

Moult, flight performance and wingbeat kinematics during take-off in European starlings *Sturnus vulgaris*

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The effects of natural moult on avian flight performance have received relatively little attention, yet moult is an important part of the annual cycle. Quantification of flight costs will help to explain the diversity of moult patterns observed in avian taxa. Take-off from the ground requires a high power output from the flight muscles compared to other modes of flight, and is an important feature of foraging and predation escape. The present study was designed to quantify the effect of natural moult and new plumage on the take-off strategy, kinematics, and flight performance of European starlings *Sturnus vulgaris*. A high-speed (185 Hz) cine camera was used to film seven European starlings on three occasions: session 1, two weeks prior to the onset of moult; session 2, during mid-moult; and session 3, two weeks after full plumage had re-grown. From subsequent film analysis, we assessed take-off speed and angle, the energy gained per wingbeat, and wingtip kinematics. Take-off strategy (measured by angle and speed) altered through the course of the three experimental sessions, i.e. ascent angle decreased and take-off speed increased. Energy gained per wingbeat did not vary, suggesting there was no significant decrease in flight performance due to moult, but there was a significant improvement in take-off performance due to renewal of flight plumage. Wingbeat amplitude increased in association with moult and after flight plumage had been completely renewed. The European starlings incurred relatively minor flight costs due to moult, when comparing before-moult with during-moult take-off performance. The apparent absence of additional flight costs associated with moult may reflect a decreased mechanical performance of year-old feathers (which are replaced during the moult) and may also help to explain the relatively long duration of the moult in this species. This study also provides evidence of the benefits of plumage renewal, as take-off performance is improved after moult has been completed.

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Take-off is known to be one of the most costly modes of flight in birds (Dial and Biewener 1993, Rayner and Swaddle 2000). Immediately after leaving the ground, the bird must use the aerodynamic lift force generated by the wings to support its weight, and to gain height and speed. The maximum power available to the bird (limited by muscular and skeletal forces) is expected to constrain the trajectory and speed of take-off. In addition to mechanical costs, take-off imposes ecological costs in that it directly affects foraging and predation escape (reviews in Witter et al. 1994, Metcalfe and Ure 1995, Kullberg et al. 1996, Rayner and Swaddle 2000).

In particular, the ability of a bird to ascend from the ground at a steep angle and at high speed is thought to be important in escaping a terrestrial predator (Lima 1993, Witter et al. 1994).

Moult is a demanding stage of the avian annual cycle. The direct energetic and physiological costs of feather production are believed to be large, especially for small birds (e.g. Lindström et al. 1993), and moult rarely overlaps with periods of breeding (Payne 1972, Jenni and Winkler 1994). There may also be substantial indirect costs associated with moult, such as increased predation risk associated with decreased flight perfor-

mance during natural (Kahlert et al. 1996, Swaddle and Witter 1997, Rayner and Swaddle 2000) and experimentally simulated (Swaddle and Witter 1997, Swaddle et al. 1999) moult.

Like many small passerine species, European starlings *Sturnus vulgaris* remain active fliers throughout the course of their annual post-breeding moult, experiencing sequential replacement of primary feathers in an ascendant order, i.e., from proximal to distal (Bährmann 1964, Feare 1984). It has often been acknowledged that consideration of the direct costs of moult alone will not fully explain the natural variation in the timing and duration of moult (King 1981, Earnst 1992, Murphy and King 1992, Lindström et al. 1993, Rayner and Swaddle 2000). Therefore, investigation and quantification of the indirect costs of moult, such as the influence of moult on ecologically important aspects of flight performance, in conjunction with the known physiological and energetic costs, are important in explaining the diversity of moult patterns observed among avian taxa (cf. Earnst 1992).

Previously, there have been relatively few studies of the influence of moult on flight performance. In general, it seems that lift production can be decreased in both gliding and flapping flight (Tucker 1991, Chai 1997, Swaddle and Witter 1997, Swaddle et al. 1999, Rayner and Swaddle 2000). But in some slow moulting species (e.g. tree sparrows *Passer montanus*), the aerodynamic effects of moult may be minimal (Lind 2001). Swaddle and Witter (1997) demonstrated that a number of flight performance measures were affected by natural and experimentally simulated moult in European starlings. Their study included an analysis of take-off strategy, but was limited in that take-off was separated into two parameters (angle and speed), thereby making direct comparisons between different experimental groups difficult to interpret. This is an issue common to almost all avian take-off studies (e.g. Witter et al. 1994, Metcalfe and Ure 1995, Kullberg et al. 1996).

