

## ON THE AERODYNAMICS OF MOULT GAPS IN BIRDS

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### Summary

**During the moult, birds sequentially replace their flight feathers and thus temporarily have gaps in their wings. These gaps will vary in size and position(s) during the course of the moult. We investigated the aerodynamic effects of having moult gaps in a rectangular wing by using a vortex-lattice (panel) approach, and we modelled the effect of moult gap size at the wing moult initiation position, of gap position in the primary tract and of two simultaneous gaps (as occurs during secondary feather moulting in many birds). Both gap size and gap position had a detrimental effect on aerodynamic performance as measured by lift curve slope, effective aspect ratio and the**

**aerodynamic efficiency of the wing. The effect was largest when the moult gap was well inside the wing, because the circulation declines close to the wing tip. In fact, when the gap was at the wing tip, the performance was slightly increased because the lift distribution then became closer to the optimal elliptical distribution. The detrimental effect of moult gaps increased with increasing aspect ratio, which could help to explain why large birds have relatively slow rates of moult associated with small gaps.**

Key words: avian moult, aerodynamics, flight, mechanical power, cost of transport, manoeuvrability, predation risk.

### Introduction

Moulting in birds is an energetically costly process (e.g. Payne, 1972) because (i) during the moult there is an energy cost of synthesizing new feathers (reviewed by Lindström et al., 1993), (ii) the insulation capacity of the plumage is reduced during the moult, which increases the energy costs of thermoregulation (Lustick, 1970; Payne, 1972), and (iii) the cost of flight increases owing to a reduction of wing area and/or wing span (Ginn and Melville, 1983). In some birds, such as ducks, swans and geese (Anseriformes), all or most of the flight feathers are shed simultaneously and the birds become flightless until the new set of feathers restores the flight capacity. In most other birds, e.g. passerines and raptors, moulting is a rather continuous process in which the flight feathers are replaced according to a preprogrammed sequence (e.g. Stresemann and Stresemann, 1966; Payne, 1972; Ginn and Melville, 1983; Jenni and Winkler, 1994). However, at northern latitudes, even passerines may moult so heavily that flight is severely hampered or even temporarily lost (Haukioja, 1971).

Furthermore, researchers studying life-history trade-offs induce elevated flight costs by experimentally reducing the wing area and/or wing span (reviewed by Mauck and Grubb, 1995). This method has also been used to study the effects of an increase in flight costs on song-flight performance in male birds (Møller, 1991; Mather and Robertson, 1992) and on the performance of a

peculiar stone-carrying behaviour in black wheatears (*Oenanthe leucura*) (Møller et al., 1995). However, a quantitative aerodynamic understanding of how flight performance is affected by wing gaps due to moulting or experimentally reduced wing area is lacking. The effects of the moult on flight performance have been studied experimentally by Tucker (1991), who measured the gliding flight performance during the primary moult of a Harris' hawk (*Parabuteo unicinctus*) in a wind-tunnel. Recently, there have also been experimental studies on the effects of moult gaps on hovering performance in hummingbirds (Chai, 1997) and on take-off escape performance in starlings (*Sturnus vulgaris*) (Swaddle and Witter, 1997).

In the present study, we adopt a computational fluid dynamics (CFD) approach by using a vortex lattice (panel) method to estimate the aerodynamic drag and lift coefficients during the moult. We investigate the effects of moult gap size, geometry and the position of the gap in the wing to mimic the situation during a normal sequence of moulting.

### Materials and methods

#### *Calculation of the aerodynamic characteristics of a wing*

For the present analysis, we assume a fixed rectangular and planar wing in steady, non-accelerated motion at a fixed angle of attack  $\alpha$ . The assumption of a planar wing should not affect

our results to any large degree because bird wings are very nearly planar. The calculations thus refer to a bird in gliding flight and are not directly applicable to flapping flight. However, for high-speed flight, especially in large birds with a low flapping frequency (i.e. a large advance ratio), the results may also be valid for flapping flight. Real birds do not have perfectly rectangular wings as assumed here but, provided that the wings have similar geometrical aspect ratios  $\mathcal{AR}$ , the effective aspect ratio  $\mathcal{AR}_e$  and lift curve slope  $a$  will be approximately the same (see Hoerner, 1965).

On the basis of the potential flow theory, the aerodynamic characteristics of a wing can be determined as follows (Katz and Plotkin, 1991): a wing moves at a forward velocity  $V$  through the air with a geometrical angle of attack  $\alpha_0$ . The applicability of potential flow theory requires small values of  $\alpha_0$  and, for the present calculations, we set  $\alpha_0$  to  $2.5^\circ$ .

The wing and the trailing-edge vortex are represented by many vortex rings, as shown in Fig. 1. The circulation ( $\Gamma$ ) of vortex rings can be determined by the boundary condition on the colocation points (centres of the vortex rings) on the wing. The lift ( $C_L$ ) and induced drag ( $C_{Di}$ ) coefficients can be calculated by using the circulation, obtained as follows:

$$C_L = \frac{2}{VS_w} \sum_{j=1}^{j=j_{\max}} \left[ \sum_{i=2}^{i=i_{\max}} (\Gamma_{i,j} - \Gamma_{i-1,j}) \Delta y_{i,j} + \Gamma_{1,j} \Delta y_{1,j} \right], \quad (1)$$

$$C_{Di} = \frac{2}{V^2 S_w} \sum_{j=1}^{j=j_{\max}} \left[ \sum_{i=2}^{i=i_{\max}} w_{\text{ind},i,j} (\Gamma_{i,j} - \Gamma_{i-1,j}) \Delta y_{i,j} + w_{\text{ind},1,j} \Gamma_{1,j} \Delta y_{1,j} \right], \quad (2)$$

where  $V$  is forward speed,  $S_w$  is the wing area,  $i$  and  $j$  are numbers of vortex rings in the  $x$  and  $y$  directions, respectively, of the  $(i, j)$ th vortex ring,  $\Gamma_{i,j}$  is the circulation on vortex  $(i, j)$  and  $w_{\text{ind},i,j}$  is the induced velocity at the colocation point  $(i, j)$ .

