The effect of simulated flight feather moult on escape take-off performance in starlings

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We investigated the effects of the plumage changes associated with moult on the anti-predator take-off performance of European Starlings *Sturnus vulgaris*. By altering the plumage to simulate moult, we have isolated the biomechanical consequences of changes in wingform from the underlying physiological and metabolic changes that may occur during natural moult. Previous analyses of avian take-off performance have relied on descriptive observations of wingtip kinematics or dual measures of take-off speed and angle. We have developed a novel method using the energy gain per wingbeat as a measure of overall take-off performance. The advantages of this measure compared with previous approaches are that it summarises the potential trade-off between height gain and speed gain, and can be related directly to lift on the wings. Analysis of high speed (100 Hz) video tapes indicated that birds in simulated moult suffer a reduction in total energy produced during the second wingbeat of take-off, resulting in a slower take-off speed. This reduction in take-off performance is also associated with a marked change to the pattern of movement of the wingtip during flight; moult-manipulated birds appear to reverse the wingtip at the top of the downstroke although there is no associated change in wingbeat amplitude or duration. Birds appeared to be able to regain, in part, their flight performance within 6 days of the manipulations, as take-off speeds returned to pre-manipulation levels. This partial return to pre-manipulation flight performance was associated with an alteration in pattern of movement of the wingtip during take-off. The relevance of this adaptation to birds in natural moult is discussed. Any reduction in take-off performance is likely to influence directly individual behaviour and survival; hence the ability to quantify take-off in different species under a common currency is of general ecological importance and will enable predictions to be generated and tested concerning the effects of natural moult in wild birds.

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Take-off is one of the most energetically demanding modes of flight in birds; it is also important in, e.g., foraging and predatory avoidance. Notably, the ability of a bird to take-off from the ground by using flapping flight from a standing start, at a high speed and at a steep angle of trajectory, is likely to reduce the probability of being captured by a terrestrial predator (Lima 1993, Witter et al. 1994). Flight feather moult is known to reduce the take-off performance of European Starlings *Sturnus vulgaris*, and hence to increase predation risk (Swaddle and Witter 1997), and therefore, it is likely that take-off performance directly influences indi-

vidual survival (Lima 1993, Witter et al. 1994). Despite their important evolutionary implications (Swaddle and Witter 1997), there have been few attempts to quantify changes in flight behaviour or aerodynamics during either natural moult (Tucker 1991, Chai 1997, Swaddle and Witter 1997) or experimentally simulated moult (Swaddle and Witter 1997).

Swaddle and Witter (1997) have indicated that both natural and simulated moult incur costs in terms of flight behaviour, daily activity routines, anti-predatory tactics and body mass regulation in the European Starling. They also observed that birds in experimentally

simulated moult appeared to offset their loss of plumage and partially regain their original flight performance within two weeks of the manipulations. This response was associated with a reduction in body mass, which may reduce flight costs (Pennycuick 1975, Rayner 1979, 1990), or permit a bird to maintain a particular speed or rate of acceleration during take-off.

From these findings it is evident that moult affects flight performance and other aspects of biology. However, neither the aerodynamic mechanisms associated with moult in a bird in flapping flight, nor the mechanisms by which a flying bird may regain flight performance after prolonged exposure to experimentally simulated moult, are known. It might be hypothesised that any reduction in wing area brings a proportional decrease in the lift generated by the wing, but it is not immediately evident that this is the case, since a slotted wing does not behave in the same way as a solid wing with the same shape and area (cf. Tucker 1993, 1995). It is arguable that the loss of a primary tip feather – producing a slot parallel to the leading edge – has only a weak aerodynamic effect on vorticity bound on the wing. Additionally, Drovetski (1996) has reported that short secondary feathers (producing a trailing edge notch) in galliforms can increase lift to drag ratio in species with very short, rounded wings. Although Drovetski considered only steady-state aerodynamics, his findings could have implications for studies of slow flapping flight (e.g. take-off) during moult stages that influence the most proximal primary feathers in species with very rounded wings. Nonetheless, the behavioural responses to simulated and natural moult indicate that there is a marked aerodynamic effect and that during some stages of moult the wings are aerodynamically sub-optimal. It seems likely that the effect of moult is to reduce the total lift or the lift to drag ratio. In take-off, pressure for rapid take-off and/or acceleration is large, and aerodynamic factors on the wings and a range of additional mechanical and physiological factors may impose constraints which prevent a bird from making a simple compensation of the kind described above. Therefore, we hypothesise that moult may reduce the maximum lift that a wing can produce. Our observations on the effect of moult under the conditions of take-off should help us to isolate the significant limiting factors both on moulting birds and on take-off flight.

