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Flying with holey wings

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I recently caught and ringed a moulting female blackbird *Turdus merula* and her young in my garden. The female had the outermost primaries growing or missing, thus having a substantially reduced wing area compared with her youngster. When releasing the birds there was a striking difference to their flight trajectories; the young bird initially ascended from my hand and then flew straight into a bush, while the female lost altitude and almost touched the lawn before gaining control and land in the same bush as her young. This observation, together with similar ones made before, clearly revealed to me that moult and its associated reduction of wing area and wingspan affect flight performance. However, as ecologists we are not satisfied only with casual observations such as this one, but we want to know what the costs are and their magnitude, and ultimately if and how they determine the life, behaviour and morphology of the bird. Ringers know that birds in mid-moult are less likely to be caught in mist nets than non-moulting birds, presumably because they change behaviour or even become flightless as a result of missing flight feathers (Haukioja 1971). But how should we approach the problem of a relevant quantification of the costs of moult and leave the domain of casual observation? First, there are direct energy costs simply due to the production of new feathers, which have been measured as elevated metabolic rate (e.g. Lindström et al. 1993). This extra energy cost must be covered by increased food intake, which is generally thought to be associated with an increased predation risk. Second, it is possible and even likely that moulting birds adjust their foraging behaviour and minimize their exposure to predators, not least because of the indirect costs of moult. Indirect costs refer to elevated flight costs due to reduced wing area/span and the risk of being killed once attacked by a predator because of lowered flight performance. Ultimately, an understanding of the costs (physiological and ecological) of moult should help us explain feats such as variation in the timing, sequence and rate of moult. At least this is what I hope for in certain moments of

optimism. Also, plucking or trimming flight feathers is being used as a technique to elevate flight costs in parent birds feeding young or performing flight displays (Møller 1991, Mather and Robertson 1992, Mauck and Grubb 1995). Until the aerodynamic effects become understood, the results from such manipulations are difficult to interpret. Hence, there are multiple reasons why we need a characterisation of the effects on flight from gaps in the wings.

Escape flight

Writing in this issue of *Journal of Avian Biology*, Williams and Swaddle (2003) report on new findings regarding escape flight performance in European starlings *Sturnus vulgaris* prior to, during and after the completion of moult. Their main findings are that the angle of the flight trajectory was reduced in moulting birds (having a gap in the wing), but the velocity did not change when compared to pre-moult conditions. The energy gain per wingbeat (sum of kinetic and potential energy) did not change between pre-moult and moulting birds, indicating that moult had small, if any, effects on flight performance. These findings are very similar to those on tree sparrows *Passer montanus* (Lind 2001), in which natural moult gaps had no measurable effect on either take-off angle or velocity. Moulting birds in these studies exhibited body mass reductions during moult and, in the tree sparrow, also an increased flight muscle (Lind and Jakobsson 2001). These physiological changes could thus have masked the expected reduction in flight performance. In contrast, when trimming flight feathers as to mimic the geometry of moult gaps (simulated moult) both starlings and tree sparrows showed measurable reductions in escape flight speed and angle of flight trajectory (see Table 1 for a summary of results from various studies). However, when tested a few days after the manipulations, most effects disappeared and flight performance returned to that of pre-moult.

Table 1. A summary of results from flight experiments of moulting birds.

Species	Factor	Effect[1]	Source
Sturnus vulgaris	Simulated moult	Reduced U_{esc} Reduced $\alpha_{take\text{-}off}$	Swaddle et al. 1996
Sturnus vulgaris	Natural moult	Unaffected U_{esc} Reduced $\alpha_{take\text{-}off}$	Swaddle and Witter 1997
	Simulated moult	Reduced U_{esc} Unaffected $\alpha_{take\text{-}off}$ Reduced U_{level}	
Sturnus vulgaris	Simulated moult	Reduced U_{esc} Unaffected $\alpha_{take\text{-}off}$	Swaddle et al. 1999
Sturnus vulgaris	Natural moult	Reduced $\alpha_{take\text{-}off}$ Unaffected U_{esc}	Williams and Swaddle 2003
Passer montanus	Natural moult	Unaffected U_{esc} Unaffected $\alpha_{take\text{-}off}$ Increased m_{muscle}	Lind 2001, Lind and Jakobsson 2001
	Simulated moult	Reduced U_{esc} Unaffected $\alpha_{take\text{-}off}$	
Archilocus colubris	Natural moult	Heliox flight failure Reduced C_L Reduced P_{mech} Increased $\dot{V}_{o_2}$ Reduced η Reduced U_{max}	Chai 1997, Chai and Dudley 1999

[1]Symbols used are defined as: U_{esc} escape flight speed, $\alpha_{take\text{-}off}$ angle of take off flight trajectory, U_{level} horizontal flight speed, m_{muscle} flight muscle mass, C_L lift coefficient [defined as $C_L = 2L/(\rho SU^2)$, where L is lift, ρ is air density, S is wing area and U is airspeed], P_{mech} mechanical power output, $\dot{V}_{o_2}$ rate of oxygen consumption, η energy conversion efficiency, U_{max} maximum horizontal speed.