Alternatively, the induced drag can be calculated by considering the Trefftz plane, which is the plane  $z$  perpendicular to the forward direction, and the induced drag coefficient is then given by:

$$C_{Di} = -\frac{1}{4V^2 S_w} \sum_{k=1}^{N_w} \Gamma_{i,\text{max},k} w_{\text{ind},k} \Delta y_k, \quad (3)$$

$$w_{\text{ind},k} = -\frac{1}{2\pi} \sum_{kk=1}^{N_w} \frac{\Gamma_{i,\text{max},kk} (y_k - y_{kk})}{(y_k - y_{kk})^2 + (z_k - z_{kk})^2}, \quad (4)$$

where  $w_{\text{ind},k}$ , the induced velocity of the trailing vortices, is calculated in the Trefftz plane,  $\Delta y_k$  is the spacing of the trailing vortices and  $N_w$  is the number of trailing vortices. The induced drag coefficients calculated from equations 2 and 4 differed by less than 3% and, since the methods yielded very similar results, we are confident that high accuracy was obtained in the calculations of the induced drag. This test is common practice in computational aerodynamics for validation of programs. We

also compared our method of calculating the lift and induced drag coefficients for a rectangular wing with the values obtained by Lan (1974) and the difference was less than 2%.

The values of  $C_L$  and  $C_{Di}$  change when the value of  $\alpha_0$  changes. However, the lift curve slope  $a$  and the effective span ratio  $\mathcal{AR}_e$  are determined uniquely when the wing planform is given. These variables are obtained as follows:

$$a = \frac{C_L}{\alpha_0}, \quad (5)$$

$$\mathcal{AR}_e = \frac{C_L^2}{\pi C_{Di}} = \left( \frac{\alpha_0^2}{\pi} \right) \frac{a^2}{C_{Di}}. \quad (6)$$

The lift curve slope  $a$  becomes close to  $2\pi$  when  $\mathcal{AR}$  approaches infinity. A wing with a larger lift curve slope  $a$  generally has a larger lift-to-drag ratio. Induced power decreases with increasing  $\mathcal{AR}_e$ , as indicated by equation 6. Therefore, a wing with a large lift curve slope  $a$  and effective aspect ratio  $\mathcal{AR}_e$  generally has a better performance than a wing of lower  $a$  and  $\mathcal{AR}_e$ . The ratio  $\mathcal{AR}_e/\mathcal{AR}$ , usually called the aerodynamic efficiency, is a variable indicating the appropriate circulation distribution along the span required to obtain an optimal performance. When the circulation distribution along the span is elliptical, the value of  $\mathcal{AR}_e/\mathcal{AR}$  is equal to unity. Theoretically, the value of  $\mathcal{AR}_e/\mathcal{AR}$  must be less than or equal to 1.

#### Performance of a wing with a gap

The characteristics of a wing were estimated using the first method outlined above. First, we estimated the characteristics of a rectangular wing with  $\mathcal{AR}=b/c=4, 6, 8, 10, 12, 16$  or  $20$ , where  $b$  is wing span and  $c$  is the wing chord of a rectangular wing with no gap. The range of  $\mathcal{AR}$  was chosen to cover the range found among birds from small passerines with short and rounded wings to large albatrosses with  $\mathcal{AR}=15$  (see Greenewalt, 1962; Pennycuik, 1982). Next, the characteristics of a rectangular wing with a rectangular gap were estimated. To