Previously, take-off performance has been analysed in a variety of ways including description of wingbeat kinematics (Norberg and Norberg 1971, Simpson 1983), measurement of leg thrust forces (Heppner and Anderson 1985, Bonser and Rayner 1996), and quantification of take-off speed and angle of trajectory (Marden 1987, Swaddle et al. 1996). All of these approaches have some limitations. For instance, qualitative descriptions of wingbeat kinematics do not allow any statistical comparisons to be made either within or among individuals, and hence are difficult to interpret.

Measurement of leg thrust forces allow comparisons to be made, but gives no indication as to the role of the wings, the major force producer during take-off, and therefore may be relatively uninformative about overall take-off performance in many species. Measuring take-off speed and angle of trajectory also allows statistical comparisons to be made among treatment groups. However, this method does not render a single measure of take-off performance and it is clear that a bird, in some situations (such as predatory avoidance), may choose to trade-off speed, acceleration and height gain, so that angle of trajectory and take-off speed are not independent. To integrate these two elements into one currency of performance we have developed a novel method of analysing take-off performance, in which the amount of mechanical energy gained per wingbeat cycle during take-off is measured. This takes into account the effects of height gain and of vertical and horizontal speed changes, giving a sum total for both kinetic and potential energy. Presumably in an escape take-off, a bird will attempt to maximise quantities measured by this parameter, and therefore it should be sensitive to the maximum lift force production of the wings. This measure of energy can be used as a standard measure, quantifying take-off performance in all birds. It may give an indication of the relative magnitudes of energy consumption during take-off under different conditions, but it cannot be related directly to the energy consumed during take-off (mean power output from the muscles, or mean metabolic power), which depends also on the efficiency of conversion of muscle force into lift by the flapping wings, on the energy-generating capacities of the flight muscle, and on work performed by the legs; the first two of these may be altered in a moulting bird, and the former may be altered in simulated moult.

In this study, by experimentally manipulating flight plumage to simulate moult, we have quantified the escape take-off performance consequences of the wing-form changes associated with moult in starlings. The changes in take-off performance that we have investigated are independent of the physiological and metabolic alterations that birds experience during natural moult. This investigation further illustrates the constraints acting on starlings during moult and indicates how these constraints are likely to influence their ecology and survival.

Methods

The experiment was performed on 21 wild-caught adult European Starlings of both sexes. When not in the experimental aviary, birds were housed in a large (2 × 5 × 2 m) outdoor aviary and supplied with turkey starter crumbs, drinking water and bathing water ad libitum.

Feather manipulation

Birds were randomly allocated to three treatment groups (N = 7 for each group) as follows. Control I: the feathers were not manipulated, but the birds were handled for an equal amount of time as those in the Control II and Moult treatments (see below). Control II: the tips of primaries four, five and six and tail feather three were removed with fine scissors, removing approximately 0.1% of the total feather area. This second control treatment was included to test whether there was a non-specific effect of removal of the feather tip (cf. Swaddle et al. 1996). Moult: primary four was reduced in length, by removal of a feather section with fine scissors, to 6.0 cm; primary five was reduced to 4.5 cm; primary six was reduced to 0.5 cm; and tail feather three was reduced to a length of 0.5 cm. This simulated a wing profile equivalent to a mid-moult stage (refer to Fig. 1 for a diagrammatic representation of the treatment groups).