A bird may make behavioural decisions when escaping a predator and these decisions will affect the angle of take-off from the ground. As the angle of trajectory will trade-off with flight speed (Swaddle et al. 1999), measures of take-off angle and speed will be affected (somewhat unpredictably) by behavioural decisions. If it is assumed that a bird performs at near-maximum when escaping a predator (which makes intuitive, evolutionary sense), a better measure of take-off is to either measure the force generated during initial flight (Swaddle and Biewener 2000), or to sum the potential and kinetic energy of the bird during take-off (Swaddle et al. 1999). Both these techniques reduce behavioural variance and more closely assess mechanical performance. We chose to adopt the latter approach, as we know this technique works well with European starlings in open aviary conditions (Swaddle et al. 1999). Essentially, this measure (termed "energy gain per wing-

beat") integrates the effects of ascent angle, speed, and acceleration, allowing take-off performance through moult to be analysed quantitatively with a single measure. In addition to analysing take-off performance (defined as energy gained by the bird per wingbeat), we also analysed take-off strategy (defined by changes in ascent angle, speed, and acceleration) in response to moult and new plumage.

Previous evidence indicates that birds may be able to alter their wingtip kinematics in response to moult. In particular, starlings have been observed to adopt a "figure-eight" wingbeat in association with experimentally simulated moult (Swaddle et al. 1999). Therefore, we analysed wingtip kinematics to test whether this form of apparent compensation happens during natural moult. Although it may appear reasonable to assume that the aerodynamic performance of a moulting bird will be impaired roughly in proportion to the decrease in wing area, aerodynamic mechanisms of the wing may confound this. While the relationships between wing shape and lift production of a fixed wing (e.g. aircraft wings) are relatively well understood, the bird wing is much more complex. A bird wing may deform and change shape in compensation for moult, for example by an alteration in feather overlap, or by a change in the angle of attack. Birds may also change wingbeat kinematics to compensate and maintain weight support and thrust production. In flapping flight, weight support and thrust production are determined primarily by the span of the wing (Rayner 1986, 1993). The effect of moult on lift may also depend on which wing feathers are missing. When more proximal primaries or secondaries are being replaced (e.g. during the mid-moult stage), it is possible that the bird could compensate for the reduction in wing area and disruption to the trailing edge simply by increasing the local angle of incidence and / or the wingtip speed. When distal primaries are being replaced, the wingtip geometry may be disturbed, and the consequences for lift may be somewhat greater. However, Hedenström and Sunada (1999) modelled the effect of moult initiation position for a hypothetical wing, and concluded that the aerodynamic performance of the wing was most detrimentally affected when the moult gap was further from the wingtip, because circulation declined closer to the wingtip. Since the bird must always at least support its weight, any changes to maximum lift production capacity may lead to a reduction in the excess thrust available for acceleration and ascending. Therefore, take-off speed may be unaffected in response to moult, but ascent angle or rate of acceleration may decrease. Observations of take-off flight during European starlings' moult support this prediction (Swaddle and Witter 1997).

The aims of this investigation were to investigate empirically how take-off performance, strategy, and wingtip kinematics of European starlings alter in response to natural moult, and the subsequent growth of

new plumage. Specifically, we filmed take-off before, during, and after moult to test the following hypotheses. First, take-off performance decreases in response to moult (comparing before and during moult). Second, take-off performance increases due to the renewal of plumage following moult (comparing before and after moult). Third, birds exhibit alterations to their wingtip kinematics that minimize the mechanical costs of moult. This study was designed to highlight the constraints acting on European starlings during natural moult, and the mechanisms by which the birds appear to minimise the adverse effects of these constraints.

Methods

The study was performed on seven wild-caught European starlings of both sexes. All of the birds appeared to have undamaged flight plumage. The experiment was carried out on three consecutive occasions. Session 1 was two weeks prior to the onset of moult, session 2 during mid-moult, and session 3 was two weeks after the full plumage had grown. While not in the experimental aviary, the birds were kept in a large outdoor aviary (approximately $2.5 \times 2.5 \times 3$ m) and supplied with turkey starter crumbs, drinking water, and bathing water *ad libitum*.