The pattern emerging is that when trimming the feathers experimentally there is a measurable effect on flight performance shortly after the manipulation due to the wing gaps, while naturally moulting birds seem to compensate for this aerodynamic effect by remoulding the flight muscle and/or body mass, and thereby effectively increasing the flight muscle ratio. Compensatory physiological changes are also seen some days after experimentally inducing moult gaps. Hence, measurements shortly after a manipulation are reflecting the aerodynamic effect before compensatory physiological adjustments conceal the effect. Such rapid physiological flexibility of flight muscles and metabolic organs have also been found in birds accumulating migratory fuel loads, and are interpreted as adaptive changes to requirements of being heavy (Piersma 2002).

Williams and Swaddle (2003) also report another interesting observation: when moult was complete the starlings demonstrated an increased escape flight speed and increased energy gain per wingbeat in relation to pre-moult conditions. This indicates the benefit of renewing the plumage, as new feathers seem more efficient than one-year-old feathers, even if wing morphology is identical before and after moult. This is, to the best of my knowledge, the second empirical demonstration that feather quality might affect flight performance quite clearly, something that is ignored by aerodynamic models of bird flight.

Hovering and U_{max}

In another elegant study, Chai (1997) investigated the effects on flight performance in hovering ruby-throated hummingbirds *Archilocus colubris*. His birds were trained to hover in a box where the air density could be manipulated by gradually replacing normal air by filling the box with normoxic heliox (21% O_2 and 79% He, density 0.40 kg m^{-3}). At some reduced air density the hummingbirds would descend rapidly to the floor, a condition taken as aerodynamic failure. Wingbeat kinematics and metabolic rate (derived from rates of oxygen consumption) were recorded simultaneously. Compared with non-moulting birds, moulting hummingbirds showed aerodynamic failure at a higher air density (Table 1). The moulting birds also exhibited reduced lift coefficient, reduced mechanical power output (P_{mech}), elevated mass-specific oxygen consumption (P_{input}) and reduced energy conversion efficiency (P_{mech}/P_{input}). In a similar experiment using hovering bumblebees *Bombus terrestris*, a 10% reduction of wing area did not affect power expenditure (P_{input}) due to opposite effects on profile and induced power and an increased resonant wingbeat frequency (Hedenström et al. 2001). The hummingbirds were also tested for maximum horizontal flight speed (U_{max}) in a wind tunnel (Chai and Dudley 1999), and moulting birds displayed decreased U_{max} compared with the pre-moulting test. This indicates that the moulting birds could not generate thrust as efficiently as before moult. Interest-

ingly, the post-moult hummingbirds showed higher U_{max} than the pre-moult birds, hence again suggesting aerodynamic advantages of having a fresh plumage. Also the hummingbirds lost weight during moult, presumably as a means to compensate for aerodynamic inefficiency.

Measuring flight performance

The experiments on escape flight performance refer to the initial take-off flight trajectory, where a caged bird is motivated to take-off as fast as it can by a 'loud vocal startle stimulus' (starlings), or by showing a model predator (tree sparrows). This method has become somewhat of a standard assay to record effects of different factors (fuel load, egg formation, moult gaps, flight feather asymmetries) on flight performance. It is cheap, quick to set up and can easily be carried into the field. A problem with it is that we do not know if the bird really is performing at its limit. An often found negative correlation between flight angle and speed is taken as support for the presence of a trade-off, and hence evidence of envelope performance. This criticism does not apply to the hummingbird experiments, since the heliox hovering and maximum flight speed assays actually revealed the aerodynamic performance limits. In the most recent starling study, Williams and Swaddle (2003) measured energy gained per wingbeat that combines the effects of acceleration and rate of climb (angle of ascent). This is an improvement compared with that of separately recording angle of the flight trajectory and speed, as speed is typically taken at some arbitrary distance from the take-off position (remember that the bird is accelerating). However, also energy gain per wingbeat is difficult to relate to more orthodox and useful measures, such as mechanical power output (e.g. Pennycuick 1989). Luckily the wingbeat frequency did not change among experimental groups in the starling study, but invariant wingbeat frequency is not likely to be universal and so this measure becomes less useful.