Take-off performance

Escape take-off was filmed in a long, narrow flight aviary (3.5 × 1.2 × 2 m). One end of this experimental aviary contained perching sites, food, drinking water and bathing water. The opposite end of the aviary was empty except for a single perch positioned 5 cm above the floor, from which birds were released, and a white perspex sheet on which standardised gridlines were drawn so that the video recordings could be calibrated accurately. This sheet was placed on the far wall of the aviary at right angles to the perch so that it was in view of the camera when birds ascended from the perch. Birds were placed by hand on the perch at the empty end of the aviary 20 cm in front of the gridlines sheet and were released with the simultaneous sounding of a
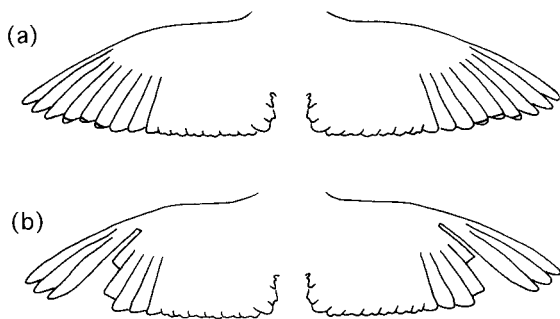

Fig. 1. Diagram of the effect of the manipulations on the wing feathers (i.e. after session 2). (a) Represents both Control I and Control II: (b) represents the effect of the Moult treatment. Wing area of Control I birds did not alter during the experiment; Control II birds experienced a minor reduction in wing area (0.09 ± 0.01%); Moult birds experienced a 9.82 ± 0.31% reduction in wing area as a result of the manipulations. Figures given are mean ± S.E.

loud vocal startle stimulus. All birds took off from the perch immediately and flew to the other end of the aviary which contained perching sites. The take-offs were recorded on a high-speed video camera (HSV-200, NAC Inc., Japan) filming at 100 Hz, the camera being placed perpendicular to the line of flight at a distance of 1.5 m from the position of the bird on the take-off perch. Take-offs of all birds were recorded on three occasions: session 1, before the manipulations were performed; session 2, immediately following the manipulations; and session 3, 6 days following the manipulations. This experimental design allowed us to investigate the immediate effects of the moult simulation treatment within individuals, and also to examine the longer-term influence of the plumage manipulations. Within each session, the take-off behaviour of each bird was recorded three times in quick succession, which allowed us to investigate the repeatability of flight behaviour. Immediately before flight trials, birds were weighed (to 0.1 g accuracy) on an electronic balance and flattened wing tracings were taken to calculate wing area and length.

Movement analysis

The high-speed video tapes were subsequently transferred to Hi-8 video through a Sony EV-S9000E video player and analysed with the public domain NIH Image program, version 1.6 (written by Wayne Rasband at the U.S. National Institutes of Health), on a Power Macintosh 8100/100AV. The first frame of take-off was taken to be the first frame when the bird's feet had left the perch. The next 15 frames were then digitised and analysed. The point of the bird's beak, the tip of the wingtip nearest to the camera (the left wing in all cases), the base and the tip of the tail were all digitised by hand using the NIH Image program. Computer software written by JMVR (for further details of the algorithms see Rayner and Aldridge 1985) was used to calculate the speed and angle of take-off and the instantaneous mechanical energy per unit mass (calculated as $\frac{1}{2}(V_x^2 + V_z^2) + gz$, where V_x and V_z are the horizontal and vertical components of flight speed, respectively, g is the acceleration due to gravity, and z is height) and the position of the wingtip during the wingbeat cycle. Velocity was calculated for every frame digitised and averaged over every wingbeat. The error associated with the digitising process was approximately 1 mm per point, which was minimised by using a smoothing method within the movement analysis program that employed Lanczos' least squares adjustment (Lanczos 1957). Body and tail angles during flight were calculated with reference to the horizontal. In addition, tail angle was also measured relative to body angle. It was not possible to accurately reconstruct the centre of gravity of each bird from the points digitised, hence the