Take-off filming

Escape take-off was filmed in a long, narrow outdoor aviary (approximately $2 \times 2.5 \times 8$ m). The bird was placed by hand on a perch, 5 cm above the ground, at one end of the aviary and a loud vocal startle stimulus was given as the bird was released. A cine camera (Photosonics 1PL; Angineux 12-120 FC lens), filming at 185 Hz was positioned perpendicular to the direction of take-off. A white Perspex sheet with 10 cm grid lines was mounted behind the bird, in full view of the camera, for subsequent film calibration. In response to the stimulus, the bird immediately left the perch and

flew to the opposite end of the aviary. Each bird was filmed twice in quick succession before being returned to the housing aviary. Immediately before filming during each session body mass (to 0.1 g accuracy on an electronic balance), fat score on a scale of 0 to 5 (Helms and Drury 1960), moult score from 0 to 35 (Ginn and Melville 1983), pectoral muscle external profile (Selman and Houston 1996), and flattened wing length measurements (shoulder to wingtip length) were taken for each bird.

Movement analysis

The cine film was viewed with a NAC Film Motion Analyser, linked to a digitising pen (Science Accessories Corporation) and computer. Digitised data were stored onto the computer using software written by J.M.V. Rayner. For each take-off, the positions of the beak tip, the wingtip of the closest wing (left in all cases), the base and tip of the tail were digitised for 65 frames after the feet of the bird had left the perch (Fig. 1). This was sufficient for analysis of the first four wingbeats after take-off. The number of frames per wingbeat varied between 11 and 16, depending on the wingbeat number after take-off, speed of flight, and wingbeat frequency. Movements of the birds were analysed by using the MOVE program, also written by J.M.V. Rayner (see Rayner and Aldridge 1985 for algorithms), to obtain values of angle of trajectory, flight speed (m/s along the flight trajectory) and instantaneous mechanical energy per unit mass (Eq. (1)),

$$E = \frac{1}{2}(V_x^2 + V_z^2) + gz \quad (1)$$

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. The MOVE program calculates the instantaneous speed and angle of digitised points, using the Lanczos' least squares adjustment smoothing method (cf. Swaddle et al. 1999 for further details) to reduce the error associated with the

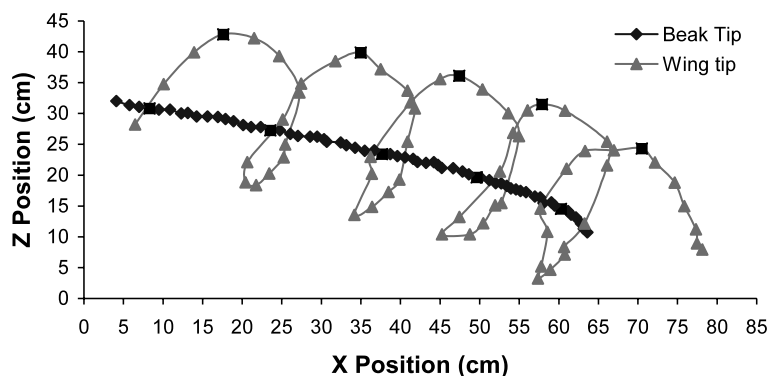


Fig. 1. An example of beak and wingtip kinematics, illustrating a take-off during mid-moult for bird 1. This take-off has a mean speed of 1.95 m/s (± 0.16), ascent angle of 18.12° ($\pm 0.60^\circ$), energy gain of 1.15 J/kg (± 0.24) and wingbeat frequency of 13.77 Hz (± 0.24), across the four wingbeats after take-off. The large squares (\square) indicate when the bird left the perch, and the end of subsequent wingbeats (1–4).

digitising process. Wingbeat frequency was calculated directly from the wingtip position data, using the first frame after the birds feet had left the perch as the start of the first wingbeat, and counting subsequent wingbeats consecutively from this position. Wingbeat amplitude was calculated by subtracting the position of the beak from that of the wingtip, and then calculating the greatest vertical distance moved by the wingtip within each wingbeat. Wing length at the top and bottom of the wingstroke was assumed to be equal to the wing length, measured from the shoulder to the wingtip for a flat wing. The mean ascent angle per wingbeat and mean speed per wingbeat were subsequently calculated by taking the mean value of all the digitised points within each wingbeat. The energy gained per wingbeat ($\Delta E/M$) was calculated by subtracting the instantaneous energy at the start of the wingbeat from that at the end of the wingbeat. In a similar manner, we also calculated energy gained per second over the first four wingbeats. Acceleration was calculated for each wingbeat from the formula (Eq. (2)), which is derived from Eq. (1),

