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Source: The Auk, 121(3) : 973-976

Published By: American Ornithological Society

URL: https://doi.org/10.1642/0004-8038(2004)121[0973:CTFWMI]2.0.CO;2

Commentary

The Auk 121(3):973–976, 2004

CONFLICTING TERMINOLOGY FOR WING MEASUREMENTS IN ORNITHOLOGY AND AERODYNAMICS

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It has come to our attention that certain frequently used terms describing wing dimensions refer to different morphological features when used by ornithologists, as opposed to physiologists or physicists working in aerodynamics. Potential for confusion certainly exists, particularly now that the study of avian aerodynamics may be entering a very active phase, given theoretical (Rayner 1979a, b; Ellington 1984b; Norberg 1995; Dickinson et al. 1999) and experimental (e.g. Chai and Dudley 1995, Dial et al. 1997, Spedding et al. 2003, Tobalske et al. 2003) advances in animal-flight research over the past few decades. Here, we describe the conflict in terminology and suggest a solution, in hopes of avoiding misunderstandings in future studies of aerodynamics by ornithologists. We also discuss how ornithologists might best take some measurements of interest in aerodynamics studies.

In aerodynamics, the definition of wing length R is distance from base of the wing to tip. For birds, that distance should be measured on a wing extended in a natural position, as during flight (see Fig. 1). Wing chord c is defined in aerodynamics as any straight-line distance between leading and trailing edges of the wing, taken perpendicular to the long axis of the wing (i.e. wing length)—and that definition appears in standard non-ornithological sources like the Oxford Unabridged Dictionary. Animal wings typically vary in chord length from base to tip (most wings become narrower distally), and mean chord of the wing is defined as $S/2R$, where S is the area of both wings (Ellington 1984a).

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The definition of wing length in ornithology has been more ambiguous. Because classical ornithology developed around use of bird specimens, the traditional measurement of wing length was the one taken most conveniently on study skins (and most mounts): distance from bend of wing (i.e. wrist joint) to tip of the longest primary feather, measured over the folded wing (Fig. 1). That is the only measurement of wing length given in most ornithology textbooks (e.g. Pettingill 1985, Proctor and Lynch 1993); in many classical works (e.g. Ridgway 1901), the measure is called simply "wing," though in one standard reference (Baldwin et al. 1931) a more accurate term, "length of closed wing," is

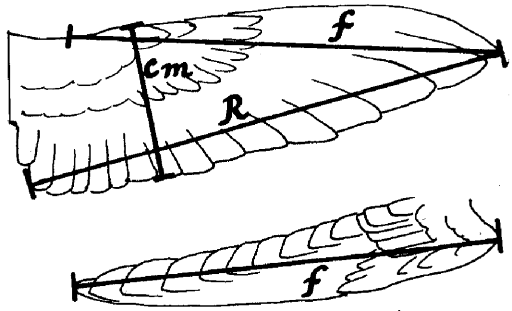

Fig. 1. Measurements of a wing of a hummingbird (male *Heliodoxa aurescens*). Top: spread wing, opened to approximate the natural extended position in flight. Bottom: the same wing in closed (folded) position, as in a perched bird (or a study skin). Abbreviations: f = length of closed (folded) wing; R = length of wing; c_m = length of (maximum) chord or "width" of wing. Note that position of wrist joint, or bend of wing, is not obvious on the planform of the spread wing. See text for details.

used. As banders and other field ornithologists began measuring more birds, it became evident that the wing length measurement could be taken in three different ways: (1) by the "classical" method, with the normal dorsoventral curvature of primaries maintained—usually called "wing chord" and taken with calipers; (2) with the primaries flattened against a ruler (usually with a vertical stop at 0)—called "length of flattened wing"; and (3) with the primaries flattened and extended to their maximum length—called "length of flattened and extended (or stretched) wing." The first method works best with study skins, because the dried wing is often difficult to lift to insert a ruler; the second and third measurements are chiefly taken on live birds in hand. Relative precision of the three wing measurements is still being debated (e. g. Parkes 1988, Winker 1998), but our point is that none of them correspond to the aerodynamics definition of wing length (and "wing chord" means very different things in ornithology and aerodynamics).

Because the aerodynamics definitions of "wing length" and "wing chord" are much more widely used, we recommend that ornithologists adopt them (Table 1). Given that the traditional ornithological measurement of wing length does not, in fact, measure the entire wing's length but only the length of the distal part (wrist to wingtip), taken over the folded (closed) wing, we recommend that ornithologists explicitly indicate that by adopting the term "length of closed wing" from Baldwin et al. (1931). Where different measurement methods are specified, we recommend "chord of closed wing"; "length of closed, flattened wing"; and "length of flattened and extended closed wing" for definitions (1), (2), and (3) above, respectively. These terms are more accurate and would avoid potential confusion in future aerodynamics studies. Their phrasing is slightly more cumbersome, but that does not seem onerous, given that they would typically appear once in the Methods section of a paper and could be abbreviated thereafter. In effect, we simply suggest that ornithologists recognize explicitly the difference between viewing bird wings as taxonomic or identification tools and viewing them as aerodynamic structures.