tip of the bill was tracked for positional information to permit calculation of our measures of flight performance. Of the four points digitised, this appeared to follow the most consistently smooth trajectory during take-off, was reliably identified in all video frames and the position of the bill relative to the centre of mass will not have altered systematically among treatment groups. Speed and angle of trajectory were defined as the mean value over the first three wingbeats of take-off, starting from the point the bird's feet left the perch. Wingtip patterns were constructed by assuming the beak to be a constant position on the body; the co-ordinate values could then be subtracted from the wingtip values to get the wingtip position within a wingbeat; this method ignores recoil of the body and subtle movements of the head during the wingbeat. From the position of the wingtip at the top and bottom of the wingbeat and knowing maximal wing length from flattened wing tracings, we estimated wingbeat amplitude (assuming that all birds achieved maximal wing extension at the top and bottom of the wingbeat). Wingbeat duration was calculated from the number of frames of video it took to complete a full wingbeat. Mechanical energy gain per wingbeat was calculated as the difference in mechanical energy between two time instants at the same phase of the wingbeat.

Statistical analyses

All analyses, unless otherwise stated, were performed on SPSS (SPSS Inc. 1988) using the MANOVA procedure with a within-subject factor (experimental session) and a between-subject factor (treatment group). Analyses of speed of take-off, angle of trajectory, body and tail angles and wingbeat amplitude during take-off were performed with body mass as a covariate. Differences between treatment groups were explored by orthogonal pairwise contrasts (see Hand and Taylor 1987) with the following comparisons: (1) Control I and Control II vs. Moult; (2) Control I vs. Control II. All tests, unless otherwise stated, were performed on the mean of the repeated measures performed on each bird within a session. The single averaged values for each bird were also used to calculate mean $\pm$ s.e. values for the figures. Two-tailed tests of significance are used throughout.

Results

Take-off performance: speed and angle of escape take-off

Speed of take-off was significantly repeatable within a session (intra-class correlation coefficient (Zar 1984) $r_1 = 0.93$, $F_{20,2} = 29.02$, $P = 0.034$); however, angle of
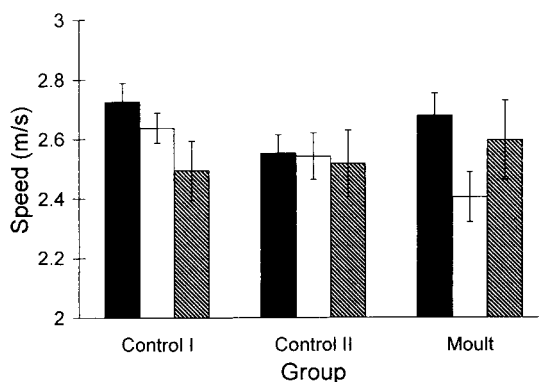

Fig. 2. Mean ($\pm$ s.e.) speed (m/s) of take-off with treatment group during the three sessions of the experiment. Filled bars represent data obtained in session 1 (before manipulations), open bars represent session 2 (immediately after manipulations), and shaded bars represent session 3 (six days after manipulations).

trajectory was not repeatable ($r_1 = 0.51$, $F_{20,2} = 3.09$, $P = 0.27$).

Comparison of take-off performance from session 1 (before the manipulations) with session 2 (immediately following the manipulations), indicated that there was a significant effect of the manipulations on speed of take-off ($F_{2,17} = 4.74$, $P = 0.023$, Fig. 2). Moult birds flew slower after the manipulations than both control groups (Control I and Control II vs. Moult, $t = 2.94$, $P = 0.009$), and there was no difference between control treatments (Control I vs. Control II, $t = 0.88$, $P = 0.39$). There was no significant effect of the treatments on angle of trajectory ($F_{2,17} = 2.67$, $P = 0.10$, Fig. 3).

