

Plumage condition affects flight performance in Common Starlings: implications for developmental homeostasis, abrasion and moult

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Variation in length and asymmetry of wing primary feathers can arise from a breakdown of developmental homeostasis, feather abrasion and incomplete growth during moult. Indirect predictions have been made concerning the impact of primary length and asymmetry on the flight ability of birds, but they have not been explicitly tested. Here we provide evidence from both natural variation in primary feather condition and experimental manipulations of primary feather length and asymmetry to indicate that these factors influence aspects of flight performance in the Common Starling *Sturnus vulgaris*. Damaged and incompletely grown primary feathers reduce escape flight performance. Experimentally reduced primary lengths reduce take-off speed; increased primary asymmetry decreases aerial manoeuvrability. A comparison of the experimental and natural plumage data indicates that birds may be able to adapt to a change in wing morphology, perhaps reducing the effects of feather loss or damage on flight. The results from this study indicate that primary feathers are under strong stabilising selection to maximise developmental homeostasis and reduce feather asymmetry. These findings are also of ecological importance to the damage-avoidance and moult strategies of these birds. This is the first experimental evidence to indicate a quantitative reduction in flight performance with feather lengths and asymmetries typical of those observed during flight feather moult and feather damage in any species.

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Primary feather lengths and asymmetries (fluctuating asymmetries, see Van Valen 1962) are known to vary within populations of birds (e.g., Balmford et al. 1993, Møller 1990, Swaddle and Witter 1994). This between-individual variation may result from differences in intrinsic developmental processes (Swaddle and Witter 1994, Witter and Swaddle 1994), rates of abrasion and damage (Francis and Wood 1989, Rogers 1990) or feather regrowth during moult (Ginn and Melville 1983). It has long been realised that such changes in plumage have implications for flight performance, from both empirical and flight-theoretical perspectives (for reviews, see Norberg 1990, Jenni and Winkler 1994).

To explain possible aerodynamic effects of avian wing asymmetry, Thomas (1993) produced a flight model based on Norberg's (1990) modification of Pennycuick's (1975) momentum jet theory of bird flight. In this model, wing asymmetry is defined as the difference in wing length between the left and right sides (Thomas 1993). It was assumed that wing asymmetries were more likely to influence wingspan than wing chord, as birds generally have wings of high aspect ratio (i.e. the length of the wing is much greater than the breadth). Thomas (1993) also suggests that the shape of the wings and the relative position along the wing where the asymmetry occurs is "unimportant provided the wings have a high aspect ratio". Under this scenario, wing

asymmetry (a) creates an asymmetry in lift (L) that results in a rolling moment (M_a), where $M_a = (La)/2$. This rolling moment may be offset by behavioural adaptations of an individual bird, such as increased flexing of the longer wing or independently adjusting the angle of attack of each wing (see Thomas 1993). These compensational changes would either result in the longer wing being shortened to match the shorter, or the lift coefficient of the shorter wing being increased. Therefore, this model predicts a reduction in turning performance in birds with asymmetric wings (Thomas 1993). These aerodynamic predictions are based on gross changes to wing length and wing area. Less consideration has been given to the biomechanical and aerodynamic consequences of changes in the length and asymmetry of individual feathers. It is noteworthy that damage and abrasion often only occur in single feathers and primary feathers are frequently shed and regrown one-by-one during moult (Jenni and Winkler 1994).

The wings of all birds are comprised of many overlapping feathers; the most biomechanically important of these are the primary feathers (Tucker 1991). Alterations to the dimensions of a single feather may not affect wing length or mean chord, depending upon the specific shape of the wing, but will always influence wing area. The extent to which area is affected will depend on the extent of overlap between adjacent feathers. Wing length may be affected if the wingtip is comprised of a single primary, which occurs in species with a very pointed wing shape (see Fig. 1). In such species, aspect ratio and wing area will be altered by changes in lengths of individual distal feathers. However, in species with more rounded wings, the wingtip (and hence the delimitation of wing length) is formed by a number of primaries with similar dimensions (see Fig. 1). Thus, damage to one of these feathers will have little effect on wing length. In any wing-shape formation, mean chord is unlikely to be greatly influenced by changes in length or asymmetry of single primaries (or small number of primaries), as the lower boundary of the wing is delimited by a number of feathers. The wingtip of the Common Starling *Sturnus vulgaris*, the subject of our study, is formed by the three most distal primaries, and so changes in wing length and wing length asymmetry can only be large if all three of these feathers are altered (Fig. 1). These observations affect the applicability of the aerodynamic predictions that have been made concerning the effects of wing length (and hence wingspan) and mean chord on flight performance (for a review, see Norberg 1990). At present, aerodynamic theory does not take account of changes in length and asymmetry of individual flight feathers. Thus, it is not possible to make quantitative predictions about the influence of individual primary lengths and asymmetries on aspects of flight. However, there is interest in addressing the flight performance conse-

quences of such changes in plumage because it is this type of change that naturally occurs during primary damage or moult in birds.

