

Body frontal area in passerine birds

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Projected body frontal area is used when estimating the parasite drag of bird flight. We investigated the relationship between projected frontal area and body mass among passerine birds, and compared it with an equation based on waterfowl and raptors, which is used as default procedure in a widespread software package for flight performance calculations. The allometric equation based on waterfowl/raptors underestimates the frontal area compared to the passerine equation presented here. Consequently, revising the actual frontal areas of small birds will concomitantly change the values of the parasite drag coefficient. We suggest that the new equation $S_b = 0.0129m_B^{0.61}$ (m²) where m_B is body mass (kg) should be used when a value of frontal area is needed for passerines.

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Aerodynamic analysis of bird flight attempts to quantify three main components of drag, i.e. induced, profile and parasite drag, which summed together results in the total aerodynamic drag (D) used to estimate the mechanical power output as $P = DV$, where V is airspeed. This yields a relationship between mechanical power and speed (Pennycuick 1989), which is used extensively to derive properties of flight behaviour and performance (Hedenström and Alerstam 1995, Pennycuick 1997, Alerstam and Hedenström 1998, Hedenström 2002). The parasite drag is the drag due to the pressure drag of the bird body, and is written as

$$D_{\text{par}} = \frac{1}{2}\rho V^2 S_b C_{D,\text{par}} \quad (1)$$

where ρ is air density, V is airspeed, S_b is body frontal area and $C_{D,\text{par}}$ is a dimensionless drag coefficient. The additional drag due to skin friction is generally presumed to be of minor importance for birds (Pennycuick 1989). Also, additional drag arising from the interference due to the body-wing juncture, as the boundary layer of wings and body interact and thicken, is usually not considered important in birds (Tucker and Heine 1990). Hence, to accurately estimate the parasite drag S_b and $C_{D,\text{par}}$ are crucial parameters. The product $S_b C_{D,\text{par}}$ is the equivalent flat plate area in aeronautical terminology, which is a reference area of fictitious shape having a $C_{D,\text{par}}$ of 1.0 and with the same drag as the body in question. Most recent literature concerns the magnitude of $C_{D,\text{par}}$ (Pennycuick et al. 1988, 1996, Tucker 1990, Pennycuick 1997, Maybury and Rayner

2001, Hedenström and Liechti 2001), while the body frontal area is either measured directly or, more often, calculated according to the following allometric equation

$$S_b = 0.00813m_B^{0.666} \text{ (m}^2\text{)} \quad (2)$$

where m_B is body mass in kg (Pennycuick et al. 1988). This equation is based on a small sample of large waterfowl and raptor species and follows an expected isometric scaling relationship. This formula is used extensively when estimating body frontal areas in birds, as it is the default formula provided in a popular model for flight performance calculations (Pennycuick 1989).

Methods

We obtained head-on photographs of 31 species of passerine birds captured at Ottenby Bird Observatory (56°12'N, 16°24'E) in spring 1999 and a few corvids captured in Lund in March 2001. Body frontal area was measured from head-on photographs of the birds when held in a flight like position with extended wings and feathers held tightly against the body (Fig. 1). Birds may often erect the body feathers when captured and held in the hand, resulting in an apparent increased projected frontal area. However, when blowing at the birds they invariably responded by folding the body feathers tightly against the body, when photos were obtained. Birds with erected body feathers were ex-

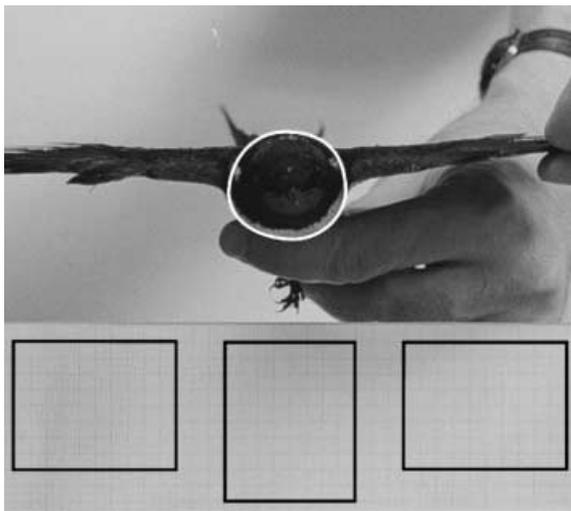


Fig. 1. Head-on photograph of a barn swallow *Hirundo rustica* illustrating how body frontal area was measured (area inside white contour). The rectangles are reference areas of 20 cm² held in the same plane as where the bird body has its widest point.

cluded from the analysis. Photos included a reference area held in the plane where the body had maximum width (Fig. 1). For comparison we also measured the body frontal area of two barn swallows *Hirundo rustica* flying in a wind tunnel at 10 ms⁻¹ and imaged from a rear view camera (Park et al. 2001). The flying birds had frontal areas of 8.66 cm² and 9.86 cm², to be compared with 8.67 cm² and 9.89 cm², respectively, using the photographic method for the same birds. Hence, our method gives similar frontal areas as those of birds in flight. Negatives or positives were scanned and converted into JPG images. Bird body frontal area and reference area were measured by using MapInfo 4.5. The bird body contour was marked as a polygon using on average 35 (range 20–49) line segments, which was converted into an area (bfa). The reference area (ref; rectangle of sides 4 cm × 5 cm) was measured marked likewise using 4 line segments (Fig. 1). The true body frontal area was then given by the ratio bfa/ref multiplied by 20 cm². The method of measuring body frontal areas from photographs was highly repeatable as revealed from repeat measurements of a random sub-sample ($r = 0.999$, $P \ll 0.001$, $N = 20$; Lessells and Boag 1987).

