

whereas residents must engage in other activities. One could test this hypothesis by comparing either fat levels or body mass per unit size of challengers and residents during takeover attempts.

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#### LITERATURE CITED

- ARCESE, P. 1989. Territory acquisition and loss in male Song Sparrows. *Anim. Behav.* 37: 45-55.
- ECKERT, C. G., & P. J. WEATHERHEAD. 1987. Owners, floaters and competitive asymmetries among territorial Red-winged Blackbirds. *Anim. Behav.* 35: 1317-1323.
- FREED, L. A. 1986. Territory takeover and sexually selected infanticide in tropical House Wrens. *Behav. Ecol. Sociobiol.* 19: 197-206.
- . 1987a. Prospective infanticide and protection of genetic paternity in tropical House Wrens. *Am. Nat.* 130: 948-954.
- . 1987b. The long term pair bond of tropical House Wrens: advantage or constraint? *Am. Nat.* 130: 507-525.
- HAMMERSTEIN, P., & G. A. PARKER. 1982. The asymmetric war of attrition. *J. Theor. Biol.* 96: 647-682.
- JAKOBSSON, S. 1988. Territory fidelity of Willow Warbler (*Phylloscopus trochilus*) males and success in competition over territories. *Behav. Ecol. Sociobiol.* 22: 79-84.
- JOHNSON, L. S., & L. H. KERMOTT. 1990. The structure and context of female song in a north-temperate population of House Wrens. *J. Field Ornithol.* (in press).
- KREBS, J. R. 1982. Territorial defence in the Great Tit (*Parus major*): do residents always win? *Behav. Ecol. Sociobiol.* 11: 185-194.
- LEIMAR, O., & M. ENQUIST. 1984. Effects of asymmetries in owner-intruder conflicts. *J. Theor. Biol.* 111: 475-491.
- MAYNARD SMITH, J. 1974. The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* 47: 209-221.
- , & G. A. PARKER. 1976. The logic of asymmetric contests. *Anim. Behav.* 24: 159-175.
- PARKER, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* 47: 223-243.
- UEDA, K. 1986. A polygamous social system of the Fan-tailed Warbler *Cisticola juncidis*. *Ethology* 73: 43-55.
- WALTON, R., & V. NOLAN JR. 1986. Imperfect information and the persistence of pretenders: male Prairie Warblers contesting for a territory. *Am. Nat.* 128: 427-432.

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## Measures of Wing Area and Wing Span from Wing Formula Data

DUNCAN STUART EVERED<sup>1</sup>

Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221 USA

The modification of wing shape is an important feature of many avian adaptive radiations, whether the differences are among major taxa (Saville 1957) or within a group of closely related species (Gaston 1974,

Fitzpatrick 1985). An accurate and convenient description of wing-shape variation is relevant to many systematic and comparative studies of birds.

Wing shape is often described by means of tracing or photographing the outline of the extended wing. However, wing formulae, long recognized as useful descriptors of wing shape (Johnson 1963, Svensson 1975), have several important advantages. For example, measuring the distance between successive

<sup>1</sup> Present address: Cincinnati Museum of Natural History, 1720 Gilbert Avenue, Cincinnati, Ohio 45202 USA.

primary tips on the closed wing is inherently more precise than obtaining the outline of an outstretched wing, because the precision with which wing outlines can be defined depends critically on the subjective control of the extension and flatness of the wing. Further, data generated from wing formulae are better suited to familiar statistical techniques than are data derived from the outlines of wings (but see Bookstein et al. 1985). Finally, wing outlines can be obtained only from material that allows the wing to be extended. In contrast, wing formulae can also be taken from study skins, which are relatively numerous in museum collections and often include rare or extinct species.

Wing span and wing area are fundamental descriptors of wing shape. Both are important variables in systematic and comparative studies of wing-shape variation (e.g. Fitzpatrick 1985) that draw on aerodynamic theory (Brown 1963, Rayner 1988). Despite considerable efforts to obtain wing areas and wing spans directly from spread wings, the limited availability of the necessary living, alcohol-preserved, or freshly killed specimens has severely restricted sample size within species and the scope of taxonomic coverage in many studies. These sampling constraints could be alleviated if adequate measures of wing span and wing area can be derived from wing formulae taken from study skins in museum collections.