We predict that decreases in primary lengths and increases in primary asymmetry will act to decrease flight performance, as either lift is reduced or asymmetric lift is generated creating a rolling moment (cf. Thomas 1993). Primary asymmetry may particularly influence the ability of an individual to perform aerial manoeuvres, as there will be asymmetry in lift coefficients between the left and right wings.

Experimental investigations of the aerodynamic costs of flight feather asymmetry have been limited to the exaggerated tail ornaments of certain bird species (Møller 1991, Evans et al. 1994). However, it has been predicted that tail asymmetry is less important to flight performance compared with primary feather asymmetry (Thomas 1993) and the aerodynamic costs of the interaction of trait length and asymmetry may be directly opposite in wings compared with tails (Thomas 1993). Thus, we have investigated the effects of trait length

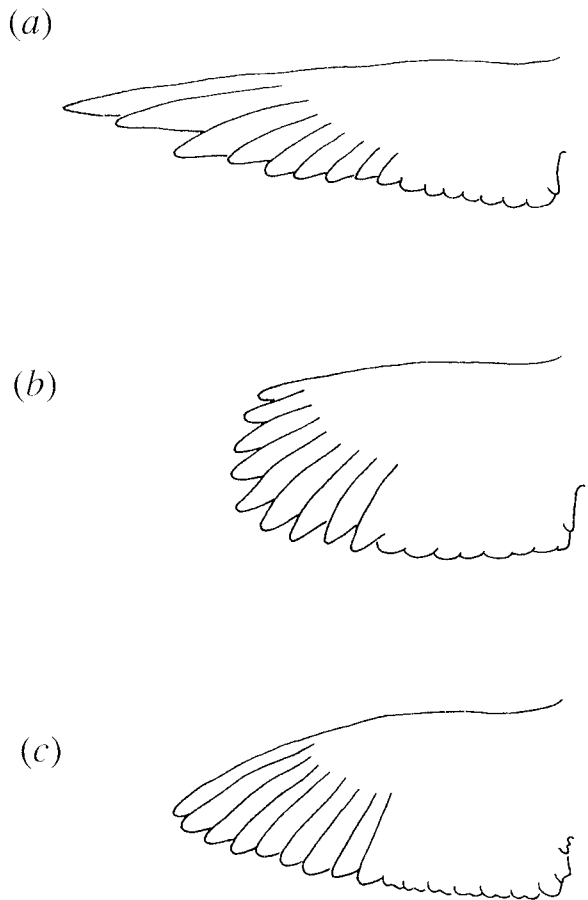


Fig. 1. Diagram of stereotypical wing outlines of (a) pointed wing; (b) rounded wing; and (c) wing of the Common Starling. Also see Rayner (1988), Norberg (1990) and Lockwood et al. (in press) for reviews of avian wing shape.

and asymmetry in the primary feathers of Starlings on three measures of flight performance: aerial manoeuvrability (defined in this study as performance through an obstacle course and so incorporates both manoeuvrability and agility, see Witter et al. 1994), trajectory of escape take-off flight and speed of escape take-off flight. These flight parameters are likely to influence aspects of individual fitness (e.g. predator avoidance) and so may be optimised by natural selection (see Hedenström 1992, Lima 1993, Witter et al. 1994). For example, many avian species rely on a short escape flight to cover to evade predation (e.g. Grubb and Greenwald 1982, Lindström 1989, Lazarus and Symonds 1992). Both the speed and trajectory of take-off have been suggested as important determinants of predation risk (Page and Whitacre 1975, Kenward 1978, Cresswell 1993, Witter et al. 1994, Metcalfe and Ure 1995). Once potential prey are airborne, manoeuvrability may be of primary importance in evading predation (Rudebeck 1950, Bijlsma 1990, Cresswell 1993).

Our study has implications beyond the assessment of the flight costs of natural variation in primary length and asymmetry. It is also relevant to length and asymmetry differences that may arise at different stages of moult or as a result of mechanical damage to feathers. Primary feather damage is common amongst birds (Ginn and Melville 1983, Rogers 1990) and moult is a key process in the regular replacement of primary feathers (Ginn and Melville 1983). The relative costs of primary length and asymmetry may influence the damage-avoidance strategies and moult strategies of birds. This is the first study, of any species, to attempt to quantify these costs and their consequences for flight ecology.