$$\frac{a}{g} = \frac{-V_1}{gt} - \frac{1}{2} \sin\theta \pm \frac{1}{2gt} \left[\frac{8\Delta E}{M} + (2V_1 - g t \sin\theta)^2 \right]^{\frac{1}{2}} \quad (2)$$

where V_1 is the speed of the beak for the first frame of each wingbeat, t is the time taken for each wingbeat (seconds), g is acceleration due to gravity (9.81 m/s^2), $\sin \theta$ is the sine of the ascent angle, and $\Delta E/M$ = the energy gain per wingbeat. Equation (2) summarizes how acceleration is determined by the velocity of the bird at the beginning of the wingbeat, the potential and kinetic energy that the bird gains during the wingbeat, and the angle of take-off.

Statistical analyses

For all take-off measurements, statistics were carried out on mean values, taken across all four wingbeats,

and two repeated take-offs for each bird, within each session. All statistical analyses were performed using SPSS (SPSS 1988) using the repeated-measures ANOVA procedure, unless otherwise indicated. A priori independent contrasts were conducted using repeated-measures ANOVAs on differences between specific pairs of treatment groups (i.e. session1 with session 2 to test for the effects of moult, and session1 with session 3 to test for the effects of plumage renewal) when the overall ANOVA was significant. Two tailed tests of significance were used throughout.

Results

A summary of all morphological and take-off measurements analysed is given in Table 1. Ascent angle, speed, acceleration, energy gain, and wingbeat amplitude measurements were calculated as mean values across the first four wingbeats of take-off, after the bird had left the perch.

Morphological measurements

Body mass did not change significantly during the course of the experiment ($F_{2,12} = 2.99$, $P = 0.088$), although it tended to be lower in pre- and mid-moult conditions and rise after new plumage had re-grown. Fat score did not alter through the course of the experiment (Friedman non-parametric repeated measures analysis of variance; $S = 7.35$, $df = 6$, $P = 0.394$), nor did pectoral muscle profile area, calculated from the pectoral muscle external profile (Selman and Houston 1996; $F_{2,12} = 1.37$, $P = 0.292$). As expected, wing area changed markedly ($F_{2,12} = 12.93$, $P = 0.001$), decreasing from session 1 to session 2 by 7.4% ($F_{1,6} = 30.21$, $P < 0.001$), and increasing from session 2 to session 3 by 7.4% ($F_{1,6} = 18.29$, $P < 0.001$), returning to the pre-moult wing area. Wing length increased as a

Table 1. Summary of all morphological, take-off, and kinematic measurements taken, across the three experimental sessions. Session 1 was two weeks prior to the onset of moult, session 2 was during mid-moult, and session 3 was two weeks after moult had been completed. Mean values are given, \pm standard error.

Category	Variable	Session 1	Session 2	Session 3
Morphological measurements	Body mass (g)	74.38 (± 2.09)	71.57 (± 2.88)	76.49 (± 2.10)
	Fat score (0–5)	0.75 (± 0.25)	0.38 (± 0.26)	0.57 (± 0.20)
	Pectoral muscle profile area (cm ²)	5.16 (± 0.15)	5.52 (± 0.11)	5.30 (± 0.12)
	Wing area (cm ²)	187.52 (± 2.18)	173.64 (± 2.86)	187.00 (± 1.84)
	Flattened wing length (cm)	15.87 (± 0.15)	15.87 (± 0.15)	16.67 (± 0.13)
Take-off measurements	Ascent angle (°)	23.08 (± 1.83)	16.57 (± 1.88)	13.56 (± 0.95)
	Speed (m/s)	2.03 (± 0.098)	2.07 (± 0.064)	2.53 (± 0.123)
	Acceleration (g)	0.29 (± 0.12)	0.24 (± 0.11)	0.80 (± 0.14)
	Energy gain (J/kg)	1.49 (± 0.25)	1.23 (± 0.27)	2.90 (± 0.44)
Kinematic measurements	Wingbeat amplitude (°)	90.15 (± 4.23)	125.89 (± 2.17)	120.10 (± 9.25)
	Wingbeat frequency (Hz)	14.89 (± 0.23)	13.98 (± 0.50)	14.86 (± 0.28)

result of growing new plumage ($F_{1,6} = 16.8$, $P = 0.006$). The increased wing length also resulted in increased aspect ratio of the wing following moult. The range of moult scores recorded during session 2 was between 21 and 25 (Ginn and Melville 1983), indicating that all the birds were fairly synchronous with one another, and in a mid-moult stage.