I evaluated the adequacy of using wing formulae to characterize the interspecific variation in wing area and wing span of 27 species of North American wood-warbler (Parulinae). I used linear regression techniques to assess how much variation can be modeled from wing-formula data, and to what extent unexplained variation is due to sampling bias and the existence of different linear relationships in the different genera (phylogenetic allometry).

Wing span and wing area can be defined graphically (Fig. 1a). When wing area and wing span are measured from a single wing, their definitions are not identical with those used in flight mechanics, which includes both wings and the body between the wing roots. However, these "single wing" definitions of wing area and wing span yield variables proportional to those used in flight mechanics, given that a bird's wings are the same size, and body size is proportional to wing size.

From 1982–1988 I recorded wing formulae from wood-warblers mist-netted in Massachusetts, Michigan, Ohio, and Ontario. Most (85%) were examined during early autumn migration to ensure most individuals had fresh, fully grown primaries. Individuals with signs of primary molt, or with worn or broken primary tips, were excluded from the analysis. I measured the distances between successive primary tips on the naturally closed wing with Mitutoyo dial calipers to the nearest 0.1 mm, and wing length (wing flattened and straightened) with a rule to the nearest 0.5 mm (Svensson 1975). From these data, I calculated

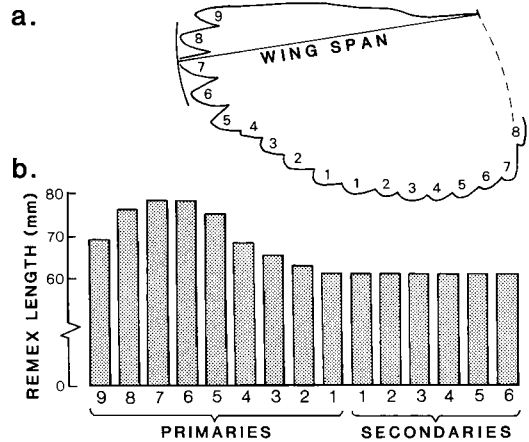


Fig. 1. Representations of the wing of the Yellow-breasted Chat (*Icteria virens*). (a) A single wing tracing to define the conventions used to measure wing span and close the wing outline (dashed line) for area measurement. (b) Average remex lengths calculated from wing formulae. The index of area was obtained by summing these remex lengths.

the distance from carpal joint to primary tip on the folded wing for each of the nine primaries (hereafter primary length). An index of area was found by summing the primary lengths and six secondary lengths (Fig. 1b). The secondaries were not measured, but they were on average the same length as the innermost primary.

Wing tracings and wing length (natural, unflattened chord to the nearest 1 mm) were obtained from fresh, window-killed wood-warblers collected from 1978–1985 in Chicago, Illinois. I measured wing span (to the nearest 1 mm) from these wing tracings with calipers. Wing outlines were completed by extending a curve that followed the inner edge of the seventh secondary (first tertial) to the proximal leading edge of the wing (Fig. 1a). The seventh secondary was chosen because its outline was more consistent than the sixth secondary in this particular set of wing tracings. The outline of each wing was digitized on a 30 cm × 30 cm Summagraphics digitizing tablet, and the wing area computed by trapezoidal integration in a BASIC program. I used the mean of two replicates to represent the area of each wing tracing. Computed areas were highly repeatable,  $r = 0.996$ , with a mean replicate difference ( $\pm$ SD) =  $0.22 \pm 0.16$  cm<sup>2</sup>. Sample sizes for the 27 species in nine genera common to these measures varied widely (Table 1).

The adequacy of the wing formula derived variables was evaluated by two linear regressions, wing area vs. index of area, and wing span vs. wing length. I assessed the influence of the general size of each species on these regressions by repeating each re-