Methods

Natural plumage condition

We performed the first experiment on 192 wild-caught adult Starlings of mixed sex. Before and during the experimental period, birds were housed in 16 large ($2 \times 3 \times 3$ m) outdoor flight aviaries and were maintained on turkey starter crumbs and water ad libitum. Because of the large number of birds used, we chose a single feather on each wing as a measure of asymmetry. In all cases, this was the eighth primary, counted from the inner-most primary feather. This feather was chosen because changes to distal primaries may have a larger impact on flight performance than similar changes to more proximal primaries (cf. Evans and Hatchwell 1993); however, the distal-most primary (primary nine) was found to be damaged or abraded in many of the birds. On three occasions between December 1993 and January 1994, all the birds were caught and had the

length of their eighth primary feather measured (to 0.01 cm with Vernier callipers) on both wings. Additionally, any damage to the primary feathers was noted. During the latter two measurement sessions we also recorded take-off escape performance in all birds. Escape was assessed in a separate long narrow aviary ($1 \times 2 \times 4$ m). Half of the aviary was open space; the other half was filled with dense vegetation, shrubs and perches (protective cover). Birds were released, in the open side of the aviary, from a perch positioned 5 cm above the ground, simultaneously with the sounding of a loud vocal startle stimulus (cf. Witter et al. 1994). Take-offs were recorded on video tape, the camera being placed perpendicular to the line of flight. The video tapes were subsequently used to derive measures of trajectory and speed. Specifically, we measured the mean angle of ascent in flight (the angle subtended at the position of the bill tip when the bird was first in flight from the position of the bill tip after approximately 0.2 s of flight) and flight speed after 0.2 s of flight (speed, calculated from the total distance moved during three consecutive frames of the video after 0.2 s of flight). These data were then used to examine the relations between primary length, primary asymmetry, feather damage and escape performance.

Experimental manipulation of primary length and asymmetry

We performed the second experiment on 42 adult Starlings of mixed sex with undamaged flight plumage. Birds were housed in identical conditions to those described above. We randomly allocated the birds to six treatment groups ($N = 7$ for each group). In each treatment group, the sixth and seventh primaries of both wings were manipulated by removing a length of feather with fine scissors. These feathers were chosen as they were predicted to influence flight behaviour and were less likely to suffer physical damage during the experiment compared with the outermost primaries. The levels of manipulation were chosen to reflect lengths and asymmetries that would be observed during natural moult. The treatment groups were as follows (see Fig. 2). Short Symmetric (*SS*, Fig. 2a), the lengths of the sixth and seventh primaries were reduced to 2 cm on both left and right wings. Short Asymmetric (*SA*, Fig. 2b), primaries six and seven were shortened to 1.5 cm on one wing and 2.5 cm on the other. This manipulation occurred with equal probability on the left and right wings. Long Symmetric (*LS*, Fig. 2c), the sixth and seventh primaries were reduced to 6.5 cm on both wings. Long Asymmetric (*LA*, Fig. 2d), primary length was reduced to 6 cm on one wing and 7 cm on the opposite wing, again with equal probability of occurring on left or right sides. Control I (*CI*, Fig. 2e) birds were handled for the same amount of time as all

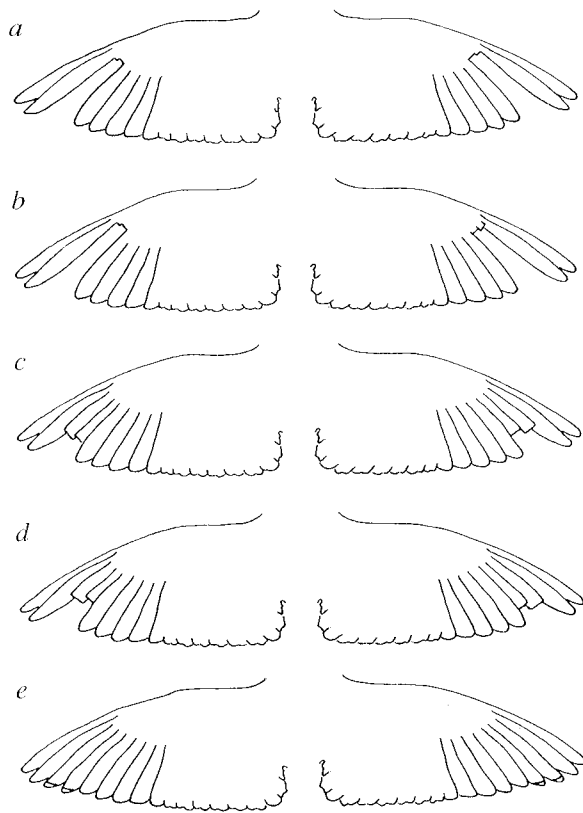


Fig. 2. Diagram of effect of the manipulations on wing outlines of starlings, (a) short symmetric, *SS*; (b) short asymmetric, *SA*; (c) long symmetric, *LS*; (d) long asymmetric, *LA*; (e) controls, *CI* and *CII*. *CI* birds were unmanipulated, *CII* birds had the tips of primaries six and seven removed. Refer to text for details of the manipulations.

manipulated birds but had none of the primary feathers shortened. Control II (*CII*, Fig. 2e) birds had the tips of primaries six and seven removed (approx. 2 mm) on both wings. Control manipulated birds had mean (\pm SE) feather lengths of 8.32 cm (\pm 0.031) for primary six and 8.77 cm (\pm 0.055) for primary seven. Mean (\pm SE) asymmetry for primary six = 0.087 cm (\pm 0.023) and primary seven = 0.055 cm (\pm 0.010).