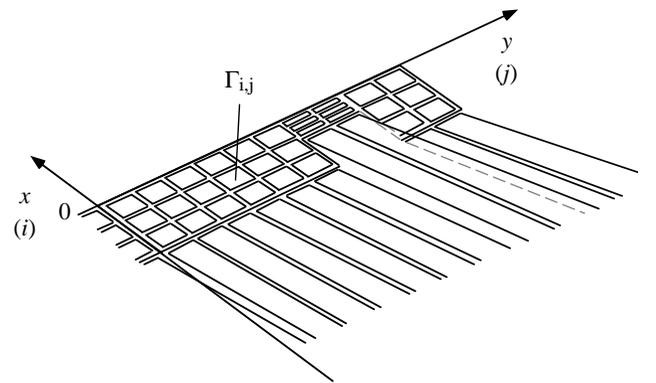
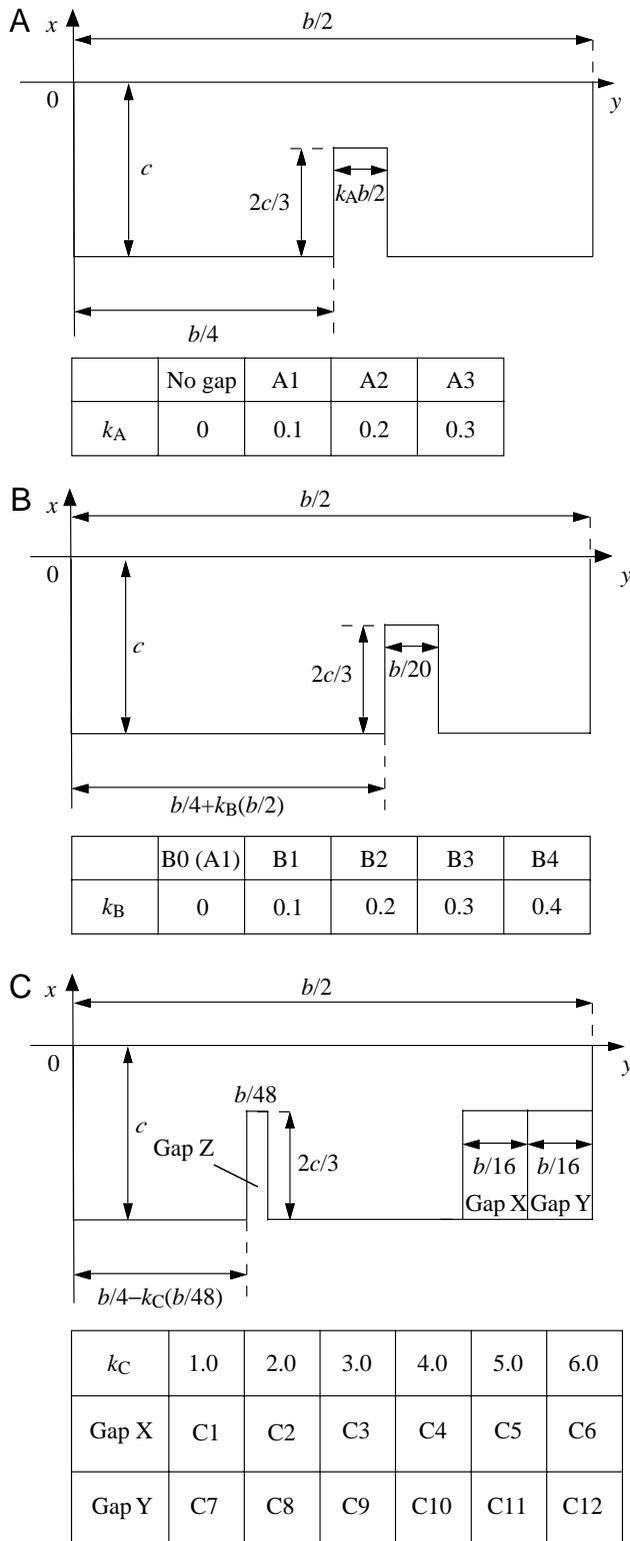


Fig. 1. Nomenclature for the vortex ring model of the wing and the trailing vortices.  $\Gamma_{i,j}$  is the circulation on vortex  $(i, j)$ ,  $x$  is the chordwise direction and  $y$  is the spanwise direction. How a gap in the wing was modelled is also shown (see text for further details).

mimic the positions and sizes of moult gaps in real birds (see Hedenström, 1998), we divided the calculations into three cases A–C (Fig. 2; Table 1). We only show the gap(s) for the semi-span of the wing, since moult gaps are generally symmetrical about the  $x$ -axis. The length of the gap in the  $x$  direction (i.e.



the length of primary and secondary feathers in relation to the wing chord) is constant at  $2c/3$  in all three cases (A–C). First, in case A (Fig. 2A), we investigate the effect of varying gap size at the position of moult initiation, i.e. the first primaries to be shed in a moult sequence. In this case, the gap is at  $-c \leq x \leq -c/3$  and  $b/4 \leq y \leq b/4 + k_A(b/2)$ , where  $k_A$  is a gap size factor ( $0 \leq k_A \leq 0.3$ ). The inner edge of the gap is fixed at  $y = b/4$ . The width of the gap in the  $y$  direction varies with  $k_A$ . Note that the wing area ( $S_w$ ) and the geometrical aspect ratio ( $\mathcal{AR}$ ) will vary with variation in  $k_A$ .

Second, in case B (Fig. 2B), we consider the effect of changing the position of a constant-sized gap in the primary wing, mimicking the sequence of primary shedding and regrowth of new feathers in most bird species (see Ginn and Melville, 1983; Jenni and Winkler, 1994). In this case, the gap is at  $-c \leq x \leq -c/3$  and  $b/4 + k_B(b/2) \leq y \leq 3b/10 + k_B(b/2)$ , where  $k_B$  determines the position of the inner edge of the gap ( $0 \leq k_B \leq 0.4$ ; Fig. 2B). The width of the gap in the  $y$  direction is  $b/20$ , which corresponds to a relative gap size of approximately 7% of the total wing area (which is typical in real birds; Hedenström, 1998). The gap moves towards the wing tip with increasing  $k_B$  and is at the wing tip in case B4. Note that case B0, with  $k_B = 0$ , is identical to case A1.

Finally, in case C (Fig. 2C), we consider the effects of two simultaneous gaps, a situation that occurs during the secondary moult in many species (e.g. Ginn and Melville, 1983; Jenni and Winkler, 1994). In this case, gaps X and Y represent gaps in the primary tract and gap Z represents a moving gap in the secondary tract. Since the first secondary is usually shed when the sixth primary is shed (Ginn and Melville, 1983), we took the innermost edge of the primary gap to be at  $y = 3b/8$ .