For measuring body mass the bird was put in a plastic cone and placed on an electronic balance, which was read to the nearest 0.1 g. Fat class was scored on the standard scale 0–6 used by ringers for 77 of the 81 birds (Pettersson and Hasselquist 1985).

Results

The data for passerines, spanning a body mass range

0.0073 to 0.53 kg, used for analyses are presented in Table 1. Fig. 2 shows a log–log plot using species mean values. Fitting an allometric equation to the data using reduced major axis regression yields

$$S_b = 0.0129m_B^{0.614} \text{ (m}^2\text{)}, \quad (3)$$

with a 95%-confidence interval $\epsilon[0.00975, 0.0170]$ for the numerical constant and $\epsilon[0.54, 0.68]$ for the exponent, i.e. the interval for the exponent includes 2/3 of expected isometric scaling. Ordinary linear regression gave an exponent of 0.58 ($r^2 = 0.90$), significantly different from 2/3 ($P < 0.05$), but we used reduced major axis regression because Equation (2) was derived by this method. For comparison the data of non-passerine birds used to derive Equation (2) are also shown in Fig. 2. A test for homogeneity of slopes revealed a significant difference between passerines and non-passerines (ANCOVA $F_{1,46} = 52$, $P < 0.001$), as well as between the intercepts ($F_{1,46} = 1197$, $P < 0.001$). This means that the slopes differ between the two data sets and that passerines have larger body frontal areas than would be estimated from Equation (2), and body frontal area increases at a slower rate with increasing body mass for passerines than for the non-passerine birds.

The passerine birds used in this study had an average fat score of 3.1 (SD = 1.12, range 1–5, $N = 77$), which represents relatively small or moderate fat stores.

Discussion

Changing the formula for estimating body frontal area does not change the parasite drag experienced by a bird, but it does change the value we should assign to $C_{D,par}$. Experiments suggest that $C_{D,par}$ should be in the range 0.1–0.2 (Tucker 1990, Pennycuik et al. 1996, Hedenström and Liechti 2001), which is considerably lower than the previously recommended default value for passerines of 0.4 (Pennycuik 1989). In that context, our Equation (3) for passerines gives twice as large frontal area for a 10 g bird compared to Equation (2), which would then require an equal reduction of $C_{D,par}$ to not change the equivalent flat plate area. In a recent study, Hedenström and Liechti (2001) measured terminal velocity in birds diving vertically or at very steep angles, and used Equation (1) to estimate $C_{D,par}$. It was assumed that at terminal velocity the drag of the body balances the pull of gravity. When calculating $C_{D,par}$, Hedenström and Liechti (2001) used Equation (2) to estimate body frontal area (S_b) for their sample of birds, and obtained a mean of $C_{D,par} = 0.37$ and a range 0.17–0.77. Using the same data and procedure, but instead using Equation (3) for S_b the mean $C_{D,par} = 0.18$ and the range 0.09–0.38. The new formula for body frontal area in passerines thus changes how the equivalent flat plate is subdivided between projected

Table 1. Body mass (m) and body frontal area (S_b) for 31 species of passerines. The values are means in cases where more than one individual was measured.

Common name	Scientific name	N	Mean m_B (kg)	Mean S_b (m ²)
Common chiffchaff	<i>Phylloscopus collybita</i>	4	0.008	0.00073
Willow warbler	<i>Phylloscopus trochilus</i>	5	0.009	0.00075
Reed-warbler	<i>Acrocephalus scirpaceus</i>	3	0.012	0.00086
Pied flycatcher	<i>Ficedula hypoleuca</i>	5	0.012	0.00099
Lesser whitethroat	<i>Sylvia curruca</i>	2	0.013	0.00075
Whitethroat	<i>Sylvia communis</i>	6	0.014	0.00109
Robin	<i>Erithacus rubecula</i>	6	0.015	0.00116
Common redstart	<i>Phoenicurus phoenicurus</i>	7	0.015	0.00092
Garden warbler	<i>Sylvia borin</i>	3	0.015	0.00125
Blackcap	<i>Sylvia atricapilla</i>	5	0.017	0.00123
Reed bunting	<i>Emberiza schoeniclus</i>	1	0.017	0.00178
Goldfinch	<i>Carduelis carduelis</i>	1	0.017	0.00095
Dunnock	<i>Prunella modularis</i>	1	0.017	0.00077
Spotted flycatcher	<i>Muscicapa striata</i>	1	0.018	0.00111
Yellow wagtail	<i>Motacilla flava</i>	1	0.018	0.00083
Barn swallow	<i>Hirundo rustica</i>	4	0.018	0.00094
Linnet	<i>Carduelis cannabina</i>	3	0.019	0.00093
White wagtail	<i>Motacilla alba</i>	2	0.020	0.00089
Tree pipit	<i>Anthus trivialis</i>	1	0.021	0.00122
Chaffinch	<i>Fringilla coelebs</i>	2	0.021	0.00134
Scarlet rosenfinch	<i>Carpodacus erythrinus</i>	2	0.023	0.00121
Ortolan bunting	<i>Emberiza hortulana</i>	2	0.024	0.00107
Red-backed shrike	<i>Lanius collurio</i>	2	0.027	0.00151
Waxwing	<i>Bombycilla garrulus</i>	1	0.048	0.00285
Hawfinch	<i>Coccothraustes coccothraustes</i>	1	0.053	0.00248
Song thrush	<i>Turdus philomelos</i>	1	0.060	0.00226
Blackbird	<i>Turdus merula</i>	2	0.098	0.00240
Fieldfare	<i>Turdus pilaris</i>	2	0.099	0.00236
Jackdaw	<i>Corvus monedula</i>	2	0.189	0.00486
Magpie	<i>Pica pica</i>	1	0.251	0.00541
Rook	<i>Corvus frugilegus</i>	2	0.507	0.00765