One week before and immediately following the manipulations, all birds were flown through a manoeuvrability course and were recorded performing take-off and escape flight, in two separate experimental procedures. Trajectory and speed of escape were recorded using identical techniques and apparatus to those employed in the first experiment. Body masses were also recorded on an electric balance to 0.1 g accuracy. The manoeuvrability course measured 1 \times 2 \times 4 m and comprised a series of rows of identical wooden poles, covered in parcel tape, suspended from the course ceiling, which the birds had to negotiate (see Witter et al. 1994). There were five rows of poles, which alternated from having three or two poles in a staggered arrangement 0.3 m and 0.25 m apart. Rows were 0.25

m apart. Branches, food and bathing water were placed at the end of the manoeuvrability course to encourage birds to fly straight through without pausing or stopping. Both wings of each bird were dipped in a standardised volume of water soluble black ink. Birds were held by an experimenter on a perch approximately 1.5 m from the floor at the beginning of the course. They were then exposed to a short vocal startle stimulus and simultaneously released. Birds flew directly through the course to the area of food and water. Any birds that did not fly through the entire course, or perched on the suspended poles, were retested until a successful trial had been recorded. This occurred on only five occasions across all the trials, with these birds being retested once. The number of rows that each individual made contact with, displayed by black ink marks on the poles, was noted (cf. Møller 1991). This design enabled the investigation of the influence of primary length, primary asymmetry and an interaction of length and asymmetry on manoeuvrability and take-off performance.

Validation of measurements and statistical analyses

Measures of primary length and asymmetry were highly repeatable, as determined by intraclass correlation coefficients and mixed-model ANOVA (see Swaddle et al. 1994, 1995; experiment 1, primary eight length, $r_1 = 0.995$, $P < 0.0001$; primary eight asymmetry, $F_{19,38} = 29.67$, $P < 0.0001$; experiment 2, primary seven length, $r_1 = 0.943$, $P < 0.0001$; primary seven asymmetry, $F_{13,52} = 6.69$, $P < 0.0001$; primary six length, $r_1 = 0.951$, $P < 0.0001$; primary six asymmetry, $F_{13,52} = 5.89$, $P < 0.0001$). Excluding damaged feathers, asymmetries approximated a normal distribution about a mean of zero (experiment 1, normal probability correlation, $r = 0.983$, one-sample t-test, $t = 0.06$, $P = 0.95$; experiment 2, normal probability correlation, $r = 0.991$, one-sample t-test, $t < 0.55$, $P > 0.59$, for both primaries). These properties are in close agreement with our previous analyses of plumage asymmetry in the Starling (see Swaddle and Witter 1994, Witter and Swaddle 1994). All analyses from the first experiment were performed on mean absolute asymmetry and mean length from the three measurement sessions, and mean measures of performance from the two escape measurements. These analyses mostly consist of analyses of covariance and least-squares regressions. Where appropriate, asymmetries have been transformed to meet the assumptions of the tests employed.

Data from experiment two were analysed using MANOVA on SPSS (SPSS Inc. 1988) with body mass entered as a covariate. Orthogonal contrasts were performed to investigate the differences between specific treatment groups. The orthogonal contrast matrix consisted of the following four comparisons, in all cases.

Table 1. Analysis of the effects of primary asymmetry, primary length and feather damage on escape performance in experiment 1.

	df	F	P
Ascent angle			
Damage	1,178	0.12	0.727
Length	1,178	0.78	0.378
Asymmetry	1,178	4.14	0.043
Damage*Length	1,178	0.49	0.483
Damage*Asymmetry	1,178	5.42	0.021
Length*Asymmetry	1,178	5.56	0.019
Damage*Length*Asymmetry	1,178	1.00	0.318
Speed			
Damage	1,176	0.15	0.696
Length	1,176	1.50	0.222
Asymmetry	1,176	1.18	0.279
Damage*Length	1,176	2.19	0.141
Damage*Asymmetry	1,176	0.16	0.688
Length*Asymmetry	1,176	0.06	0.810
Damage*Length*Asymmetry	1,176	0.00	0.980

(1) The effect of primary length, *CI* and *CII* vs. *LS*, *LA*, *SS* and *SA*; plus *LS* and *LA* vs. *SS* and *SA*. (2) The effect of primary asymmetry, *LS* and *SS* vs. *LA* and *SA*. (3) The effect of an interaction between length and asymmetry, *LS* and *SA* vs. *LA* and *SS*. (4) Differences between control treatments, *CI* vs. *CII*. Two-tailed tests of probability are used throughout.

