

## THE RELATIONSHIP BETWEEN WING AREA AND RAGGEDNESS DURING MOLT IN THE WILLOW WARBLER AND OTHER PASSERINES

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**Abstract.**—Molt involves increased metabolic cost due to the energy required to synthesize new feathers and increased cost of thermoregulation because the insulation capacity is reduced. Flight cost is also increased because wing span and wing area are reduced when remiges are missing or growing. However, data on the reduction of wing area during molt (necessary for calculating aerodynamic performance) is lacking. I show how standard molt scores (converted into a raggedness score) can be used to estimate the reduction of wing area due to molt in Willow Warblers (*Phylloscopus trochilus*) and selected other passerines. Maximum wing area reduction associated with maximum raggedness score of the birds examined was approximately 10%. Wing loading will therefore become increased during molt and flight performance will be reduced in similar ways as during migratory fattening.

### LA RELACIÓN ENTRE EL ÁREA DEL ALA Y LA DESALINEZ DURANTE LA MUDA DE PHYLLOSCOPUS TROCHILUS Y DE OTRAS PASERINAS

**Sinopsis.**—La muda incluye aumentos en costos metabólicos por la energía requerida para sintetizar plumas nuevas y al costo de termoregular, porque la capacidad de insulación se reduce. Los costos de volar también aumentan porque la expansión y el largo del ala se reducen cuando las remeras faltan o están creciendo. Sin embargo, faltan datos sobre la reducción del área del ala (necesarios para poder calcular la ejecución aerodinámica) durante la muda. Aquí muestro como registros regulares de muda (convertidos en datos de desalinez) pueden usarse para estimar la reducción del área del ala debido a la muda en *Phylloscopus trochilus*, y en otras aves paserinas seleccionadas. La reducción máxima del área del ala asociada con la mayor desalinez en las aves examinadas fué de aproximadamente un 10%. Por lo tanto, el empuje del ala aumentará durante la muda y la ejecución de vuelo se reducirá en forma similar como durante el engordamiento migratorio.

Molt in birds is associated with elevated energy costs because (1) there is an energy cost to synthesize new feathers (reviewed by Lindström et al. 1993), (2) the insulation capacity of the plumage is reduced during molt which increases the energy costs of thermoregulation (Lustick 1970, Payne 1972) and (3) the cost of flight increases due to a reduction of wing area and/or wing span (Ginn and Melville 1983). The latter cost is difficult to estimate since current aerodynamic theory for bird flight (e.g., Pennycuik 1989) is based on momentum-jet theory of flight and requires only the wing span as the morphological characteristic of the wing. However, some researchers studying life-history trade-offs of parent birds feeding young (reviewed by Mauck and Grubb 1995) and song-flight performance (Mather and Robertson 1992, Møller 1991) have experimentally reduced the wing area in order to induce elevated flight costs.

Gaps in the wing will affect the lift distribution and hence flight performance. Therefore, in addition to the position of gaps it is important to know the relative wing area during molt in order to estimate the associated flight costs accurately, although at present no straight forward

method is available of calculating these costs unless using so-called panel methods (cf. Katz and Plotkin 1991). However, wing areas of birds are rarely reported and wing areas during molt are virtually non-existent in the literature. In the present short paper I show that the standard molt scoring technique may be used to estimate the relative wing area during molt in the Willow Warbler (*Phylloscopus trochilus*) and a few other passerine species.

#### METHODS

Passerines were captured in a subalpine birch forest at Lake Tjulträsk (520 m elevation) near Ammarnäs (65°58'N, 16°07'E) in Swedish Lapland during their prebasic molt (July 1992), as part of the LUVRE project (Enemar et al. 1984). Birds were aged and sexed on the basis of plumage and molt characteristics and, in the Willow Warbler, on the basis of size (Svensson 1984). All birds were in their second calendar year or older. Molt in each bird's left wing was recorded according to Ginn and Melville (1983): old feathers were scored 0; new, fully grown feathers were scored 5; missing and growing feathers were scored between 1 and 4. The outermost reduced primary was excluded in the analysis because its contribution to the total wing area is negligible. By using these molt scores, an estimate of the gaps caused by missing or growing feathers can be obtained from the wing raggedness score introduced by Haukioja (1971). Raggedness is calculated as 5 minus the molt score for missing and growing feathers; old and new (fully grown) feathers receive raggedness score of 0. The total raggedness score for one wing can theoretically vary between 0 (complete wing) and 60 (nine primaries and six secondaries shed simultaneously).