Methods for taking the three measurements of (closed) wing length *f* are well known in ornithology. Methods for measuring aerodynamic

Table 1. Suggested terminology and definitions for wing-length measurements.

Recommended term	Definition	Present ornithological term(s)
Wing length	Distance between base and tip extended during natural flight position.	Total wing length
Wing chord	Distance between leading and trailing edge during natural flight position.	Wing width
Length of closed wing	Distance between wrist joint and tip of longest feather, over folded wing.	Wing, wing chord, wing length
(1) Chord of closed wing	As above, with curvature of primaries maintained	Wing, wing chord, wing length
(2) Length of closed, flattened wing	As above, with primaries flattened against a ruler.	Length of flattened wing
(3) Length of flattened and extended closed wing	As above, with primaries flattened and extended.	Length of flattened and stretched wing
Wing span	Distance between outer tips of left and right wings during natural flight position.	Wing span

wing length *R* are less available to ornithologists, and we present a brief description here. Animal wings obviously differ from airplane and helicopter wings, and two of the differences make measurement of animal wings less straightforward. First, animal wings are more pliable and typically exhibit considerable torsion axially. Second, positions and degrees of overlap of feathers of bird wings vary over the course of a wingbeat. Both wing torsion and wing area in birds will thus change as a function of wing position, direction, and velocity. Ideally, measured wing lengths and chords should correspond to the position at which most power is generated (i.e. during the middle portion of the downstroke or, for larger soaring birds, the position while ascending, as in a thermal).

The technique we recommend is to hold the wing in the mid-downstroke position against graph paper and take a digital photograph. The only challenge in that technique is determining the correct wing position. While the photograph is being taken, the bird should be held with its body parallel to the edge of the paper and flush against it, and the wing should be extended—slightly anterior to the perpendicular of the paper's edge—to permit the inner secondaries to fall naturally into place. Usually, the tips of most of the secondaries and inner primaries fall along a nearly straight line roughly parallel to the leading edge of the wing, the outer primaries tapering distally to the wingtip. The base of the outermost primary should continue the similarly nearly straight line from wing base along the leading (carpal) edge of the wing; the tips of the outer, longest primaries should be evenly spaced (as in a slotted wing). (Note that whereas the forearm bones and carpometcarpus join at a slight angle, the patagium normally maintains the straight leading edge of the wing; hence, one should avoid pressing inward while tracing that edge to avoid distortion.) Because it is often difficult to determine precisely the location of the shoulder joint, distance from tip of the innermost long secondary to tip of the longest primary is a reasonable approximation to "true" wing length. (We specify the innermost long secondary because the proximal 1–3 secondaries are usually much shorter than the rest, serving mainly to cover the latter when the wing is folded, and do not appreciably extend proximally, such that using the innermost secondary could underestimate wing length).

Digital images of the wing are inexpensive, accurate, archivable, and downloadable to a computer. For analysis, the images can be imported into image-analysis software, such as NIH Image for Macintosh users (available at rsb.info.nih.gov/nih-image/), with which one can measure wing length, wing area, and length-specific wing chord (e. g. Altshuler 2001).

An alternative procedure that works well for small birds when a digital camera is not available is to press the wing in appropriate position against the paper and make a tracing of the wing. That tracing can then be cut out and its area measured with the appropriate software or a leaf-area meter (e.g. Stiles 1995). If wing position is standardized, in our experience the two techniques give comparable results.

We should note that pressing the wing against the paper eliminates the normal dorsoventral curvature of the primaries; the resultant figure is a planform of the flattened wing (analogous to the measure of length of the flattened, closed wing); the width of the planform (measured at the level of the tip of the first or second primary) will exceed the chord of the unflattened wing (effectively, the maximum chord c_m) measured at the same point. Because curvature or camber (convex dorsally, concave ventrally) of the primaries is relatively slight, that difference is usually small: for a sample of 15 hummingbird species varying from 38 to 75 mm in wing length, the mean difference was 1.75% ± 0.27% (F. G. Stiles unpubl. data). Because the basal part of the wing (where the secondaries insert) is much more strongly cambered, care should be taken to exert any pressure on the primaries rather than the secondaries when restraining and positioning the wing, to reduce distortion of its normal form.

These measures can be taken on live birds or recently dead ones. Dead birds that have been kept for some time in a freezer may become desiccated and may require, in addition to thawing, soaking in cool water to relax the wing so that the feathers fall naturally into position. For live birds, the most important requisite for avoiding injury to the flight muscles is that the wing be completely immobilized. For small birds, such as hummingbirds, one person can hold the bird and take a wing tracing unassisted; the photographic method requires two people, one holding the bird and the other taking the photograph. For birds larger than small passerines, more than one person may be needed to restrain the bird; in such cases, the photographic method is superior, because it requires immobilizing the wing for considerably less time (using a prefocused camera). A small, black cloth hood, placed over its head, often helps keep the bird calm and immobile while a wing tracing is taken. Wing length and wing area having been measured, one can calculate mean wing chord and various other parameters of interest in aerodynamics studies, including first, second, and third moments of wing area (Weis-Fogh 1973, Ellington 1984a).

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Received 31 May 2002, accepted 29 March 2004
Associate Editor: K. G. Smith