Results

Natural primary asymmetry and escape performance

Across all of the individuals measured, there was a significant negative relation between asymmetry and length, but the relationship differed between damaged and undamaged primaries (length, $F_{1,188} = 30.25$, $P < 0.001$; damage, treated as a binary categorical variable, $F_{1,188} = 22.23$, $P < 0.001$; length*damage, $F_{1,188} = 20.62$, $P < 0.001$). There was no significant linear relationship between primary asymmetry and length in the undamaged feathers (Asymmetry = $0.749 - 0.034 * \text{Length}$, $F_{1,135} = 0.74$, $P = 0.391$), as would be expected for traits under stabilising selection (Møller and Pomiankowski 1993). However, for damaged primaries there was a strong negative relationship between asymmetry and length (Asymmetry = $3.90 - 0.360 * \text{Length}$, $F_{1,53} = 26.08$, $P < 0.001$). This demonstrates the important point that trait-damage can create a negative relationship between trait length and trait asymmetry because damage both decreases mean trait length (undamaged feathers, 9.4058 ± 0.0196 cm, damaged feathers, 9.2043 ± 0.050 cm; $t = 3.75$, $P < 0.001$) and increases mean asymmetry (undamaged feathers, 0.0546 ± 0.0054 cm, damaged feathers, 0.2579 ± 0.0591 cm; $W = 11017.0$, $N_1 = 55$, $N_2 = 137$, $P < 0.0001$). There-

fore, it is vital that damaged individuals are identified in any investigation of fluctuating asymmetry, as damage can lead to a spurious negative relationship between trait size and asymmetry that may influence the interpretation of asymmetries within and between populations, especially in situations where asymmetries are purported to have signalling properties (see Cuthill et al. 1993, Sullivan et al. 1993, Swaddle et al. 1994, 1995).

The analyses of the relationships between primary asymmetry, primary length, damage and escape performance are shown in Table 1. Speed was not significantly related to damage, length, asymmetry or any interaction of these variables. The angle of ascent in flight decreased with increasing primary asymmetry; although the effects of primary asymmetry differ according to feather length and damage. Examining damaged and undamaged feathers separately (Table 2) revealed that in the damaged feathers angle of ascent was significantly negatively related to primary asymmetry, with the effect of asymmetry being larger in shorter feathers (Fig. 3). There was no relation between ascent angle, length and asymmetry in the undamaged feathers (Table 2).

Manipulated primaries and manoeuvrability

There was an overall effect of the manipulations on aerial manoeuvrability ($F_{5,35} = 2.91$; $P = 0.027$; Fig. 4). This effect was due to a reduction in flight performance with increasing primary feather asymmetry, as symmetrically manipulated birds made contact with fewer rows than asymmetric birds ($F_{1,35} = 6.35$; $P = 0.016$). There was no effect of primary length on manoeuvrability ($F_{2,35} = 2.41$; $P = 0.104$), nor was there evidence of an interaction between primary feather length and asymmetry ($F_{1,35} = 0.09$; $P = 0.772$). There was no difference in manoeuvrability between the two control treatments ($F_{1,35} = 0.36$; $P = 0.550$).

Manipulated primaries and escape performance

The manipulations significantly affected take-off speed ($F_{5,35} = 7.20$; $P = 0.010$; Fig. 5b). A reduction in primary length decreased the speed of escape flight

Table 2. Analysis of the effects of primary asymmetry and primary length on angle of ascent in flight in the damaged- and undamaged-feather groups from experiment 1.

		df	F	P
Undamaged	Asymmetry	1,127	1.92	0.169
	Length	1,127	0.57	0.453
	Asymmetry*Length	1,127	1.80	0.183
Damaged	Asymmetry	1,51	11.84	0.001
	Length	1,51	0.27	0.604
	Asymmetry*Length	1,51	12.68	0.001