## Results

The results showing how  $a$ ,  $\mathcal{AR}_e$  and  $\mathcal{AR}_e/\mathcal{AR}$  vary in relation to  $\mathcal{AR}(b/c)$  and the position and size of wing gaps (cases A–C; Fig. 2) are presented in Figs 3–6. Note that the value of  $\mathcal{AR}_e/\mathcal{AR}$  must theoretically be less than or equal to unity but, because the panel number in the model of the wing is finite, a few values for wings of low aspect ratio are slightly greater than

Fig. 2. Three cases of moult gaps and how they were modelled:  $b$  is wing span and  $c$  is wing chord. (A) The effect of gap size at the position of primary moult initiation with the inner edge of the gap fixed at  $y = b/4$ ;  $k_A$  is introduced as the gap size factor. (B) The effect of gap position where a fixed gap moves from  $y = b/4$  towards the wing tip;  $k_B$  represents the position of the inner edge of the gap. (C) The effect of two simultaneous gaps in the outer primary and secondary tracts. The position of the more proximate gap Z ( $k_C$ ) moves progressively towards the body in cases C1–C12. The effect was calculated for two distal gaps: gap X is a gap not influencing the wing tip and gap Y is at the wing tip. The three different cases are referred to in the text as A, B and C, with number suffixes representing different increasing values of  $k_A$ ,  $k_B$  and  $k_C$  as shown below each figure, where  $k_A$  represents increasing gap size (for A),  $k_B$  represents the position of a primary feather gap (for B) and  $k_C$  represents the position of a secondary feather gap (for C).

Table 1. Geometrical aspect ratio for the different gap types and sizes investigated

Type of gap	Aspect ratio, $\mathcal{A}$						
No gap	4	6	8	10	12	16	20
Cases A1, B	4.3	6.4	8.6	10.7	12.9	17.1	21.4
Case A2	4.6	6.9	9.2	11.5	13.8	18.5	23.1
Case A3	5.0	7.5	10.0	12.5	15.0	20.0	25.0
Case C	4.5	6.8	9.0	11.3	13.5	18.0	22.5

$\mathcal{A} = b^2/S_w$ , where  $b$  is wing span and  $S_w$  is wing area.  
 Note that in cases B and C the relative gap size does not change.  
 Gap geometry is defined in Fig. 2.

unity (Figs 3C, 4C, 5C, 6C). However, these values of  $\mathcal{A}_e/\mathcal{A}$  can be considered to be very close to 1.

The presence of a gap makes the wing shape, and therefore the distribution of circulation, undesirable in all cases except in case B4 (Fig. 4). The values of  $a$ ,  $\mathcal{A}_e$  and  $\mathcal{A}_e/\mathcal{A}$  generally decrease with the presence of a wing gap (Figs 3–6). The decreases in  $\mathcal{A}_e$  and  $\mathcal{A}_e/\mathcal{A}$  are proportionally larger for wings of increasing  $b/c$  (Figs 3B,C, 4B,C, 5B,C), but the reduction in lift curve slope is somewhat smaller for wings of increasing  $b/c$  (especially in case C; Figs 3–6). In case B4 (see Fig. 2B), there is a gap at the wing tip, but in this case the distribution of circulation is closer to the optimal elliptical distribution than for the rectangular wing without a gap and hence gives an improved performance (Fig. 4).

In case A, the reduction of the lift curve slope  $a$  due to a gap is approximately independent of  $k_A$ , i.e. the size of the gap (Fig. 3A). For the effective aspect ratio  $\mathcal{A}_e$ , the largest gap (case A3; Fig. 3B) gives the smallest reduction in performance. This is because the larger the gap, the larger is the geometrical aspect ratio (Table 1), which counteracts the adverse effects of the gap itself on performance. However,  $\mathcal{A}_e/\mathcal{A}$  shows a performance reduction in proportion to gap size (Fig. 3C).

For a constant-sized gap moving towards the wing tip (case B), the values of  $a$ ,  $\mathcal{A}_e$  and  $\mathcal{A}_e/\mathcal{A}$  increase with increasing  $k_B$ , i.e. with increasing proximity to the wing tip (Fig. 4). Hence, performance is worst during the initial stages of the primary moult and increases as the gap moves distally along the wing, since the circulation becomes smaller near the wing tip. In fact, the performance for case B4 was slightly better than for the rectangular wing without a gap, as explained above (Fig. 4). The reduction in performance is proportionally larger with increasing aspect ratio.

Finally, we investigated the effect of having two gaps in case C (Fig. 2C), which represents the situation that usually occurs during the second half of wing feather moult. The effects on  $a$ ,  $\mathcal{A}_e$  and  $\mathcal{A}_e/\mathcal{A}$  in relation to the position of the fixed-size gap Z and aspect ratio are shown in Figs 5 and 6. The position of the gap Z has a small detrimental effect as it moves from mid-wing towards the body (Figs 5, 6), but the effect on  $a$  is negligible (Figs 5, 6). With a gap at the wing tip (gap Y, cases C7–C12; Fig. 2C), the effect of gap Z moving from mid-wing towards the body is similar to the case with gap X (cases C1–C6; Fig. 2C), but both cases give reduced values relative

to values for the rectangular wing with no gaps (compare Figs 5 and 6).

In conclusion, we investigated the effect of gaps of various sizes and positions on the performance of a rectangular wing. Generally, performance is reduced by increasing the size of the gap and when the gap is positioned at a distance from the wing tip. The effect of the position of a second gap (which occurs during the moult of the secondaries) had only a small effect on performance.