frontal area and $C_{D,par}$. By way of example, provided a given value of $C_{D,par}$ and everything else equal, using

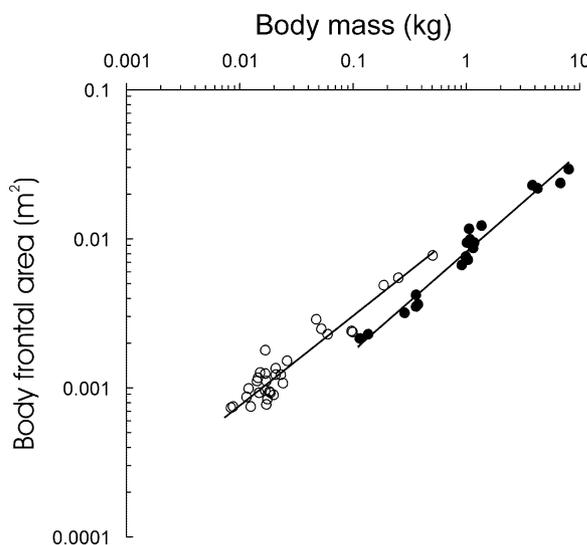


Fig. 2. Log-log plot of body frontal area in relation to body mass for 31 passerine bird species (open symbols) and, for comparison, the data on non-passerine species (filled symbols) from Pennycuik et al. (1988). The lines represent the equations $S_b = 0.0129m_B^{0.614}$ (m²) for passerines and $S_b = 0.00813m_B^{0.666}$ (m²) and were fitted to the data by reduced major axis regression.

our Equation (3) for passerine body frontal area will translate into a 30% reduction of calculated flight range for an 'ideal bird' compared to Equation (2) (proportionality 5a in Alerstam and Hedenström 1998).

The reason for the discrepancy between Equations (2) and (3) is most likely that waterfowl/raptors are more elongated and streamlined compared to passerines. There is a possibility that the discrepancy arose due to different methods used for estimating frontal areas. Pennycuik et al. (1988) measured body depth (z) and width (w) at the widest point and calculated the frontal area assuming an elliptic shape from $\pi wz/4$. Our method of taking head-on photographs of hand held birds gave very similar results as those obtained from a bird flying in a wind tunnel. For comparison we also measured body height and width from the photographs and calculated the area for an ellipse, which yielded a nearly identical result as that from the true body shapes (slope of regression $b = 0.994 \pm 0.013$, $\pm 95\%$ confidence limit), and hence confirm the assumption that bird body frontal areas can be calculated as ellipses. For these reasons we believe that the difference between Equations (2) and (3) is real.

Most birds carried small or moderate fat deposits as indicated by the visual fat scores. Subcutaneous fat deposits should increase the frontal area in relation to a lean bird, if fat is uniformly distributed around the

body. However, fat is not uniformly distributed but tends to be stored on the belly, in the tracheal pit and on the throat. Exactly to what extent fat deposition affects the frontal area is unknown at this stage. In the present sample the fat stores were relatively small and did not bulge excessively, and moreover, fat loads will be included as extra body mass when deriving Equation (3). The fat loads of the non-passerine birds were not reported (Pennycuick et al. 1988), and therefore, it is unknown if the two samples differed or not with respect to fat loads.

Larger birds typically fly at faster airspeed than small birds, and so they experience an increased parasite drag ($\propto V^2$) compared to small birds flying at lower speed. This effect is countered to some extent by the higher Reynolds number for large birds (Pennycuick 1989). Therefore, selection for streamlining the body shape may be stronger in large birds, which is reflected in the difference between Equations (2) and (3). Taken together, our results show that Equation (2) is not valid for accurately estimating projected body frontal areas for passerine birds. We therefore suggest that Equation (3) should be used when body mass is known and an estimate of body frontal area is needed for a passerine bird species.

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