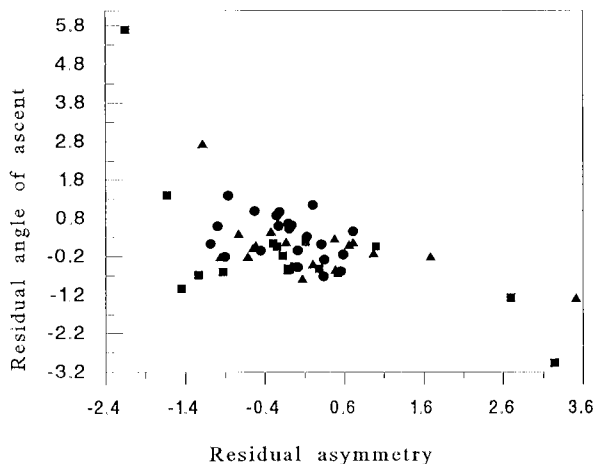


Fig. 3. Angle of ascent in flight versus primary asymmetry controlling for effects of feather length in the damaged feather group from experiment 1. To illustrate the length-asymmetry interaction, symbols are shown in three length categories: the 12 shortest feathers (■), the 12 intermediate feathers (▲) and the 11 longest feathers (●). The relationship between asymmetry and angle of ascent is strongest in the shortest feathers and becomes progressively less strong in the other length categories (Short feathers, $r_{12} = -0.645$, $P = 0.013$, intermediate feathers, $r_{12} = -0.591$, $P = 0.026$, long feathers, $r_{11} = 0.168$, $P = 0.583$).

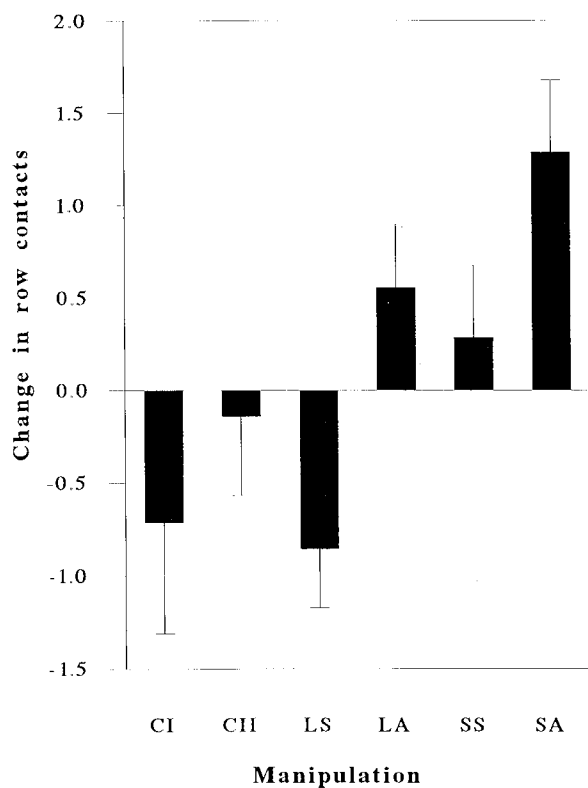


Fig. 4. Mean (+ SE) change in the number of row contacts for each treatment group from before to after the manipulations. Treatment abbreviations refer to short symmetric, *SS*; short asymmetric, *SA*; long symmetric, *LS*; long asymmetric, *LA*; and control groups, *CI* and *CH*. Refer to text for details of the manipulations employed.

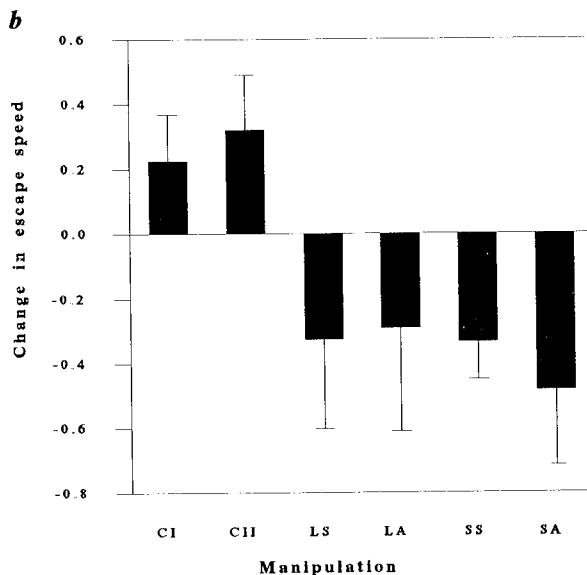
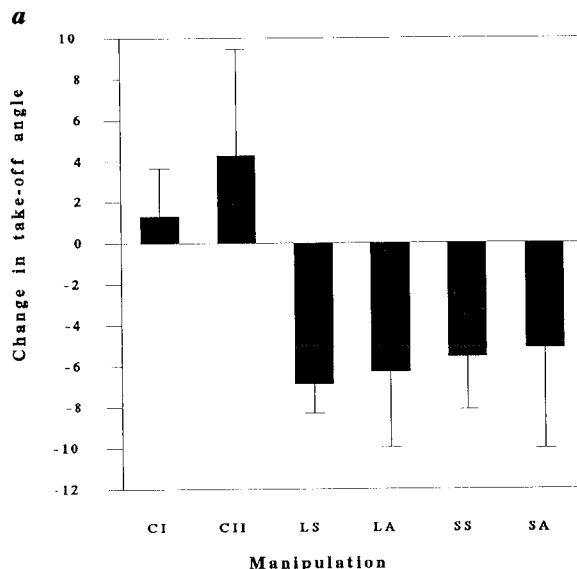


