, *PC1* is not the real area of the wing (Chandler and Mulvihill 1988).

In 1990 Evered suggested a simple index of wing area calculated as the sum of the lengths of 9 primaries (*P2* to *P10*, numbered ascendantly, from the wing tip towards the body as defined by Jenni and Winkler 1994 and Busse 2000) and of 6 secondaries (*S1* to *S6*, numbered descendantly). This text uses the ascendant convention for numbering primaries, which is the SE European Bird Migration Network standard. But many other ringing schemes, such as the British Trust for Ornithology (*e.g.* Ginn and Melville 1983) number primaries descendantly from the carpal joint to the wing tip. For consistency, we have converted all references to our numbering system, even when the original author, such as Evered, used the other convention.

Evered (1990) proved that the mean values of his index calculated for 27 species of birds were strongly correlated with the wing area calculated for these species based on the outline of their wings. The advantage of indices derived from the lengths of remiges to estimate the wing's area and shape is that these measures can be taken quickly and are repeatable (Busse 1967, Jenni and Winkler 1989, Evered 1990, Calmaestra and Moreno 2001). These measurements can be also taken from specimens in museums where the outline of wings cannot be traced (Evered 1990, Svensson 1992). The indices can be also used to analyse measurements collected for years by the large networks of bird-ringing stations, such as the SE European Bird Migration Network (SEEN) and the European-African Songbird Migration Network (EASMN). But ringing stations that work according to the SEEN standard measure only 7 primaries (*P2* to *P8*, Busse 2000), so the index of wing area suggested by Evered (1990) cannot be used with their data.

The wing area depends not only on the length of remiges but also obviously on their width (*e.g.* Marchetti *et al.* 1995). The remiges' width has not been considered in analyses of wings' flight properties yet, either in calculations of indices for the wing area (Pennycuick 1989, Evered 1990) or in analyses of the wing pointedness and sym-

metry using different indices (for review see Lockwood *et al.* 1998 and Busse 2000). The width of the remiges is also seldom considered in the analyses with the *PCA* method (*e.g.* Chandler and Mulvihill 1988, Senar *et al.* 1994, Marchetti *et al.* 1995, Calmaestra and Moreno 2001, Alonso and Arizaga 2006, Arizaga *et al.* 2006, Peiro *et al.* 2006) or the Size-Constrained Components Analysis (*SCCA*) method derived from it (Lockwood *et al.* 1998). The width of feathers, mainly of the rectrices, has been analysed so far mostly in the context of birds' signals in intraspecific communication (Bortolotti *et al.* 2006, Grégoire *et al.* 2007) and in breeding behaviour (Andersson 1994, Mřller and Hedenström 1999, Badyaev and Landeen 2007), as well as in the determination of sex and age in some species (*e.g.* Svensson 1992, McCloskey and Thompson 2000). Its use as a parameter has been restricted because of the difficulty of measuring the width of remex in a small live passerine, whose feathers are usually ruffled when taken from a mist-net or trap. The only way to overcome these difficulties is to find other parameters reflecting a bird's size that are strongly correlated with the width of its flight feathers and are easy to measure.

This paper proposes a simple index that reflects the wing area in passerine birds. It considers the width of the remiges and is derived from standard measurements that are taken at bird-ringing stations working according different procedures.

METHODS

Dead Blue Tits were collected on roads in northern Poland in 2006-2007 during the intensive autumn migration, the time when feathers of immature birds are seldom heavily worn. We collected only immatures with intact left wings and primaries that showed no visible losses or wear. We analysed the measurements of 14 males and 16 females in which sex was determined with a high certainty using the criteria laid out by Busse (1984) and Svensson (1992).

The birds were measured using the standard methods of the SE European Bird Migration Network (Busse 2000), but adjusted to measuring dead birds. The maximum length of folded wing (Busse 2000) was measured with a stopped ruler to the nearest 0.25 mm. The standard measurement in live birds is taken with a ruler without a stop to the nearest 1 mm. Folded wing of a dead bird was fully stretched and flattened on the ruler to obtain its real length. This procedure provides higher accuracy and greater repeatability of the measurement than can be obtained from live birds. The improvements reduced the variance in the results, which allowed us to apply statistical analyses to smaller samples, but they did not change the line of reasoning when applied to measurements taken strictly according to the standard (with lower accuracy). The wing formula, *i.e.* the distances from the tip of folded wing to the tips of consecutive primaries from *P2* to *P8*, numbered ascendantly (compare with Svensson 1992, Busse 2000), were measured according to the standard with accuracy of 1 mm.