## Discussion

We have shown that aerodynamic performance is reduced in birds when experiencing moult gaps or wing area reductions for other reasons, e.g. damaged wings or experimentally removed flight feathers. Both gap size and gap position affect flight performance. Large gaps have a greater effect than small gaps, and moult gaps in the middle of the wing have a larger effect than more distal gaps. The latter effect is because the circulation is reduced close to the wing tip (since the lift distribution is nearly elliptical and lift is therefore smaller near the wing tips because of the trailing vortices), and a gap here cannot therefore affect the circulation to the same extent as a gap further inwards along the wing, where the circulation is larger.

During the final stages of the moult (or the initial stages of the moult in birds with an ascendant moult sequence, i.e. when the moult begins with the outermost primary and proceeds inwards, as in the spotted flycatcher *Muscicapa striata*; Stresemann and Stresemann, 1966; Ginn and Melville, 1983), the wing span may also be reduced, which will affect the aspect ratio. By calculating the new aspect ratio, the approximate effect of such a reduction can be assessed from Figs 3–5.

In general, the effects of moult gaps on flight performance were surprisingly small. These rather small effects may be the reason why some dunlins (*Calidris alpina*) can be found in active moult during their autumn migration (Holmgren et al., 1993). Traditionally, moult and migration have been considered to be incompatible (e.g. Payne, 1972; Walsberg, 1983), and active moulting during migration has only been observed during the autumn migration, which is presumably a comparatively relaxed migration. In addition to elevated flight costs during the moult (increased induced drag), there will also

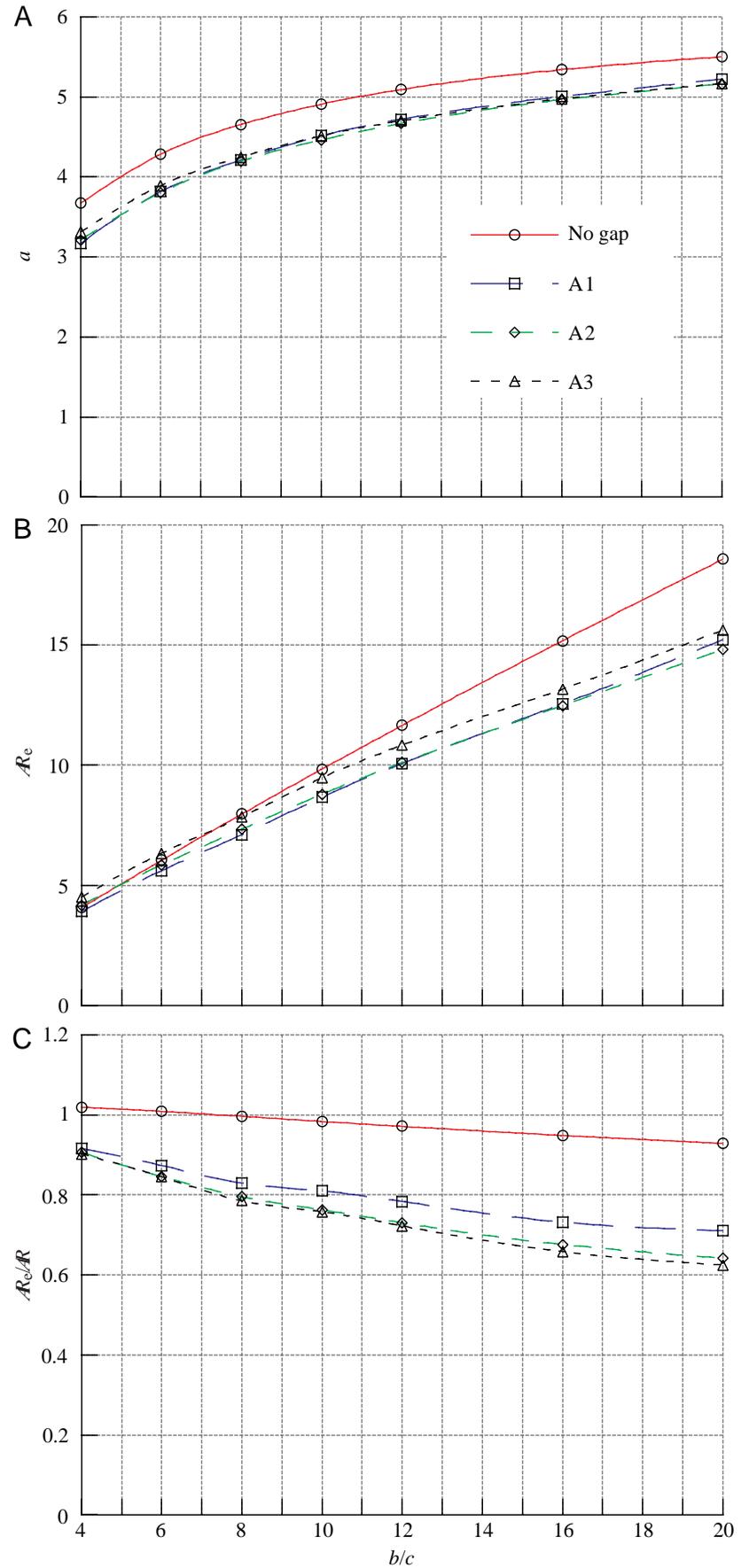


Fig. 3. The effect of gap size at the position of primary moult initiation (case A, see Fig. 2A) on three aerodynamic measures and in relation to geometrical aspect ratio  $\mathcal{R}(b/c)$ : (A) lift curve slope  $a$ ; (B) effective aspect ratio  $\mathcal{R}_e$ ; (C)  $\mathcal{R}_e/\mathcal{R}$ . For an explanation of the different cases, see Fig. 2A.