Birds regained flight performance, at least partially, 6 days after the manipulations, as there was a significant increase in speed of take-off from session 2 (immediately following the manipulations) to session 3 (6 days
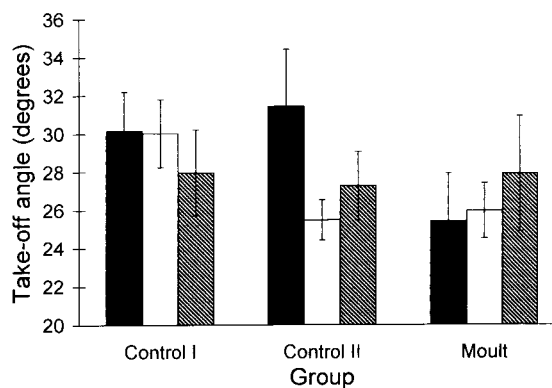

Fig. 3. Mean ($\pm$ s.e.) angle (°) of trajectory of take-off with treatment group during the three sessions of the experiment. Filled bars represent data obtained in session 1 (before manipulations), open bars represent session 2 (immediately after manipulations), and shaded bars represent session 3 (six days after manipulations).
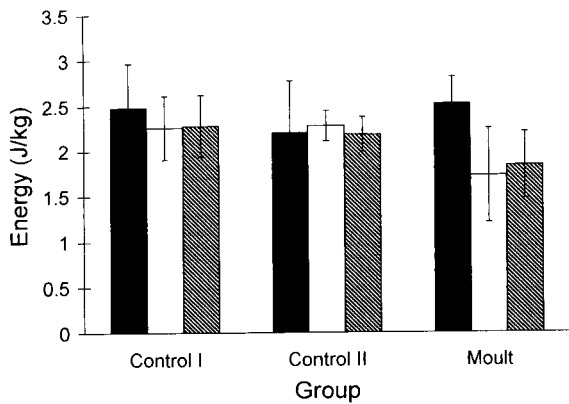
Fig. 4. Mean ($\pm$ s.e.) energy gained per unit mass (J/kg) during the second wingbeat of take-off during the three sessions of the experiment. Filled bars represent data obtained in session 1 (before manipulations), open bars represent session 2 (immediately after manipulations), and shaded bars represent session 3 (six days after manipulations).

after the manipulations) ($F_{2,17} = 3.73$, P = 0.046, Fig. 2). This difference was due to an increase in take-off speed in Moult birds (Control I and Control II vs. Moult, t = 2.58, P = 0.019); control birds did not differ (Control I vs. Control II, t = 0.70, P = 0.49). This is further supported by the observation that take-off speed did not differ between session 1 and session 3 across the treatment groups ($F_{2,17} = 1.92$, P = 0.18). Angle of trajectory during take-off did not differ with treatment group between session 2 and session 3 ($F_{2,17} = 1.47$, P = 0.26), or between session 1 and session 3 ($F_{2,17} = 1.66$, P = 0.219, Fig. 3).

Take-off performance: energy gain per wingbeat

The energy gained per wingbeat per unit body mass during take-off was not repeatable for either the first ($r_1 = 0.050$, $F_{20,2} = 1.10$, P = 0.581) or second wingbeat ($r_1 = 0.16$, $F_{20,2} = 1.00$, P = 0.614). However, there were no systematic differences between repeats in energy gained during each wingbeat (first wingbeat: $F_{2,40} = 3.063$, P = 0.058; second wingbeat: $F_{2,40} = 0.677$, P = 0.514); therefore, we used average values across repeats within a session in all subsequent analyses. Additionally, the energy gained during the second wingbeat was far greater than that gained during the first (paired t-test: $t_{20} = 6.89$, P = 0.0001); and hence further analyses concentrated on the second wingbeat alone.

The manipulations significantly affected the energy gained in the second wingbeat of take-off (session 1 vs. session 2, $F_{2,18} = 5.30$, P = 0.016, Fig. 4). Moult birds gained less energy than controls (t = 3.06, P = 0.007), but there was no difference between control groups (t = 1.10, P = 0.287). There were no differences in energy gained with treatment group between sessions 2

and 3 ($F_{2,18} = 0.28$, P = 0.759), and similar results apply to absolute as well as to mass-specific energy gain, and hence there is little evidence that Moult birds were able to regain flight performance in terms of energy gain within 6 days post-manipulation.