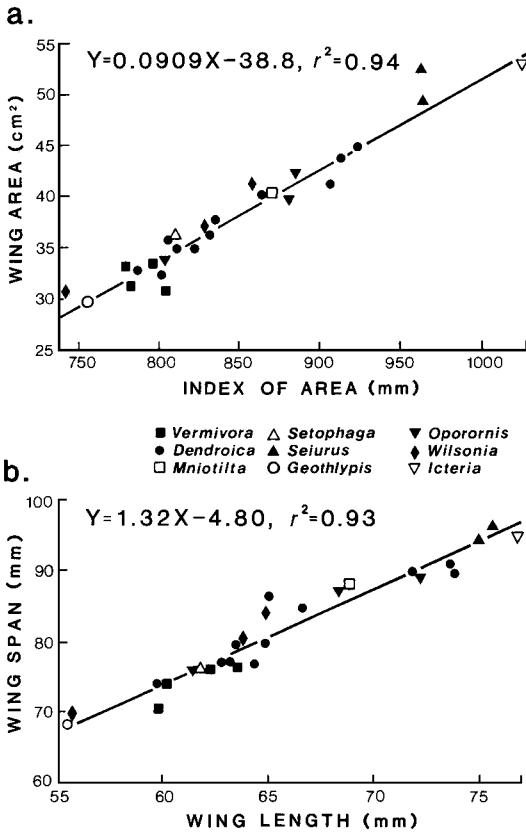


Fig. 2. Regressions of (a) wing area vs. index of area, and (b) wing span vs. wing length; sample means used for each species. There was no significant difference between different genera in the form of either of these linear relationships.

gression with wing variables made independent of size. The size-independent wing variables used were residuals from separate linear regressions of each original variable against the geometric mean of 54 linear skeletal measurements ( $n = 20$  for each species, from Ostroff 1985). I assessed the effect of sampling bias on the fit of the regression models by weighting each species by either the tracing sample size, wing formula sample size, or product of these sample sizes. Allometric effects due to phylogeny were investigated by testing for the significant effect of genus. I performed the general linear model of the analysis of variance (ANOVA) and covariance (ANCOVA) on SYSTAT (Wilkinson 1988).

Strong relationships exist between index of area and actual wing area, and between wing length and wing span (Fig. 2). Furthermore, a substantial proportion of the scatter around these regression lines was attributable to sample heterogeneity. For both regressions, weighting by the product of the sample

TABLE 1. Sample sizes for 27 species of Parulinae used in the wing tracing and wing formula datasets.

| Species                      | Sample size  |              |
|------------------------------|--------------|--------------|
|                              | Wing tracing | Wing formula |
| <i>Vermivora chrysoptera</i> | 1            | 4            |
| <i>V. peregrina</i>          | 8            | 62           |
| <i>V. celata</i>             | 1            | 11           |
| <i>V. ruficapilla</i>        | 7            | 30           |
| <i>Dendroica petechia</i>    | 3            | 13           |
| <i>D. pensylvanica</i>       | 1            | 29           |
| <i>D. magnolia</i>           | 11           | 111          |
| <i>D. tigrina</i>            | 3            | 23           |
| <i>D. caerulescens</i>       | 2            | 15           |
| <i>D. coronata</i>           | 4            | 58           |
| <i>D. virens</i>             | 4            | 26           |
| <i>D. fusca</i>              | 2            | 6            |
| <i>D. palmarum</i>           | 1            | 16           |
| <i>D. castanea</i>           | 4            | 26           |
| <i>D. striata</i>            | 1            | 65           |
| <i>Mniotilta varia</i>       | 5            | 47           |
| <i>Setophaga ruticilla</i>   | 6            | 59           |
| <i>Seiurus aurocapillus</i>  | 10           | 5            |
| <i>S. noveboracensis</i>     | 2            | 27           |
| <i>Geothlypis trichas</i>    | 19           | 41           |
| <i>Oporornis formosus</i>    | 3            | 6            |
| <i>O. philadelphia</i>       | 10           | 17           |
| <i>O. agilis</i>             | 1            | 6            |
| <i>Wilsonia citrina</i>      | 1            | 8            |
| <i>W. pusilla</i>            | 4            | 21           |
| <i>W. canadensis</i>         | 9            | 23           |
| <i>Icteria virens</i>        | 2            | 22           |
| Mean ± SD                    | 4.8 ± 4.5    | 30.4 ± 24.5  |

sizes substantially improved the fit (Table 2). The excellent fit of data to the regression models is especially noteworthy, because weighting by sample size can only incompletely account for age/sex bias and does not account for the likely geographic sources of variation between samples.

Size variation among species did not appreciably inflate the strength of these relationships. The proportion of variation explained in the regressions was only slightly decreased when each variable was replaced by its size-independent analogue. After weighting by the product of sample sizes,  $r^2 = 0.92$  in both regressions.