I traced the contour of one wing onto paper (cf. Pennycuick 1989) in order to obtain the wing area. For aerodynamic purposes, the area of the body between the wings is included in the total wing area (Pennycuick 1989). Therefore, I measured the width of the body between the wings at the centerline of the wing chord (chord is here used in the aeronautical sense, i.e. the distance from leading to trailing edge of the wing), to the nearest 1 mm with Vernier calipers. This measurement, multiplied by the chord of the wing at the wing root gave the area of the body between the wings. The wing tracings were later copied onto high quality paper, cut out and the area was determined gravimetrically by weighing the "wings" on a high precision balance. I also determined the wing area with a planimeter (computer digitizer), and the results from the two methods were practically identical ( $r = 0.99$ ,  $P < 0.001$ ,  $n = 41$ ), and so I used the data obtained by the gravimetric method in the analyses. The areas of complete wings were constructed for each bird in molt, by constructing the outline of the wing had it been complete on the basis of wing tracings for birds of the same species which were not in molt. Hence, the relative wing area is the wing area during molt divided by the wing area of the complete wing. Birds are only represented once in the data set. I also measured the wing span to the nearest 1 mm when the wings

TABLE 1. Summary statistics for each species of data used in analyses: sample size ( $n$ ), body mass ( $m$ ), raggedness value ( $R$ ; mean and range), wing area before molt ( $S$ ), wing area during molt ( $S_{\text{molt}}$ ), relative wing area ( $S_{\text{molt}}/S$ ; mean and range) and wing loading during molt ( $N_{\text{molt}}$ ; mean and range).

Species	$n$	$m$ (g)	$R$	$S$ (cm <sup>2</sup> )	$S_{\text{molt}}$ (cm <sup>2</sup> )	$S_{\text{molt}}/S$ (%)	$N_{\text{molt}}$ (Nm <sup>-2</sup> )
<i>Motacilla flava</i>	4	16.4	17 (8–21)	105.2	95.8	91.0 (88.3–93.9)	16.8 (15.2–19.0)
<i>Prunella modularis</i>	3	19.3	10.3 (8–12)	95.7	91.9	96.1 (93.6–98.5)	20.7 (19.6–21.4)
<i>Luscinia svecica</i>	5	18.3	10.6 (7–15)	108.3	102.0	94.1 (90.7–97.0)	17.6 (16.0–18.6)
<i>Phylloscopus trochilus</i>	21	9.1	11.2 (2–19)	78.1	73.5	94.2 (88.6–98.1)	12.2 (10.3–13.9)
<i>Ficedula hypoleuca</i>	1	11.8	11	88.1	84.9	96.4	13.6
<i>Parus major</i>	1	16.5	8	115.7	111.5	96.4	14.5
<i>Fringilla montifringilla</i>	3	21	5 (2–7)	125.6	123.2	98.0 (96.5–99.4)	16.8 (15.3–18.9)
<i>Carduelis flammea</i>	2	12.4	6 (5–7)	83.4	82.2	98.6 (97.5–99.7)	14.8 (14.3–15.4)
<i>Emberiza schoeniclus</i>	1	19.9	16	117.0	102.4	87.5	19.1

were stretched out to represent a normal flight position (Pennycuik 1989). Finally, the body mass was measured to the nearest 0.1 g using a Pesola spring balance. When calculating the wing loading I used the body mass measurement recorded when the bird was caught, i.e., during molt.

#### RESULTS AND DISCUSSION

I obtained data on wing area for 41 passerines of which 21 were Willow Warblers (Table 1). The maximum wing area reduction was 12.5% associated with a raggedness score of 16 in a Reed Bunting (*Emberiza schoeniclus*) (Table 1). Maximum raggedness scores are usually around 20 (Bensch and Grahn 1993) and scores of 16 or more yielded an average wing area reduction of 10% ( $n = 5$ ). The relationship between relative wing area and raggedness score was highly significant for the pooled sample of nine species (linear regression;  $r = -0.72$ ,  $P < 0.001$ ,  $df = 39$ ; Fig. 1); for the Willow Warbler alone the relationship was also significant ( $r = -0.60$ ,  $P < 0.01$ ,  $df = 19$ ; Fig. 1). Hence, the raggedness score predicted the relative wing area and therefore also the molt gap size. The variation found was due to the fact that the same molt score can be given to a range of feather lengths (e.g., score 3 is when the new feather is between one- and two-thirds grown; Ginn and Melville 1983). The fact that the primaries are longer than the secondaries also contributes to the variation.