Take-off performance: energy gain during flight

There was a significant change in the mean energy gain per wingbeat per unit mass over the course of the experiment ($F_{2,12} = 13.36$, $P = 0.001$; Fig. 2a). There was no change in energy gain associated with moult ($F_{1,6} = 1.28$, $P = 0.300$). However, birds showed a significant energy gain associated with the effects of plumage renewal ($F_{1,6} = 14.28$, $P = 0.009$). We observed an identical pattern when analysing energy gain per second during take-off. Energy gain per second did not differ in association with moult ($F_{1,6} = 1.79$, $P = 0.229$), but increased in association with growth of new plumage ($F_{1,6} = 18.13$, $P = 0.005$).

Take-off strategy: speed, angle and acceleration

Mean ascent angle decreased during the course of the experiment ($F_{2,12} = 11.33$, $P = 0.002$; Fig. 2b). There was a significant decrease in angle of ascent during moult ($F_{1,6} = 6.60$, $P = 0.042$), and also following the complete renewal of flight plumage ($F_{1,6} = 28.28$, $P = 0.002$). In contrast, mean take-off speed (average speed along the trajectory of flight over the first four wingbeats) increased over the duration of the experiment ($F_{2,12} = 8.37$, $P = 0.005$; Fig. 2c). This increase in speed was not associated with moult ($F_{1,6} = 0.30$, $P = 0.603$), but with an increase in take-off speed during session 3, after new flight plumage had grown back into the wing ($F_{1,6} = 8.07$, $P = 0.030$).

A Reduced Major Axis (RMA) regression analysis was carried out on the mean acceleration (in the direction of flight) during take-off and the mean sine of the ascent angle for each session, to investigate whether there was evidence of a trade-off between ascent angle and acceleration during take-off across individuals (Fig. 3). There was a significant negative relationship between the mean acceleration and the mean sine of the ascent angle for session 1 (pre-moult; $R^2 = 76.5\%$, $F_{1,5} = 13.02$, $P = 0.011$), suggesting that the pre-moult birds were trading-off acceleration and ascent angle against each other. This regression was not significant in either mid- or post-moult, although we had small sample sizes and the slopes of all lines indicated a negative relationship between acceleration and sine angle of ascent (Fig. 3).