The length of ulna and the lengths and widths of all selected primaries were also measured. The ulna was measured after dissection with a calliper to the nearest 0.1 mm. Four remiges were measured – the second, the fifth and the eighth primaries (*P2*, *P5*,

P8) and the first secondary (*S1*) – after they were plucked from the wing. Their lengths were obtained with the feathers maximally stretched and flattened on the stopped rule to the nearest 0.25 mm. These remiges were washed in water with detergent, rinsed and dried, then moistened over steam and dried in a slow stream of warm air to restore the natural shape of their vanes. The feathers were then laid on graph paper, pressed flat under glass and photographed. Their width was measured on the photographs at what we define as the "standard widest point of a feather" determined separately for each type of remex. For primary *P2* it was 13 mm from the tip of feather, for *P5* – 14 mm, for *P8* – 7 mm and for *S1* – 6 mm. The distance between the "standard widest point of a feather" and the feather's tip was determined as the mean of the distances between the widest point and the tip of each feather.

All measurements were taken by the same person (J.K. Nowakowski).

RESULTS

The wing tip of the Blue Tit is usually formed by the fourth and the fifth primary (*P4 + P5*), more rarely by other combinations of primaries, but always including the fifth (*P5 + P6* or *P4 + P5 + P6*). It means that the length of *P5* should be strongly correlated with the length of wing, which proved true (Pearson's correlation coefficient: $r_p = 0.93$, $p < 0.001$, $N = 30$). We found that the length and the width of this primary were also correlated ($r_p = 0.56$, $p = 0.001$, $N = 30$). In consequence we determined indirect correlation between the width of *P5* and the length of the whole wing ($r_p = 0.51$, $p = 0.004$, $N = 30$). Moreover, we determined that the length of wing was correlated with the sum of the widths of all the remiges we measured (*P2 + P5 + P8 + S1*; $r_p = 0.42$, $p = 0.020$, $N = 30$).

The wing lengths plotted against the widths of all measured remiges from males are scattered around a slightly different regression line than the one for females (Fig. 1). Thus these measurements correlated better when calculated separately for each sex than for both sexes combined (but this, of course, makes samples smaller and influences significance). The correlation coefficient for males was $r_p = 0.69$, p = 0.007, $N = 14$ for females – $r_p = 0.47$, $p = 0.069$, $N = 16$.

We also found that the length of ulna correlated with the length of folded wing ($r_p = 0.56$, $p = 0.005$, $N = 24$).

INDICES OF THE WING AREA
AND DISCUSSION OF THESE INDICES

The wing area in passerines can be approximately described by two geometric figures. The first figure, similar to a sector of circle, is formed by the primaries; the second – resembles a trapezium and is formed mainly by the secondaries (Fig. 2A). The suggested simplified index for the wing area reflects the part of the area formed by the primaries. The extended index reflects the area of the whole wing.
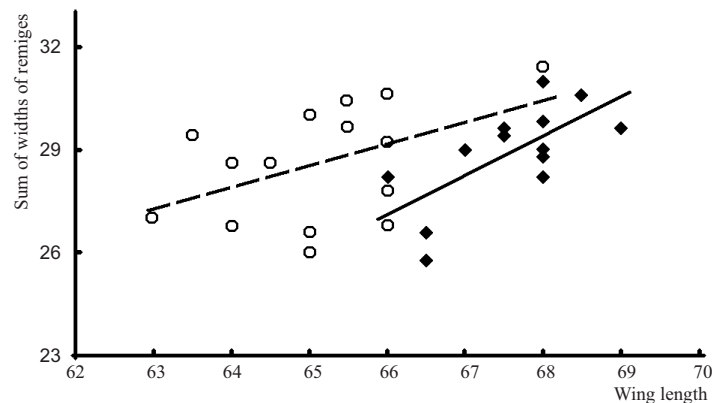
Fig. 1. Relation between the wing length and the sum of widths of four remiges ($P2 + P5 + P8 + S1$) and the fitted regression lines in males (filled squares, solid line) and females (open circles, dashed line) of the Blue Tit

Simplified index of the wing area

Let us measure the maximum length of the folded wing (W), then open the wing and form an arc with the radius $r = W$ whose centre is located where the 0 of the ruler was placed when measuring the folded wing (Fig. 2). This arc is tangent to the longest primary or primaries ($P4$ and $P5$ in Figure 2). Let us define L_i as the distance between the tip of a primary P_i and this arc (Fig. 2B). Each of these distances equals the distance between the wing tip and the tip of each consecutive primary determined when measuring the wing formula (Busse 2000). We obtain the modified wing length W' by calculating the mean L_i and subtracting this value from the wing length:

$$W' = W - \sum_{P_i=2}^{P_i=8} L_i / 7$$

where:
- W' – the modified length of folded wing,
- W – the length of wing,
- L_i – the distance between the tip of a primary (P_i) and the wing tip (see the wing formula measurement in Busse 2000).