There was also a significant relationship between relative wing area and primary molt score (the sum of individual primary scores) ( $r = 0.57$ ,  $P < 0.001$ ,  $df = 39$ ). This correlation arose because there was a significant correlation between primary molt score and raggedness score ( $r = 0.54$ ,

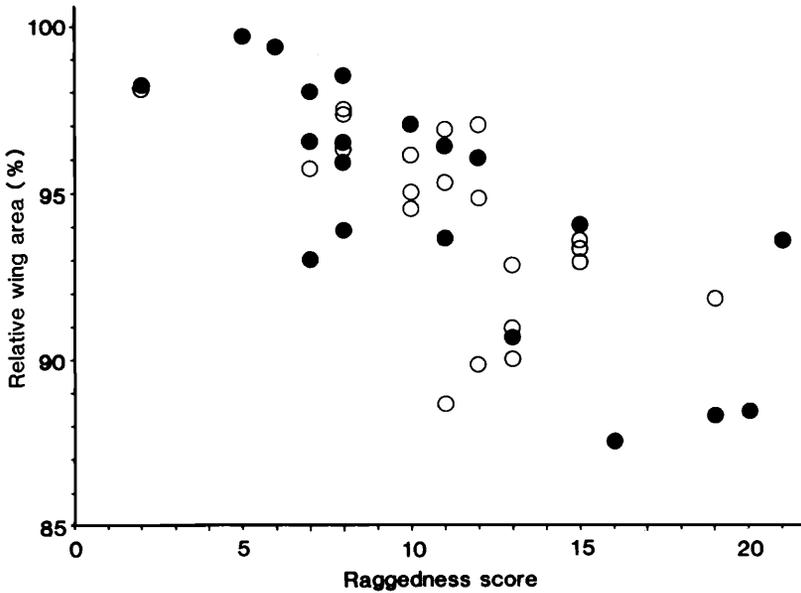


FIGURE 1. The relationship between relative wing area (%; ordinate) and raggedness score (abscissa) for nine passerine species. Regression for all species pooled is  $Y = 100.2 - 0.52 X$ ,  $r^2 = 0.51$ ,  $P < 0.001$ ,  $n = 41$ , and for the Willow Warbler only (open symbols)  $Y = 99.5 - 0.47 X$ ,  $r^2 = 0.37$ ,  $P < 0.01$ ,  $n = 21$ . Species included are (sample size separated on sex given within parentheses): *Motacilla flava* (4F), *Prunella modularis* (3M), *Luscinia svecica* (5M), *Phylloscopus trochilus* (10M; 11F), *Ficedula hypoleuca* (1F), *Parus major* (1F), *Fringilla montifringilla* (1M; 2F), *Carduelis flammea* (1M; 1F), and *Emberiza schoeniclus* (1M).

$P < 0.001$ ,  $df = 39$ ). However, this effect was largely due to the fact that data from the second half of the molt were underrepresented in my sample. With an even distribution of data over the molt we would theoretically expect a U-shaped relationship between relative wing area and primary molt score, with a minimum wing area at intermediate primary molt scores (associated with maximum raggedness), and thereafter the wing area approaching 100%, while the primary molt score approaches 45 (i.e., molt completed). However, the relationship between raggedness score and relative wing area will not be affected by a biased sample, where birds from a certain molt stage are over-represented.

The minimum turning radius, which may affect the ability to escape predators (Howland 1974), is directly proportional to wing loading (weight per unit of wing area). For example, in the Willow Warbler with the largest molt gap, wing loading increased from  $10.7 \text{ Nm}^{-2}$  to  $12.0 \text{ Nm}^{-2}$  (a 12% increase) during molt, with an associated raggedness score of 11. This change in wing loading will increase the theoretical minimum turning radius from 1.1 m to 1.25 m (a 14% increase).

Changes in flight performance similar to those during molt will also

be experienced by birds with temporary weight increases, for example due to migratory fat accumulation (Hedenström 1992), or if equipped with a radio transmitter. The increase in wing loading due to maximum fattening in migrant Dark-eyed Juncos (*Junco hyemalis*) was 14–16% (Chandler and Mulvihill 1992), which is of similar magnitude as found in molting birds in the present study. Empirical support for reduction in flight performance associated with fattening and weight increase in passerines has recently been obtained in cage experiments measuring take-off performance (Kullberg et al. 1996, Metcalfe and Ure 1995).

The aspect ratio ( $AR = b^2/S$ , where  $b$  is wing span and  $S$  is wing area) is an index of the shape of the wing, and high values are associated with high aerodynamic performance and low flight costs (e.g., Katz and Plotkin 1991). When the molt does not affect the wing span, only the wing area is reduced and hence the aspect ratio is increased. This counteracts the detrimental effect of the molt gap itself to some degree (Hedenström and Sunada, in press).

In conclusion, I have shown that molt scores can be used to predict relative wing areas during molt in willow warblers and selected other small passerines, and they may be generally useful for this purpose. Relative wing area is an important parameter when estimating the aerodynamic performance of birds during flight with reduced wing area, such as when molting. Because wing areas during molt is rarely reported it is possible to get information (required for estimating aerodynamic performance) about wing area in molting birds by using the raggedness score obtained from standard molt scores.

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