It seems as if the hummingbird study revealed quite dramatic effects on flight performance of moult gaps, while the escape flight assays found small or negligible effects during natural moult. One reason for this could be that the actual gaps were much larger in the hummingbirds than in the starlings (22% wing area missing versus 7.4%). Admittedly, the birds were also studied under completely different circumstances-hovering, forward flight in a wind tunnel and take-off flight. Even so some congruent results emerged that are likely to reflect real changes in aerodynamic performance. A bird in escape flight presumably aims at maximizing its acceleration (linear or centrifugal), which is achieved by maximizing the force and hence the lift coefficient. The lift coefficient was reduced in the moulting hummingbirds and hence the premature aerodynamic failure in this group. Even if nicely conducted as experiments, the take-off assays are fraught with uncertainties, particularly regarding the aerodynamic mechanism by which moult gaps affect aerodynamic performance. Williams and Swaddle (2003) saw a change in wingtip amplitude, and a former study observed a wing tip reversal in simulated moult experiments (Swaddle et al. 1999). What these observations mean is currently difficult to assess, but a change in amplitude is consistent also with the hummingbird study (Chai 1997). This applies to take-off flight itself, which is not well understood from an aerodynamic point of view. We can for example not rule out that transient unsteady high-lift phenomena such as 'clap-and-fling' operates at high wingbeat amplitude in birds (Weis-Fogh 1973). Recent measurements on pressure dynamics along the wing of Canada geese *Branta canadensis* during take-off flight show that force generation may vary both spatially and temporally in complicated ways (Usherwood et al. 2003).

The beating wings of a bird generate a force by depositing momentum in the wake, which conveniently rolls up as vortices. In principle the aerodynamic force could be determined from these vortices by using the technique devised by Spedding et al. (2003). The effect of moult gaps should be traceable in the wake vortices. Aerodynamic theory provides little help regarding the cost of moult gaps, and the only attempt at predicting these costs suggests rather small effects during steady cruising flight (Hedenström and Sunada 1999). These predictions, however, still remain to be tested, which should be straightforward in a wind tunnel. Only then will it be possible to quantify the aerodynamic costs of cruising flight from moult gaps in a way useful to ecological and behavioural modelling. So far, I consider the escape flight experiments as qualitative demonstrations that moult gaps have detrimental aerodynamic effects, but they cannot easily be converted into ecological costs. It is also clear that birds are able to adjust their body mass and flight muscle as requirements change due to holey wings or fuel load. The immediate effect from an experimental manipulation must therefore always be treated with caution, and the net effect might not be the one we think as rapid physiological flexibility can buffer increased aerodynamic costs. Research is now beginning to disentangle these complex processes between morphology, physiology and ecological requirements. It is indeed compelling to realize the cheer complexity of these interactions taking place within a small bird.

Prospects

We now have some evidence about in what ways moult gaps reduce flight performance. The escape flight experiments focus on predation risk, which is indeed

an interesting problem itself (Lank and Ydenberg 2003). If attacked by a predator, the risk of actually being seized is determined by the relative flight performance between the prey and predator (Hedenström and Rosén 2001), but quantitative data on such interactions are still lacking. In the hummingbird system we get data approaching usefulness to the ecological modeller. Incidentally, in models of optimal annual routines of birds in which the best policy for the timing of breeding, migration and moult are calculated using state dependent dynamic programming (Holmgren and Hedenström 1995), a specific state variable termed 'feather quality' has been introduced to get the model birds into moult. Characteristically, this variable is decreasing in value from its maximum at the end of moult. The data on both hummingbirds and starlings suggest clear advantages of having a fresh plumage and also provide the theorists with some comfort regarding their own ecological intuition. It also tells us that, from an aerodynamic viewpoint, a bird in fresh plumage cannot be considered as identical with the same bird ten months later. Even if superficially equipped with the same wing morphology as the fresh bird, the bird with worn feathers probably pays higher costs of flight and cannot get away from a predator as fast as it could with new feathers. Aerodynamic models do not account for this. It might for example turn out that worn feathers are less efficient at depositing the wake momentum into vortices. Worn feathers probably lose their stiffness and aerodynamic bite, although both the mechanisms and functional consequences of feather wear are virtually unknown. Current and future students of bird flight definitely have some quite challenging and potentially rewarding experiments ahead.

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