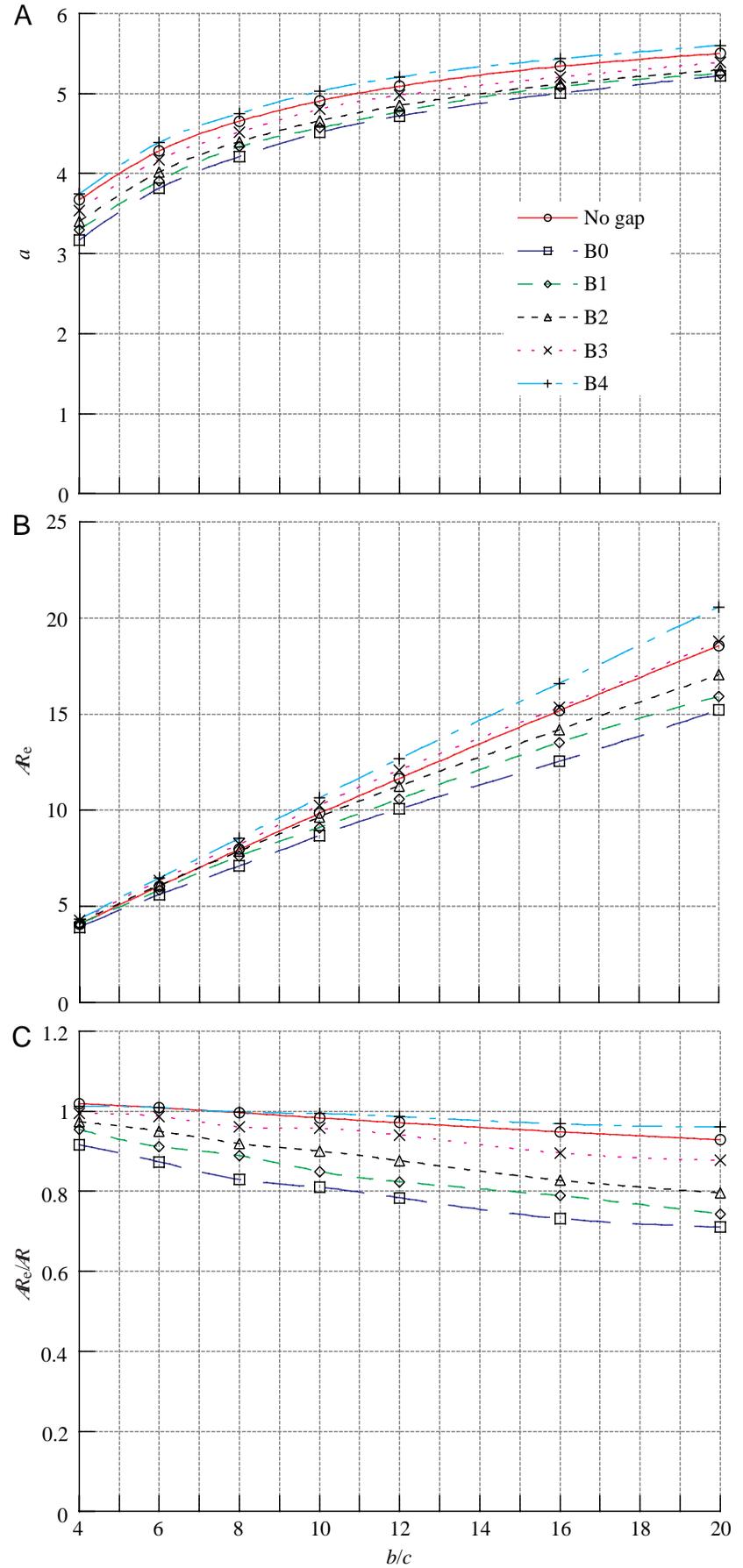


Fig. 4. The effect of primary moult gap position (case B, see Fig. 2B) on three aerodynamic measures and in relation to geometrical aspect ratio  $AR(b/c)$ : (A) lift curve slope  $a$ ; (B) effective aspect ratio  $AR_e$ ; (C)  $AR_e/AR$ . For an explanation of the different cases, see Fig. 2B.