Body and tail angle

Body and tail angles were analysed with data obtained from 0.06 to 0.15 s after the bird had left the perch, and always incorporated at least one full wingbeat. The first 0.05 s of take-off were ignored as it was felt that this period of take-off would be dominated by the posture of the bird on the perch and the bird would be too close to the ground to move its tail effectively.

There was no effect of the manipulations on mean (averaged among video frames) body angle during take-off (comparing session 1 with session 2, $F_{2,17} = 0.84$, P = 0.447). Neither was there an effect of the moult manipulation on variance in body angle across frames within a session (comparing session 1 with session 2, $F_{2,17} = 2.33$, P = 0.127). However, there was a significant effect of moult on mean tail angle between session 1 and session 2 ($F_{2,17} = 4.29$, P = 0.031, Fig. 5), in which Moult birds held their tail in a relatively more horizontal position in comparison with controls (Control I and Control II vs. Moult, t = 2.14, P = 0.048; Control I vs. Control II, t = 1.98, P = 0.061). There was no difference in mean tail angle between session 2 and session 3 ($F_{2,17} = 2.19$, P = 0.142). There was also no effect of the manipulations on variance in tail angle across frames within a session (comparing session 1 with session 2, $F_{2,17} = 1.65$, P = 0.221). Additionally, tail angle relative to the position of the body (tail angle of attack) was not influenced by the manipulations (comparing session 1 with session 2, $F_{2,17} = 0.78$, P = 0.475).
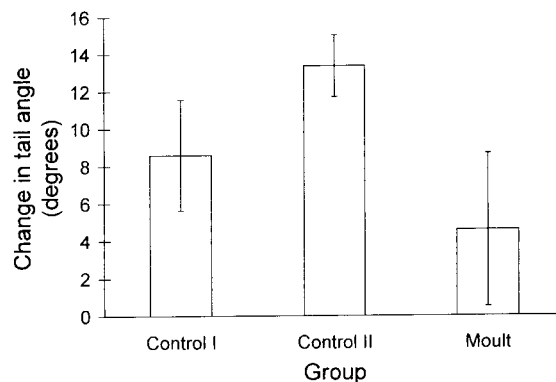

Fig. 5. Mean ($\pm$ s.e.) change in tail angle (°) relative to the horizontal due to the manipulations (i.e. difference between sessions 1 and 2). A larger angle signifies a greater downward deflection of the tail; hence, Moult birds held their tails in a more horizontal position during take-off than either control group.
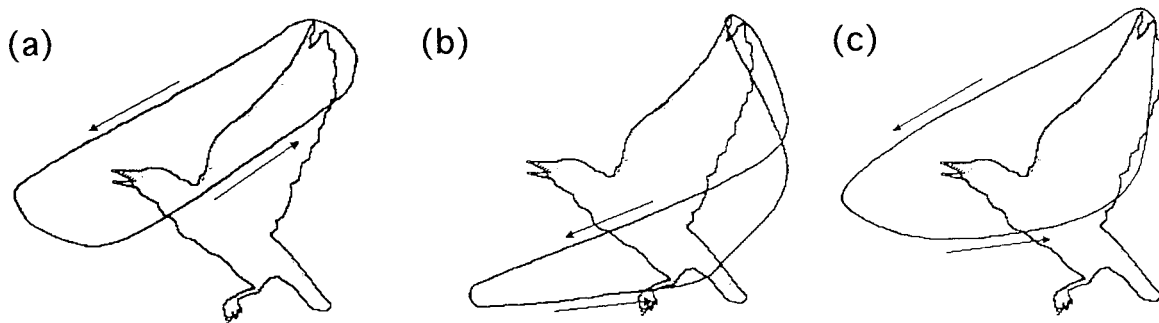
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Fig. 6. Diagram of wingtip kinematic patterns of a typical bird from the Moult treatment during the three phases of the experiment: (a) session 1; (b) session 2; and (c) session 3. All birds from this treatment group showed a consistent pattern of wingtip reversals during session 2. Throughout the whole experiment, birds in the other treatment groups exhibited the normal wingtip kinematic pattern observed in session 1 of Moult birds.