Fig. 5. Mean (+ SE) change in (a) angle of escape flight ($^{\circ}$) and (b) speed (m s^{-1}) for each treatment group from before to after the manipulation. Treatment abbreviations refer to short symmetric, *SS*; short asymmetric, *SA*; long symmetric, *LS*; long asymmetric, *LA*; and control groups, *CI* and *CH*. Refer to text for details of the manipulations employed.

($F_{2,35} = 6.28$; $P = 0.005$). However, increasing asymmetry did not influence take-off speed ($F_{1,35} = 0.35$; $P = 0.559$). As in the case of aerial manoeuvrability, there was no indication of an interaction of length and asymmetry affecting escape flight speed ($F_{1,35} = 0.25$; $P = 0.622$) and there was no difference between control treatment birds ($F_{1,35} = 0.03$; $P = 0.856$). There was no significant effect of the manipulations on escape angle ($F_{5,35} = 5.66$; $P = 0.063$; Fig. 5a). However, angle of ascent followed a similar pattern to those observed in

the flight speed data; birds with shortened primaries tended to take-off at a shallower angle (Fig. 5).

Discussion

The results from the first experiment indicate that natural variation in full-grown primary feathers is not related to escape performance of Starlings, unless the feathers are damaged. Individuals that have suffered asymmetric feather damage exhibit decreased angle of escape. These data suggest that large, asymmetric damage impairs escape performance. However, these relations are correlational and may be confounded by other between-individual differences. For example, these data are equally compatible with the view that birds that are poor fliers are more prone to large asymmetric plumage damage. Therefore, these data alone do not allow causal relations to be drawn between asymmetry, length, damage and escape performance. Hence, we performed the second experiment in which primary length and asymmetry were factorially manipulated. This enabled us to distinguish experimentally the relative effects of primary feather length and asymmetry on escape take-off performance and aerial manoeuvrability. It also allowed the investigation of the predicted interaction of primary length and asymmetry on flight performance (Evans and Hatchwell 1993, but see Thomas 1993).

The data from the second experiment indicate that both primary length and primary asymmetry directly influence aspects of flight in Starlings; but they appear to affect different aspects of flight differentially. Increasing primary asymmetry had no significant effect on take-off, but did influence manoeuvrability. Reducing primary length influenced take-off, but manoeuvrability was not significantly affected.

Birds with the shortest primaries had a lower take-off speed than birds with longer feathers and controls. This may be due to a decrease in wing area in birds with shortened primaries that results in a relative loss of thrust and lift generated by the wings (reviews in Pennycuik 1975, Norberg and Rayner 1987, Norberg 1990). Asymmetric lift generation, as would be expected in the asymmetric treatments, did not have a significant influence on this measure of escape performance. Interestingly, natural variation in plumage damage and asymmetry were associated with changes in angle of escape flight, but not speed, whereas the plumage manipulations influenced speed of escape flight; trajectory of the escape response was not significantly affected by the experimental manipulations. Previous analysis of escape response in Starlings has demonstrated that angle of take-off can be affected by experimental mass changes; increasing the mass of a bird decreases the angle at which it takes-off from the ground (Witter et al. 1994). Increasing body mass and reducing primary

lengths will both act to increase wing loading. There may also be a direct trade-off between angle and speed of escape flight (Witter and Cuthill 1993). The apparent differences present between the data obtained from natural observations and the experimental treatments may reflect compensational changes of the birds to the loss of sections of the wing. Birds in the experimental treatments were assessed immediately following the manipulations, perhaps not allowing time for any compensatory response. This contrasts with the birds in the natural plumage condition experiment, where they may have had time to adapt their take-off behaviour to their change in flight plumage. These compensations may take the form of changes in musculature or other components of body mass (see Swaddle and Witter unpubl.); or behavioural responses such as independent flexing of wings, or adjustments of angle of attack and camber on each wing separately (see Thomas 1993). Our data are consistent with the view that birds may undergo compensational responses to changes in flight morphology, and that through these changes they appear to conserve escape take-off speed to the detriment of the angle of their escape trajectory (Witter et al. 1994). It is noteworthy that Starlings' escape-flight speed was reduced when tested immediately after the addition of artificial loads, but loads had no influence on escape-flight speed if birds were tested several days after the addition of extra mass (see Witter et al. 1994).