I found no significant effects (ANCOVA) due to genus for either the wing-area or wing-span relationships. However, significance may be difficult to demonstrate as species numbers were low in most genera (Table 1). To effectively increase sample size, I considered individuals in the relationship between wing span and wing length. The regression relationship between the wing length and wing span of individuals was similar to that obtained using species' means,

TABLE 2. The effect of weighting the wing area and wing span regressions by sample size (*n*).

| Weighting variable                            | Proportion of variance explained |                 |
|---|----------------------------------|-----------------|
|   | Area regression                  | Span regression |
| None  | 0.94                             | 0.93            |
| Wing formula, <i>n</i> <sub>1</sub>           | 0.96                             | 0.96            |
| Wing tracing, <i>n</i> <sub>2</sub>           | 0.98                             | 0.97            |
| <i>n</i> <sub>1</sub> × <i>n</i> <sub>2</sub> | 0.99                             | 0.98            |

$$\text{WING SPAN} = 4.16 + 1.21 \times \text{WING LENGTH},$$

$$r^2 = 0.93.$$

The species effect in this regression model was significant and due to two species (Table 3). The Tennessee Warbler (*Vermivora peregrina*) had a disproportionately short inner wing, and the Black-and-white Warbler (*Mniotilta varia*) a relatively long inner wing. This implies that significant allometric effects are demonstrable, but because the species are in different genera, there was a lack of appreciable phylogenetic allometry.

I suggest that wing length and an index of area obtained from wing formula data are adequate surrogate variables for wing span and wing area, at least for the purposes of interspecific comparisons within the Parulinae. The regression equations obtained separately for each genus were not significantly different, despite the overall morphological diversity of these parulines. I recommend that phylogenetic allometry be tested whenever possible, as its importance may vary in different taxa.

I measured wing formulae on live birds, but the utility of the arguments made here concerns taking wing formulae from museum specimens. In my experience, wing formulae from study skins produce reliable descriptions of wing shape. Care must be taken in the selection of specimens because damage that is due to shot, poor setting of the wings, and years of physical abuse may distort the specimen. The effects of more subtle changes in the relative position of the primary tips, due to uneven wing shrinkage or the deformation of primaries caused by some preparation techniques, can be minimized by sampling from several independent series.

The index of area I used reflected the flight feather configuration of wood-warblers (nine primaries and six secondaries). For taxa with different numbers of remiges, different indices of area will be more appropriate. The treatment of the secondaries as equal in average length to the innermost primary is an assumption that should be qualified, especially in taxa with more rounded wings.

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TABLE 3. A partial decomposition of the sums of squares (SS) for the species effect in the wing span vs. wing length ANCOVA, *R*<sup>2</sup> = 0.97.

| Source                     | SS     | df | <i>P</i> |
|----------------------------|--------|----|----------|
| Wing length                | 334.61 | 1  | <0.0001  |
| <i>Vermivora peregrina</i> | 100.98 | 1  | <0.0001  |
| <i>Mniotilta varia</i>     | 52.06  | 1  | 0.001    |
| Other species              | 96.56  | 16 | 0.05     |
| Error                      | 266.05 | 83 |          |

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LITERATURE CITED

BOOKSTEIN, F. L., B. CHERNOFF, R. L. ELDER, J. M. HUMPHRIES, G. R. SMITH, & R. E. STRAUSS. 1985. Morphometrics in evolutionary biology. Acad. Nat. Sci. Philadelphia, Spec. Publ. 15.

BROWN, R. H. J. 1963. The flight of birds. Biol. Rev. 38: 460-489.

FITZPATRICK, J. W. 1985. Form, foraging behavior, and adaptive radiation in the Tyrannidae. Pp. 447-470 in Neotropical ornithology. Ornithol. Monogr. 36.

GASTON, A. J. 1974. Adaptation in the genus *Phylloscopus*. Ibis 116: 432-450.

JOHNSON, N. K. 1963. Biosystematics of sibling species of flycatchers in the *Empidonax hammondi-oberholseri-wrightii* complex. Univ. California Publ. Zool. 66: 79-238.

OSTROFF, S. J. 1985. A phenetic study of the wood-warblers (Parulidae). Ph.D. dissertation, Toronto, Univ. Toronto.

RAYNER, J. M. V. 1988. Form and function in avian flight. Curr. Ornithol. 5: 1-66.

SAVILLE, D. B. O. 1957. Adaptive evolution in the avian wing. Evolution 11: 212-224.

SVENSSON, L. 1975. Identification guide to European passerines. Naturhistoriska Riksmuseet, Stockholm.

WILKINSON, L. 1988. SYSTAT: the system for statistics. Evanston, Illinois, Systat Inc. (version 4).

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