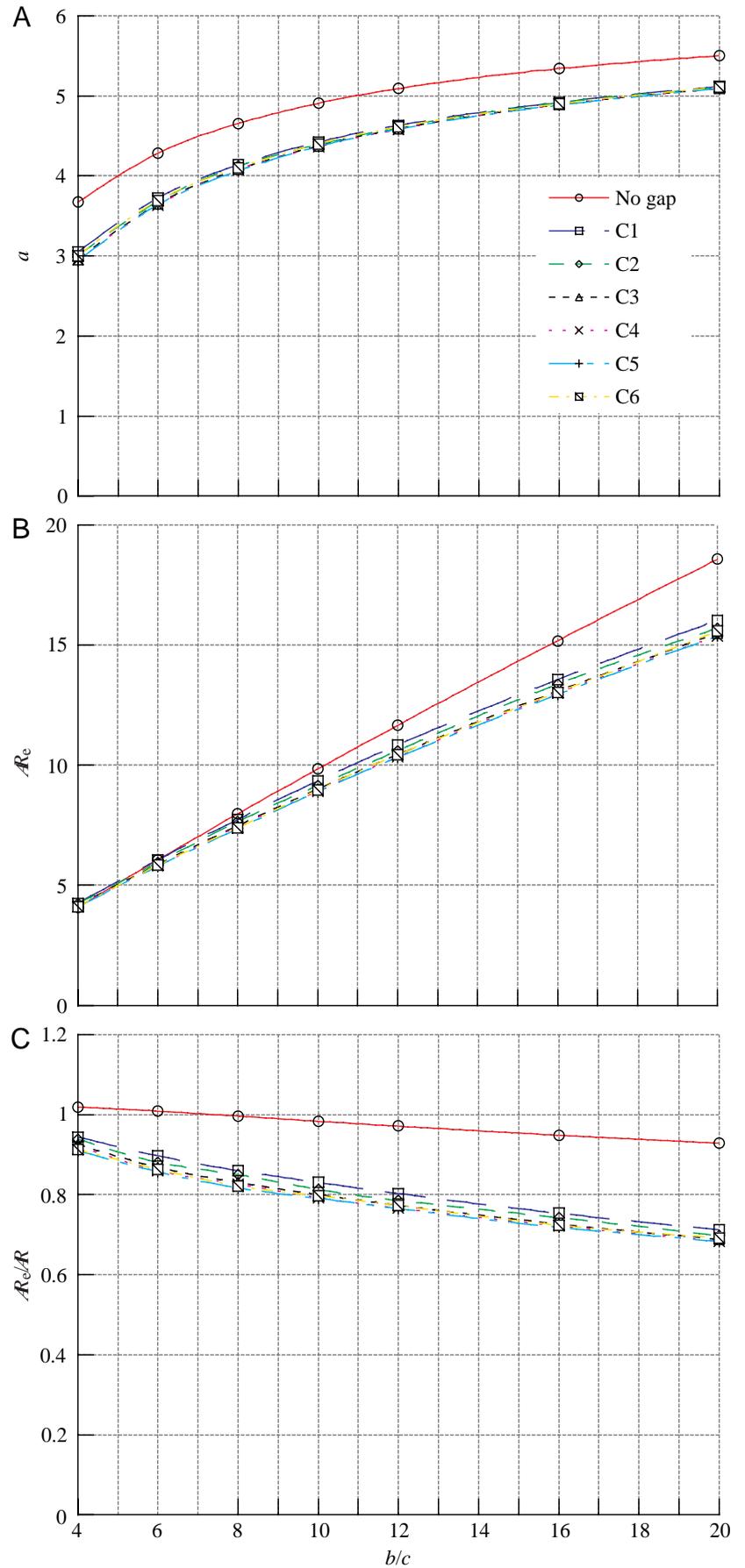


Fig. 5. The effect of secondary moult gap position and a primary moult gap not affecting the wing tip (case C with gap X, see Fig. 2C) on three aerodynamic measures and in relation to geometrical aspect ratio  $\mathcal{A}R$  ( $b/c$ ): (A) lift curve slope  $a$ ; (B) effective aspect ratio  $\mathcal{A}R_c$ ; (C)  $\mathcal{A}R_c/\mathcal{A}R$ . For an explanation of the different cases, see Fig. 2C.