Increased asymmetry decreased performance through the manoeuvrability course. This is most likely to be due to asymmetry creating differential lift on left and right wings along the roll axis (see Thomas 1993). The effect of asymmetry did not appear to differ at different feather lengths. Perhaps one would expect a non-additive (i.e., interaction) effect of reduced feather length and increased asymmetry on flight performance. This might be predicted because the relative costs of asymmetry are believed to be smaller at shorter feather lengths (Evans and Hatchwell 1993, Swaddle and Witter 1994). Shorter feathers may lie nearer to the roll axis, depending upon the configuration of the wing, so equal levels of asymmetry create smaller turning forces about this plane in shorter feathers. Contrary to these predictions, we found no evidence for such an effect.

All the manipulations that were performed in the second experiment resulted in lengths and asymmetries outside the natural range observed in these primaries at full growth. However, the manipulations did result in lengths and asymmetries that are typical of those observed during moult and feather regrowth in the Starling (Swaddle and Witter 1994, J. P. Swaddle, unpublished data). Although final primary feather lengths may possess little asymmetry, earlier stages of feather growth can be associated with relatively large asymmetries (up to approximately 3 cm, Swaddle and Witter 1994). Therefore, these results have implications for moulting strategies in Starlings and, perhaps, other

similar species. There have been few previous experimental investigations of the effects of moult on aspects of avian flight. Tucker (1991) observed that natural moult reduces the lift to drag ratio during gliding of a Harris' Hawk *Parabuteo unicinctus*. This change in flight performance appeared to be U-shaped over the period of moult. We have found that both natural patterns of moult and experimental simulations of different stages of moult affect a number of flight parameters in the Starling (Swaddle and Witter unpubl.). Unlike Tucker (1991), we did not find evidence for a U-shaped change within moult stages, although our study was limited to just three stages of moult. We did, however, find that moulting birds had reduced escape performance, reduced ability to perform aerial manoeuvres and flew slower during level flapping flight (Swaddle and Witter 1996). Anecdotal and observational accounts of bird behaviour during moult support these findings; there are reports of moulting birds having reduced flying ability and exhibiting less conspicuous behavioural patterns (e.g. Newton 1966, Dolnik and Blyumental 1967, Haukioja 1971, Ginn 1975).

This study is the first to show that the reduced feather lengths and increased asymmetries, typical of those associated with moult in the Starling, affect flight behaviour in specific ways. Reduced primary length reduces take-off and escape flight speed; increased primary asymmetry reduces aerial manoeuvrability. Birds may attempt to minimise the effect of this loss of flight performance by maximising feather growth rates whilst relaxing developmental control, as the cost of asymmetry does not appear to be greater at shorter feather lengths (*contra* Swaddle and Witter 1994). However, because the flight performance consequences of individual asymmetric primary feathers may differ according to wing shape, we might expect trade-offs in feather growth rate to differ between species with different wing shapes. Examining the patterns of change in plumage asymmetry as the primaries grow during moult in species with different shaped wings may be revealing in this context.

These findings also have implications for moult strategies, as it has been recognised that the physiological and energetic costs of feather replacement during moult may not be sufficient to explain the separation of moult from other aspects of the annual cycle of most bird species, especially in species that exhibit slow or partial moults (Murphy and King 1992). Also, moult is often associated with a reduction in other energetically costly activities and the energetic costs of moult may be counterbalanced by behavioural adaptations to conserve energy (King 1980, Lindström et al. 1993). This study provides experimental support for the notion that moult entails functional costs beyond those measured in studies of physiology, nutrition and energetics (e.g. King 1980, Murphy et al. 1990, Murphy and King 1991, 1992, Dietz et al. 1992, Lindström et al. 1993).

These indirect functional costs may be just as relevant in helping to explain the timing, duration and pattern of moult as the direct physiological costs (cf. Earnst 1992). Similarly, our results also have implications for damage and wear avoidance strategies of birds. Primary feathers are often damaged or abraded as a result of a number of different factors, e.g. bacterial infection, photochemical processes, physical abrasion (Ginn and Melville 1983, Rogers 1990, Burt 1986, Francis and Wood 1989). Damage and abrasion of feathers can result in feather lengths and asymmetry changes more dramatic than those illustrated here and so will have significant effects on flight performance. One way of avoiding these costs may be by the deposition of melanin at the tips of feathers to reduce primary abrasion (cf. Burt 1986, Bonser and Witter 1993). A systematic investigation of the flight consequences of length and asymmetry in different primaries may illustrate the relative costs associated with damage of distal and proximal primaries and so may help to explain patterns of melanin deposition.

In summary, these results indicate that primary feather length and asymmetry influence flight performance in Starlings. Decreasing primary length reduces escape flight speed; whereas increasing feather asymmetry reduces aerial manoeuvrability. These results have consequences for feather abrasion and damage, flight-feather moult and the developmental homeostasis of feather development.

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