Let us define L'_i as the distance between the tip of the primary P_i and the arc constructed as described above but with radius $r = W'$ (Fig. 2). L'_i would have a positive value if the measured primary is longer than W' and a negative value if it is shorter. The sum of L'_i for all measured primaries equals 0 (in Figure 3A: $L'_2 + L'_3 + L'_4 + L'_5 + L'_6 + L'_7 + L'_8$ = [-4.5] + 2.4 + 2.9 + 2.9 + 0.6 + [-0.2] + [-4.1] = 0).

With the same length of folded wing W the value of modified wing length W' would be larger in birds with more rounded wings, *i.e.* with smaller differences in the length between the primaries (Fig. 3A) and smaller in birds with more pointed wings, *i.e.* with greater differences in the length between primaries (Fig. 3B; Busse 2000). A pointed wing of a certain length has a smaller area than a rounded wing of the
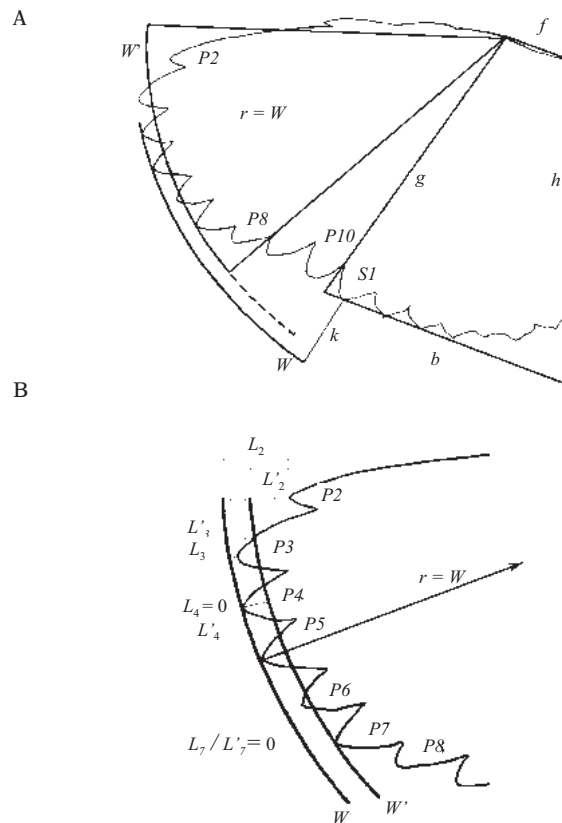
Fig. 2. The wing of the Blue Tit: (A) geometric approximations of the wing area and the measurement of maximum length of folded wing presented on the open wing; (B) measurement of the wing formula on the open wing in relation to the modified length of folded wing. W – the length of folded wing; W' – the modified length of folded wing; L_i – the distance between the tip of a primary (P_i) and the wing tip; L'_i – the distance between the tip of a primary (P_i) and the arch formed by W'; k – the Kipp's index; f – the forearm length; g, h, b – the sides of the trapezium reflecting the forearm part of the wing, their detailed description provided in the text.

same length by the definition of the term wing pointedness (Busse 1967, Busse 2000). By this reasoning, the W' value should be more strongly correlated with the wing area than W.

Hence, we can conclude that using the modified length of folded wing to calculate an index for the wing area allows us to consider the relationship between the wing's pointedness and its area.