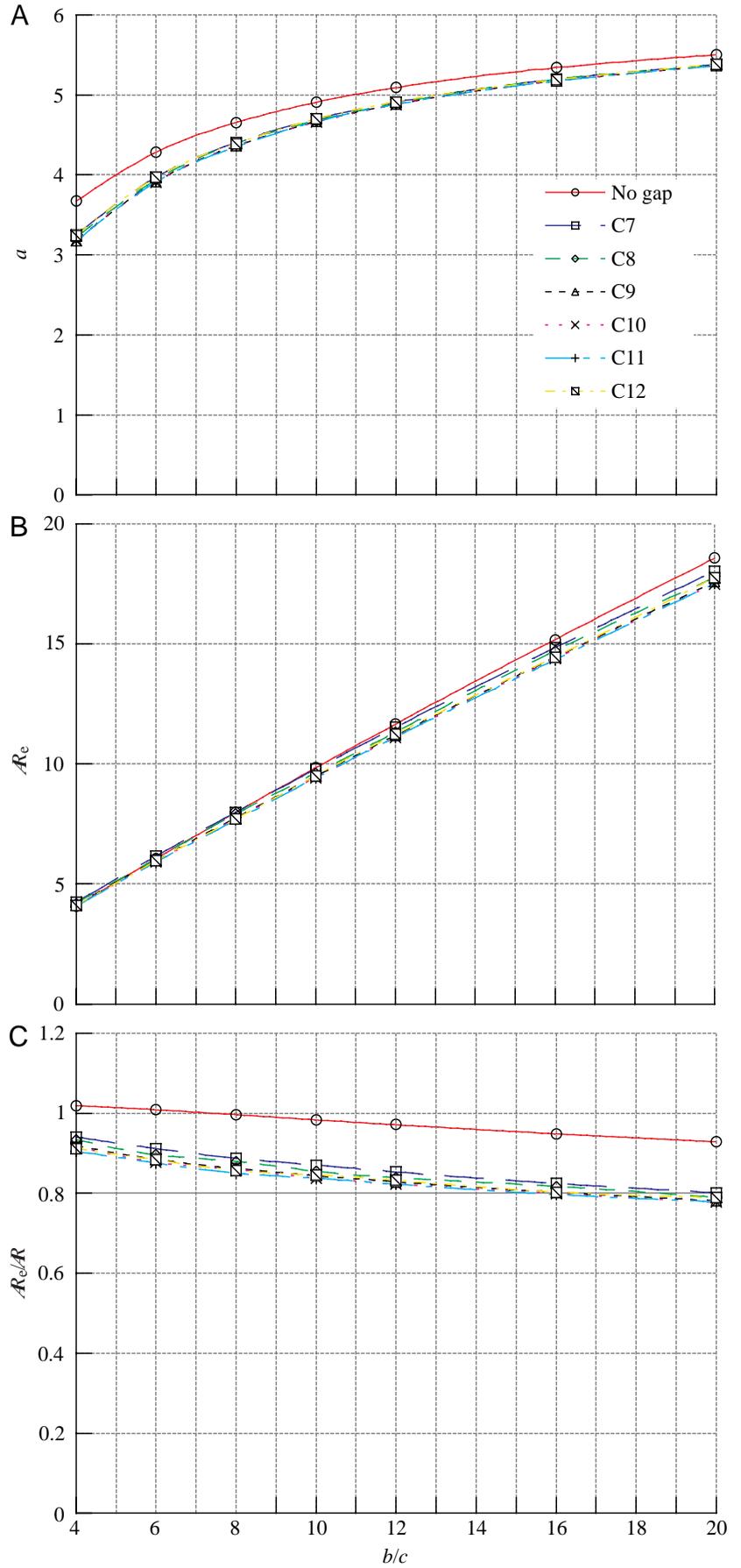


Fig. 6. The effect of secondary moult gap position and a primary moult at the wing tip (case C with gap Y, see Fig. 2C) on three aerodynamic measures and in relation to geometrical aspect ratio  $AR$  ( $b/c$ ): (A) lift curve slope  $a$ ; (B) effective aspect ratio  $AR_e$ ; (C)  $AR_e/AR$ . For an explanation of the different cases see Fig. 2C.

be increased costs of feather synthesis (e.g. Lindström et al., 1993) and, taken together, these costs may have a significant effect on the resulting overall migration speed (see Alerstam and Lindström, 1990; Hedenström and Alerstam, 1997). This effect is probably too large to allow moulting during spring migration when there is severe competition for breeding territories and rapid migration is therefore of great importance.

Further support for our relatively low predicted additional flight costs from having moult gaps comes from an experimental study by Slagsvold and Dale (1996), in which breeding female pied flycatchers (*Ficedula hypoleuca*) had primaries 4, 5 and 6 (counted from the inside outwards) on each wing experimentally cut off. In spite of this manipulation, no signs of increased energetic stress could be detected in the experimental birds compared with controls, which suggests that the power required for flight was not dramatically increased by the reduction in wing area. However, the pied flycatchers with reduced wing areas experienced increased predation levels, presumably by sparrowhawks (*Accipiter nisus*) (Slagsvold and Dale, 1996), indicating that the experimental manipulation had had a significant impact on their ability to evade predator attacks. For example, the minimum turning radius, which is a measure of the ability to escape attacking predators (see Howland, 1974), is directly proportional to the reciprocal of the wing area (e.g. Pennycuick, 1975). By way of example, a wing area reduction of 10% will increase the minimum turning radius by 11.1%. Recently, Swaddle and Witter (1997) showed experimentally that moult gaps have a negative effect on a number of flight performance measures, such as level flight speed, initial angle of escape take-off and speed of take-off.

Tucker (1991) measured the lift-to-drag ratio in a gliding Harris' hawk (*Parabuteo unicinctus*) in a wind-tunnel before, during and after the completion of the primary moult. He found a minimum lift-to-drag ratio during the moult of 69% of the pre-moult value, which is a much greater reduction than the values we predicted for moult gaps using our model. However, the primaries in the Harris' hawk are used as wing tip slots and make the wing non-planar by spreading the vorticity both horizontally and vertically (Tucker, 1995). Therefore, the loss of primaries where they serve as wing tip slots should result in a greater reduction in performance than the loss of ordinary flight feathers. Chai (1997) measured the effects of hovering performance during natural moulting and of artificial wing area reductions in ruby-throated hummingbirds (*Archilochus colubris*). The loss of the outer primaries had a larger impact than the loss of the secondaries on hovering flight performance, but the increased flight costs were compensated for by mass loss during natural moulting.

We assumed perfectly symmetrical moult gaps in both wings, but during natural feather re-growth asymmetries will occur (Swaddle and Witter, 1994) and these will reduce flight performance further (Thomas, 1993; Swaddle et al., 1996).

The increased effect of moult gaps with increasing aspect ratio is of great ecological significance since it could help to explain why large birds show relatively slow rates of moulting

that are associated with rather small gaps, for example in albatrosses (e.g. Prince et al., 1993).

This study is a first attempt to estimate theoretically the aerodynamic effects of gaps in the wings due to moulting in birds. The predictions of negative effects on flight performance are likely to have important ecological significance (see Swaddle and Witter, 1997).

### List of symbols

$AR$	geometrical aspect ratio
$AR_e$	effective aspect ratio
$a$	lift curve slope
$b$	wing span (m)
$C_{Di}$	induced drag coefficient
$C_L$	lift coefficient
$c$	wing chord (m)
$(i,j)$	panel number
$k, kk$	summation variables
$k_A, k_B, k_C$	parameters determining wing gap size and position
$N_w$	number of trailing vortices
$S_w$	wing area (m <sup>2</sup> )
$V$	forward speed (m s <sup>-1</sup> )
$w_{ind}$	induced velocity (m s <sup>-1</sup> )
$x, y, z$	coordinates of vortex elements
$\alpha$	angle of attack (degrees)
$\alpha_0$	geometrical angle of attack in the vortex method (2.5°)
$\Gamma$	circulation (m <sup>2</sup> s <sup>-1</sup> )

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