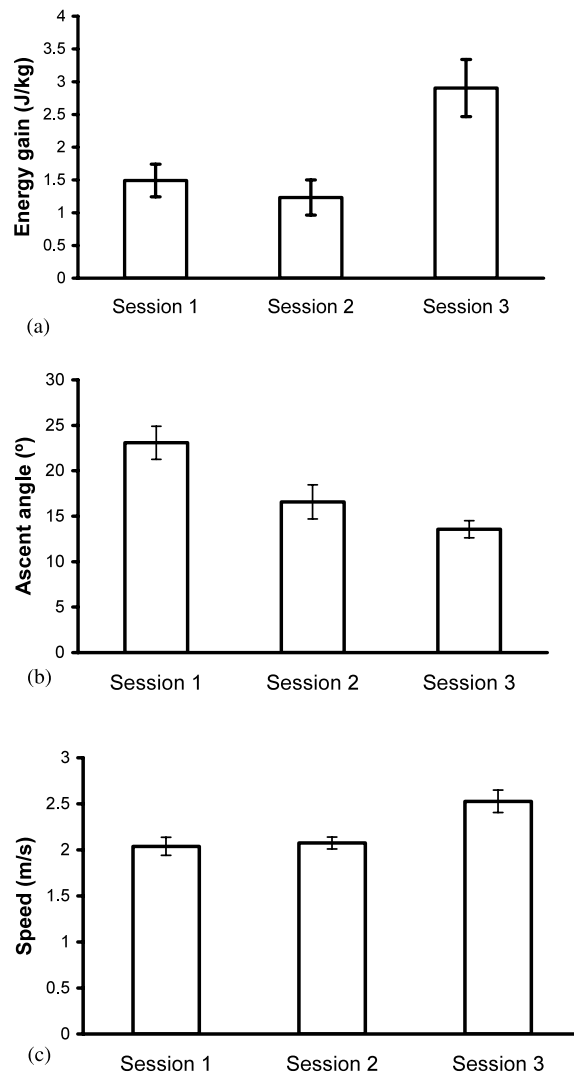


Fig. 2. (a) Mean (\pm s.e.) energy gain (J/kg) for session 1 (pre-moult), session 2 (mid-moult) and session 3 (post-moult) $F_{2,12} = 13.36$, $P = 0.001$. (b) Mean (\pm s.e.) ascent angle ($^{\circ}$) for session 1 (pre-moult), session 2 (mid-moult) and session 3 (post-moult) $F_{2,12} = 11.33$, $P = 0.002$. (c) Mean (\pm s.e.) speed (m/s) for session 1 (pre-moult), session 2 (mid-moult) and session 3 (post-moult) $F_{2,12} = 8.38$, $P = 0.005$. (d) Mean (\pm s.e.) wingbeat amplitude ($^{\circ}$) for session 1 (pre-moult), session 2 (mid-moult) and session 3 (post-moult) $F_{2,12} = 10.04$, $P = 0.003$.

Wingtip kinematics

The wingtip traces throughout the course of the experiment show a loop shape with no wingtip reversals, which would be illustrated by a “figure-eight” wingtip trace and was previously observed under experimentally-simulated moult (Swaddle et al. 1999). There was a significant change in the wingbeat amplitude across

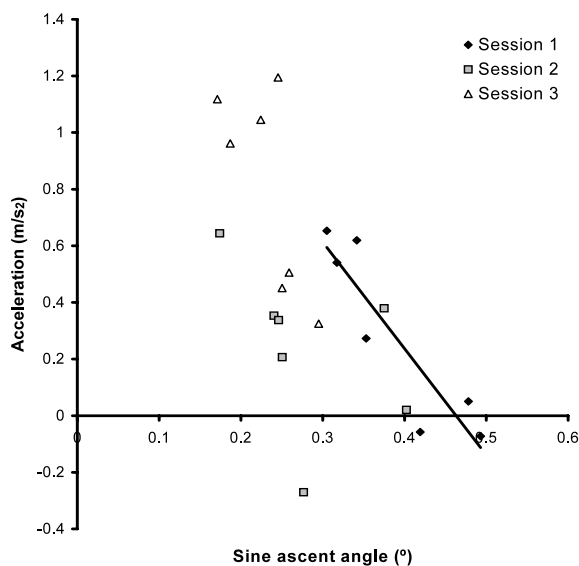


Fig. 3. Acceleration (m/s^2) against sine ascent angle for session 1 (pre-moult; acceleration = $-4.07 \times \text{sine angle} + 1.85$ and $R^2 = 76.5\%$, $F_{1,5} = 13.02$, $P = 0.011$), session 2 (mid-moult; acceleration = $-3.67 \times \text{sine angle} + 1.27$ and $R^2 = 17.6\%$, $F_{1,5} = 0.85$, $P = 0.392$), and session 3 (post-moult; acceleration = $-10.06 \times \text{sine angle} + 3.20$ and $R^2 = 46.2\%$, $F_{1,5} = 3.44$, $P = 0.113$). Acceleration was significantly correlated with ascent angle only in session 1.

the three phases of the experiment ($F_{2,12} = 10.04$, $P = 0.003$; Fig. 2d), increasing both in response to moult ($F_{1,6} = 51.41$, $P < 0.001$) and new plumage ($F_{1,6} = 7.805$, $P = 0.031$). Wingbeat frequency did not alter significantly throughout the course of the experiment ($F_{1,6} = 1.205$, $P = 0.333$).

Discussion

Birds in moult decreased their angle of ascent during moult, compared with before moult (i.e. comparing session 1 with session 2; Fig. 2b) but showed no alteration in their speed of take-off (Fig. 2c). This is consistent with previous analyses of take-off behaviour in moulting captive European starlings (Swaddle and Witter 1997), and is consistent with aerodynamic theory. Take-off speed is less likely to be affected by a decrease in wing area, because weight support and thrust production are determined primarily by the span of the wing (Rayner 1986, 1993). The wingspan of the mid-moult birds in the present study remained unchanged compared with the wingspan pre-moult.