The size of the section of circle formed by the primaries depends on how far the wing is opened. In passerines a completely open wing describes less than a quarter of a circle, or less than 90° between the outer edge of primary $P2$ and the inner edge of $P10$ (Fig. 2 and 3). The width of the primaries is one of the main factors that limit this maximum angle of opened wing. That is why these widths affect the wing area and the lift it generates. Moreover, the narrower are feathers, the greater are gaps be-
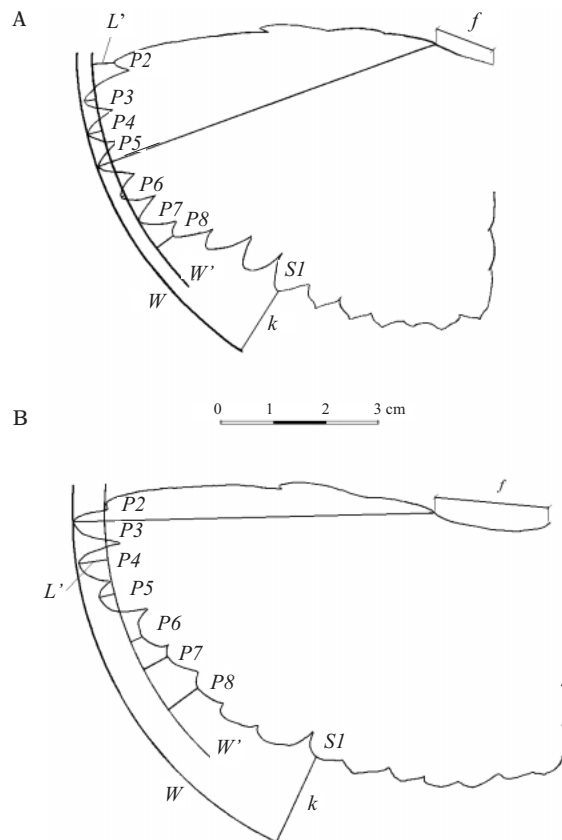
Fig. 3. Measurements of different lengths in the wing of the Blue Tit (A) and the Willow Warbler
(B) with the same 6.8 mm wing length. Explanations of symbols as in Figure 2.

tween their trailing edges at their tips and the leading edge of the next primary at its tip when the wing is open. These gaps increase the wing's aerodynamic performance by suppressing turbulence, but do decrease the wing area and the lift it generates (Tucker 1995, Videler 2006). Overlapping remiges provide an unbroken surface that generates more lift. Therefore the width of feathers should be considered when designing an index for the wing area, especially if it is to be used to calculate an index of wing loading. As proved in the results, the sum of the feathers' widths is correlated with the wing's length. So the wing length can be used as an indicator of the width of remiges. We suggest that the simplified index of the wing area (S') can be used. It is calculated as the product of the modified wing length W', reflecting its pointedness, and the maximum length of folded wing W, reflecting the width of remiges, expressed in mm², according to the equation:

$$S' = W' \times W$$

where:
    S' – the simplified index of the wing area.

The suggested simplified index of wing area reflects only the area formed by primaries *P2* to *P8* (Fig. 2), because only these feathers are measured at bird-ringing stations working to the SEEN standard. Material collected at stations working to the EASMN standard or gathered in special studies may consider the lengths of all primaries that are not reduced, as in passerines, by including them in the calculations of the modified length of the folded wing. In this case the equation would have the form:

$$W' = W - \sum_{P_i=2}^{P_i=10} L_i \, / \, 9$$

The extended index of the wing area

The extended index of the wing area (*S*) considers also the forearm part of the wing area where the lifting surface is formed by the secondaries. This part of the wing has the shape of a trapezium, in which the length of the top side (*f*) is approximately the length of the forearm bones (ulna and radius), the length of the sides (*g* and *h*) correspond with the length of the secondaries plus the width of the forearm bones and the bottom (*b*) corresponds with the width of the trailing edge of the secondaries (Fig. 2A). As we showed in the results, the length of the larger of the two forearm bones (the ulna) is correlated with the wing length within a species. The length of the side g of this trapezium equals approximately the wing length diminished for Kipp's index (*k*), *i.e.* the distance between the wing tip and the tip of the first secondary *S1*, measured on the folded wing (Kipp 1959, Fig. 2). Kipp's index is a standard measurement taken at bird ringing stations in the EASMN network, but has been taken as an additional measurement at some stations working according to the SEEN standard.

The angles of the trapezium formed by the secondaries, and thus the length of the bottom (*b*) of the trapezium depend on how much the wing is opened. Depending on how far the wing is opened we can obtain a rectangle with one side equal to *f* and the second one equal to *W – k*. Because *f* is correlated with *W* we suggest an approximation of the area of this part of the wing with the formula: $W \times (W - k)$. This is justified because the maximum extent the forearm part of the wing can be opened is related to the width of secondaries. We assume that the width of secondaries within a species is related to the wing length, as in this paper the total width of the remiges including *S1* was correlated with the wing length (see later discussion).

The extended index for the wing area is the sum of the approximate areas of both parts of the wing, the hand part and the forearm part, expressed in mm², calculated from the equation:

$$S = S' + W \times (W - k) = (W - \sum_{P_i=2}^{P_i=8} L_{Pi} \, / \, 7) \times W + W \times (W - k)$$

where:
    S – the extended index for the wing area,
    k – Kipp's index.