Wingtip kinematics

The first wingbeat was relatively abbreviated in amplitude compared with the second ($t_{20} = 5.01$, P = 0.001), hence kinematic analyses were performed only on the second wingbeat (first wingbeat amplitude = 117.1° ± 2.7; second wingbeat amplitude = 131.4° ± 3.4). The wingtip pattern during take-off was uniform between all three treatment groups in session 1, and in the Control I and Control II groups during sessions 2 and 3. The body is steeply inclined; the wingtip follows a shallow arc anterior to the head during the upstroke, as the leading edge of the wing is held at an acute angle to the body axis; during the downstroke the wrist is moderately flexed and the wingtip follows an approximately linear path.

In all seven of the Moult birds this pattern altered markedly following plumage manipulation (session 2). Instead of the smooth curve observed in session 1, loops appeared in the pattern, indicating wingtip reversal during the latter phase of the upstroke, and during most of the downstroke the leading edge was at an obtuse angle to the body axis. This altered pattern was consistent among all Moult birds. The wingtip pattern observed in session 3 was less disrupted, but was still dissimilar to that observed during session 1 or in the control birds (Fig. 6). There was no significant alteration of wingbeat amplitude ($F_{4,35} = 2.58$, P = 0.054) or wingbeat duration ($F_{4,35} = 1.08$, P = 0.381) across all three experimental sessions (Table 1).

Discussion

The repeatability of speed of take-off within individual birds within each experiment indicates that birds were displaying similar flight responses each time they were released. The discrepancy between repeatability of speed and angle of take-off may indicate that take-off angle is more influenced by the posture of the bird on the perch and the forces generated by the legs during jumping. These elements may have added more variability to the angle and energy data between repeats, but will not have affected the treatment groups in different ways and hence do not compromise our statistical findings.

The significant reduction in take-off speed in the moult group, comparing session 1 (pre-manipulation) with session 2 (immediately post-manipulation), indicates that simulated plumage moult does have an effect on take-off performance in starlings. However, angle of the take-off trajectory was not significantly affected. This is consistent with our previous investigations (Swaddle and Witter 1997).

Even though there was a large amount of variability in the data among repeated measures within a session, Moult birds produced significantly lower energy output during their second wingbeat, and therefore significantly lower mean lift. This may be in part because the birds were flying slower at this time as a result of impaired aerodynamic performance during the first wingbeat. This observation supports our hypothesis that moult reduces the maximum lift generated by the wings. This analysis also reveals interesting information about the first wingbeat cycle of take-off. The first wingbeat is significantly less powerful than the second; presumably as the first wingbeat is relatively abbreviated in amplitude.

The reduction in escape take-off performance that we recorded is of general ecological importance as it is likely to influence directly the probability of individual survival in the wild (references in Swaddle and Witter 1997). Interestingly, the speed of take-off returned to pre-manipulation levels within a six-day period. This result is in agreement with previous findings and suggests that wild birds have a capacity to partially offset the costs of plumage damage in the longer term and regain higher speed take-off. However, the energy gained per wingbeat per unit mass remained depressed after six days indicating that birds cannot entirely

Table 1. Mean (s.e.) body mass, wing loading, wingbeat amplitude and wingbeat duration of starlings in the three treatment groups for the three sessions of the experiment: session 1 (before manipulations), session 2 (immediately after manipulations), and session 3 (six days after manipulations).