Interestingly, there was a significant negative relationship between sine of ascent angle and acceleration across the birds during the pre-moult session (Fig. 3). Birds that took off at steep ascent angles had a low acceleration, and vice versa. This is consistent with the presence of a trade-off between sine of ascent angle and acceleration.

Wingtip kinematics did not appear to alter in response to moult, for example with the introduction of a wingtip reversal, as is seen immediately following feather trimming to simulate a moult wing geometry in European starlings (Swaddle et al. 1999). We were unable to estimate any deformation of the wing that may have occurred in response to moult, such as a change in feather overlap, or any change to the angle of attack. Wingbeat amplitude increased significantly in response to moult (Fig. 2d), although the increased lift resulting from the increase in speed of the wing appears not to have been great enough to maintain ascent angle to pre-moult levels. Wingbeat frequency did not alter throughout the course of the experiment.

Interestingly, there was no significant effect of moult on overall take-off performance, measured by energy gained per wingbeat (Fig. 2a) or energy gained per second. This is in contrast to experimentally simulated moult (Swaddle et al. 1999), where energy gain was found to decrease immediately after manipulation in a similar population of European starlings. Evidently, during natural moult the birds were able to adjust to their change in wingform and maintain their take-off performance over time. In the simulated moult experiment, although there was a subsequent rise in mean take-off speed six days after wing manipulations, this did not restore energy gain to pre-manipulation levels (Swaddle et al. 1999). A comparison of pre-manipulation performance to performance one week post-manipulation is probably more comparable with the effects of the mid-moult stage in the present study, since birds had time to adjust take-off performance and strategy to their moult plumage. Unfortunately, it is not possible to say if and when the birds in the simulated moult study would have regained their pre-manipulation take-off performance, if they had been given further time to adjust. Therefore, evidence from this study indicates that adjustments which occur during the natural moult of the European starling are finely tuned over time to maintain take-off performance while undergoing plumage renewal. This finding may help to explain why European starlings (and other similar passerines) have a relatively prolonged moult and shed feathers sequentially rather than simultaneously.

The significant decrease in take-off angle and increase in take-off speed in response to plumage renewal (i.e. comparing session 1 with session 3) are in contrast to the previous published examination of the influence of natural moult on take-off parameters in European starlings (Swaddle and Witter 1997) and further indicate that birds may be making strategic decisions concerning their flight behaviour.

Our data also illustrate the benefits of moulting into new plumage. Although we selected individuals with apparently undamaged plumage for this study, renewed

plumage after moult was functionally more efficient than year-old plumage. An increase in the functional efficiency of new feathers may have important implications for other putative indirect costs of moult, such as water repellence, thermal insulation and visual appearance of display plumage. It is also worth considering that moult is not restricted to renewal of flight feathers, or indeed of plumage; moult also entails renewal of many underlying tissues (reviews in Jenni and Winkler 1994, Murphy 1996), which could also influence flight performance through changes in physiological and structural efficiency. We know from a previous study that European starlings can alter the size of their flight muscles to minimise costs associated with take-off (Swaddle and Biewener 2000), as well as altering their body mass (Swaddle and Witter 1997). In addition, tree sparrows appear to alter both their body and pectoralis muscle mass in association with moult and decreased wing area (Lind and Jakobsson 2001).

The kinematic data reveal there was a significant increase in wingbeat amplitude in response to new plumage (Fig. 2d). Together with the new wing profile, this may have created the significant increase in energy gained, by increasing the wingtip speed. It may be that amplitude increased initially in response to feather loss and was maintained after new feathers grew back, resulting in greater force generation when feathers were completely replaced.

Overall, this study demonstrates that European starlings do not suffer from a relative loss of take-off performance in response to moult compared with flight performance before moult commences. A similar finding has been reported in tree sparrows, in which extent of flight feather moult does not correlate with take-off ability (Lind 2001). These observations could be explained in two non-mutually exclusive ways. First, flight performance is not significantly affected by moult. Second, flight performance is significantly decreased in year-old feathers (i.e. the flight plumage just before moult commences) compared with plumage once it has been renewed (i.e. immediately after moult). Therefore, losing feathers slowly from the wing may be no more costly than possessing year-old flight feathers. In addition, the European starling may have the potential to defend take-off speed during moult, possibly by increasing wingbeat amplitude. Theoretically, this latter issue is important in avoiding excessive flight costs from a low speed of take-off.

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