Simplifying the equation for the extended index of the wing area yields the form:

$$S = W \times (2W - \sum_{P_i=2}^{P_i=8} L_{Pi} \, / \, 7 - k)$$

Discussion on the indices for the wing area

The suggested indices for the wing area are based only on standard measurements that have been collected for years at bird-ringing stations. The extended index can be applied to measurements taken according to the EASMN standard. Stations operating according to the SEEN standard take measurements that allow to calculate only the simplified index for wing area. However, in the 1960s and the 1970s Kipp's index was also measured in tens of thousands of passerines at SEEN stations. The suggested indices use measurements that have been taken for decades, so they can be used on material that has already been collected. SEEN's databases alone contain records from about a million individuals measured over the past 50 years. The indices would allow new research that includes this material, such as an analysis of evolutionary changes in the flight properties of wings connected with global climate warming for partial migrants (Nowakowski in prep.).

We should emphasise that SEEN and EASMN use different standards to measure the wing formula. In the SEEN standard (Busse 2000), the distance between the tip of each primary and the wing tip is measured, directly giving us the values of L_i. In the EASMN standard (Bairlein 1995), which is also used at many ringing stations that do not belong to this organisation, such as those in the UK and the USA (*e.g.* Evered 1990), the length of each primary is measured separately and the approximate values of L_i can be calculated as the difference in length between the longest primary and each primary P_i. As proved by Przemysław Busse (unpubl. data) values of L_i calculated this way do not correspond exactly with the values of L_i obtained from direct measurements, because the hand bones of the manus on which the primaries are fixed are not perpendicular to the axis of the measurement during the operation, because the places where consecutive remiges are fixed are located at different distance from the wing tip. The value of L_i during direct measurement is determined by the difference in the length of measured primaries and by the place they are fixed on the manus, but L_i calculated from measurements taken under the EASMN standard reflect only differences in the length of measured primaries. Thus values for the proximal primaries L_i measured directly are larger than those calculated from the difference in the length of primaries, but for distal primaries L_i from the direct measurement are smaller than those from calculated L_i. Because these differences are relatively small, in our opinion L_i obtained from both methods can be used to calculate the indices of the wing area presented in this paper. Nevertheless, indices calculated with the use of L_i obtained by the different methods should not be directly compared. Conversion factors must be calculated for each species if L_i obtained by different methods are compared.

The indices for the wing area suggested in this paper are based on correlations between the lengths and the widths of different elements of the wing that are demonstrated using the Blue Tit as an example. Some of these elements are not functionally connected and are formed by different tissues. So their correlated size, such as the correlation of the wing length and the length of the ulna, might seem puzzling. But

the wing bones and wing feathers in juvenile passerines, which are mainly altricial, grow in the relatively short time the young birds stay in the nest. So the growth of these elements is controlled by the same favourable or unfavourable environmental conditions, such as food abundance and temperature. Thus, we can assume that other small passerines also show the same correlations between the described elements of the wing and that the suggested equations can be successfully applied in intraspecific comparisons for a wide range of bird species. However, the proportions of the parts of wing differ among species, which can be seen in Figure 3 from the comparison of wings of the Blue Tit and the Willow Warbler (*Phylloscopus trochilus*). Compare for example the wing length *W* and the forearm length *f* of these species. The results of this paper suggest that intraspecific comparisons of the real wing areas and the values calculated using the indices are strongly correlated, though the regression is not necessarily linear. The sizes and parameters of regression curves for different species will likely vary greatly, especially among species of different ecological groups and among resident and migratory species. Because of that the suggested indices are not particularly suitable for interspecific comparisons, but should be applied only in comparisons of closely related species or in analyses of very general trends. The index suggested by Evered (1990) has the same fault. Moreover, differences in the described proportions may also occur within a species, for example between the sexes, as suggested by the results of this paper.

The indices for wing area presented in this paper are based on similar assumptions to the indices of wing shape suggested by Hołyński (1965) and Busse (1967), however, they extend and supplement them. In particular, it is difficult to interpret the index of wing pointedness (Busse 1967, 2000) because that index describes the shape and the area of wing at the same time. With the same wing length, higher values of this index mean greater differences between the wing tip and the tips of consecutive primaries, hence a more pointed wing with smaller total area. But more pointed wings are usually less symmetrical (Hołyński 1965). The simultaneous use of all three indices – wing pointedness, symmetry and area – in multi-factorial analysis, such as the General Linear Models (GLM), allows researchers to draw credible conclusions about wing properties and in what proportions the different factors influence the studied phenomenon. This gives us a tool to look for links between the flight properties of the wing and birds' biology, feeding technique, social rank and the migration tendencies of individuals in a population, and of populations of one species.

In conclusion we can state that the suggested indices for wing area provide a relatively precise tool for intraspecific comparisons though the outline of the wing remains the best tool in interspecific comparisons and in analyses where we need the exact wing area.

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