	Group	Session 1	Session 2	Session 3
Body mass	Control I	73.7 (1.1)	71.7 (1.3)	73.1 (1.3)
(g)	Control II	74.9 (0.7)	73.0 (0.9)	74.9 (0.8)
	Moult	73.3 (1.4)	71.9 (1.2)	72.0 (1.4)
Wing loading	Control I	36.5 (0.8)	35.5 (0.9)	36.3 (0.9)
(N/m²)	Control II	38.4 (0.6)	37.8 (0.7)	38.8 (0.6)
	Moult	37.7 (1.2)	40.1 (1.2)	40.2 (1.2)
Wingbeat amplitude	Control I	130.9 (7.4)	128.9 (3.0)	136.0 (4.2)
(degrees)	Control II	127.0 (2.9)	136.2 (2.4)	128.1 (4.3)
	Moult	136.3 (6.1)	144.2 (6.1)	127.1 (4.3)
Wingbeat duration	Control I	62.4 (1.3)	62.4 (0.9)	62.4 (1.3)
(ms)	Control II	61.9 (0.6)	61.9 (0.6)	61.9 (0.4)
	Moult	62.4 (1.3)	61.4 (0.4)	59.5 (0.4)

alleviate the aerodynamic effects of moult. In wild birds the wing form will be constantly changing during natural moult as feathers are continually dropped and regrown. Therefore, there will be less opportunity for birds in natural moult to adapt their flight behaviour to any one wing feather geometry.

An obvious consequence of plumage moult is a decrease in the surface area of the wing. It is not obvious that this automatically results in a proportionate reduction in lift-generating capabilities, although the changes we observe in wingbeat kinematics imply there is a marked effect on lift generation. One way in which birds may respond to this reduction in wing area is to produce additional lift with the tail. Moult birds held their tails in a relatively more horizontal position than control birds, but it is not clear if this change in tail angle affected lift or any aerodynamic factors during take-off as angle of attack of the tail did not vary among treatment groups (Thomas 1993).

Previously, wingbeat kinematics have been used as a tool to describe take-off (Lorenz 1933, Norberg and Norberg 1971, Simpson 1983). This is a purely descriptive form of analysis, but by combining our quantitative measures with these descriptive observations, it is possible to infer some effects of changes in wingbeat kinematics on take-off performance. Presumably the wingbeat used by control birds and by birds before manipulation (Fig. 6, phase 1) is in some sense aerodynamically and anatomically optimal. Flow visualisation experiments (Williams et al. 1998) reveal that all aerodynamic work is generated in the downstroke since the wake comprises isolated ring vortices; the wingbeat geometry is consistent with this pattern. The wingtip reversals seen in the upstroke in Moult birds immediately after manipulations presumably represent some form of response to the manipulation. Tip reversal upstroke in the pigeon has been associated with upstroke lift generation (Brown 1963), although it is not evident from flow visualisation that the upstroke produces any useful force in pigeons in slow flight (Spedding et al. 1984, Rayner 1995); this form of

wingbeat is not normally observed in starlings. Six days after the manipulation the wingbeat had returned to a more conventional pattern and the wingtip path in the downstroke was straighter. The immediate post-manipulation wingbeat may be an inefficient but immediate response to the change in wing area, and over the following period the bird learns the most appropriate movement to regain previous take-off performance; it is however remarkable that the same response was observed in all seven birds in the Moult group. Alternatively, the consistent alteration of the wingtip kinematics in Moult birds (inversion of the wingtip on the upstroke) may be a passive reflection of loss of integrity of the wing due to feather removal. The plumage manipulation did not remove feathers from the wingtip itself, hence this explanation may not apply in this case but should be considered in moult patterns and experimental manipulations that alter the morphology of more distal primary feathers.

Overall, this study has indicated that the plumage changes observed during moult can give rise to a quantifiable reduction in escape take-off performance in starlings. Moult birds produced less energy from their wings during take-off, resulting in a slower escape speed. This reduction in take-off performance is of general ecological importance, as reduced escape ability is linked with increased predation risk and a lower probability of survival. This study is also important in that we have generated a novel way of quantifying avian take-off performance, energy used per wingbeat, that can be applied to theoretical and empirical studies of take-off performance in other bird species.

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