P_{flight}	power (metabolic) during flight, related to speed in flapping flight but not in gliding flight
R	resulting distance from departure point after a number of flight steps
r	mean vector length
s	angular deviation
T	thrust; track vector
t_0	search or settling time at new stopover site
V	flight velocity
V_{bg}	speed of best glide ratio in gliding flight
V_c	climbing speed when circling in thermals
V_{flight}	flight speed on migration .
V_{max}	maximum airspeed in flapping flight
V_{migr}	total speed of migration, taking into account flight as well as fuel deposition
V_{min}	minimum (stalling) speed in gliding flight
V_{mp}	minimum power speed in flapping flight
V_{mr}	maximum range speed in flapping flight
V_{ms}	speed of minimum sink in gliding flight
V_{mt}	speed in flapping flight for minimum migration time
V_x	cross-country speed in thermal soaring flight
V_z	sinking speed in gliding flight
W	wind vector
Y	flight range

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Aerodynamics and behaviour of moult and take-off in birds

J.M.V. Rayner and J.P. Swaddle

1. Introduction

Moult is a costly period of the annual cycle for most birds, during which most or all of the feathers, representing up to 30% of the lean dry mass of a bird, are shed and replaced (Jenni and Winkler, 1994; Murphy, 1996). Assessment of the costs and benefits of the processes involved in moult are crucial to explaining the diversity of moult patterns (timing, duration, extent, sequence), their adaptive radiation across avian taxa, and the ways in which moult affects and interacts with other important stages of the annual cycle such as breeding and migration. In this paper we briefly review the costs of moult, and stress the importance of biomechanical considerations associated with flight when making such a cost–benefit analysis. In particular, we focus on the impact of moult on the most demanding mode of avian flight—that is, take-off from the ground—and we also indicate the factors that constrain take-off flight (*Figure 1*). The ability to take-off quickly and at a steep angle of ascent is likely to have a direct influence on fitness and survival: for example, increased take-off performance aids predatory avoidance (Cresswell, 1993; Grubb and Greenwald, 1982; Page and Whitacre, 1975; Witter *et al.*, 1994). For this reason we wish to highlight the necessity for behavioural and evolutionary biologists to consider and quantify biomechanical costs and constraints in order to gain a comprehensive view of the factors influencing important life-history strategies in birds.

2. Avian moult

2.1 *Physiology and energetics of moult*

Moult imposes both direct and indirect costs on a bird. Any moult strategy will evolve after a trade-off between these costs, a range of aspects of behaviour and life-history, and wing and body morphology. In this section we briefly review the direct

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Figure 1. *The effect of moult on flight. (a) Lappett-faced vulture* Torgos tracheliotus *making a running take-off into a strong headwind. This species is the largest African vulture, with a body mass of around 8 kg. It undergoes a very slow and irregular moult, and this individual is missing one distal primary on each wing (J.M.V.R., Kenya, 1982). (b) Lesser black-backed gull* Larus fuscus *making a sharp turn in gusty winds despite moult of secondary feathers and at least one distal primary, and considerable disruption to the trailing edge and abrasion of tail feathers (J.M.V.R., North Yorkshire, 1985).*

physiological costs of moult, which have been the subject of extensive research. Subsequently we consider the indirect costs arising from change, probably impairment, to the animal's aerodynamic performance.

Direct physiological costs of moult are well documented for numerous avian species, and have been studied and quantified from several perspectives (Lindström *et al.*, 1993; Murphy, 1996; Murphy and King, 1992; Murphy *et al.*, 1990; Murton and Westwood, 1977; Payne 1972). A full moult is surprisingly inexpensive, protein replacement requiring only a 2% increase in daily energetic expenditure or 6% increase in basal metabolic rate (review by Murphy (1996)). However, energy conversion into new tissues and feathers during moult is extremely inefficient: only 40–60% of metabolized energy is actually deposited as feathers during moult (Lindström *et al.*, 1993), and therefore estimates of energy demands of moult based on plumage and tissue renewal are likely to be gross underestimates. In addition to the increase in protein synthesis during moult (to produce feathers and skin), the rates of protein degradation and turnover also increase to up to 8.5 times greater than daily protein deposits (Murphy, 1996; Taruscio and Murphy, 1995).

Energetic expenditure during moult has predominantly been assessed by using three techniques: oxygen consumption (Dietz *et al.*, 1992; Lindström *et al.*, 1993), metabolized energy (Blackmore, 1969; Dietz *et al.*, 1992), and overnight loss of body mass (Dol'nik, 1965, 1967). Oxygen consumption can rise by 9–11% of normal non-moulting levels (this varies greatly with rate of moult, body size, and the thermal environment). Metabolized energy renders similar estimates of energy expenditure to those of oxygen consumption, but the technique has been criticized as birds can alter their energy expenditure during the day by engaging in less strenuous activities (Murphy, 1996). If a constant caloric equivalent of mass loss is assumed (normally 13.8 kJ g^{-1}), then energy expenditure can be estimated from overnight body mass loss. Dol'nik (1965, 1967) used this method for 15 passerine species, and estimated energy costs to be approximately double the estimates from other methods. The assumptions of constant energy expenditure overnight and a constant caloric equivalent to body mass have been criticized, so this method is not used very commonly (Murphy, 1996).

Although these estimates of energetic costs of moult appear relatively low, especially when compared with the costs of egg production (daily energy expenditure in a typical full moult is approximately 20% of the energetic expenditure involved in producing one egg), the energetic costs are calculated without consideration of the energy expended on processing the nutrients to generate the necessary tissue (feathers and skin). Hence, there are also additional nutritional costs.

Water requirements are also greatly elevated during moult: Chilgren (1975) estimated that water requirements of moulting birds can be almost double those of non-moulting birds, probably because of increased metabolism and thermoregulation problems. Obtaining access to a reliable water supply may be the most challenging dietary problem posed by moult, and much of this cost will be manifest in the time and energy expended in selecting a suitable habitat. This will vary greatly among species, as do the nutritional demands on moult, and also vary geographically as some habitats will have more abundant suitable food and water sources than other habitats.

Other compositional changes during moult can include an alteration of blood constituents (DeGraw *et al.*, 1979; Driver, 1981), which can often result from a dilution effect as a result of higher blood volumes during moult, and hypertrophy of the thymus, possibly reflecting increased production of lymphocytes as a result of expansion of blood volume (Ward and D'Cruz, 1968).

It is important to realize that moult entails not only replacement of plumage but also significant regrowth and alteration of underlying tissues, including blood vessels supplying the growing feathers, the integument surrounding the feather base, the horny covering to legs, feet and bills, and (in some cases) increased turnover of calcified bone (Murphy, 1996; Murphy *et al.*, 1992; Payne, 1972).

2.2 *Phenotypic plasticity*

These dramatic physiological changes have implications for the mass and body composition of birds during moult. There is a large and growing body of evidence that body condition and composition in birds are highly dynamic throughout the annual cycle, with not only replacement and regeneration of worn tissues, but with systematic adaptive control of body mass seasonally and in response to short-term conditions, and with organs being reduced at times when they are not required. This suite of phenomena is increasingly recognized as a major component of the avian life-history, and collectively is referred to as *phenotypic plasticity*. Moult should not be viewed simply as a restricted period of physiological and behavioural stress (although it is undoubtedly a demanding period), but also as a component of this broader pattern of phenotypic plasticity. It may be that these processes are more pronounced in birds than in other groups owing to the high energy costs of flight, and the premium of physiological and behavioural strategies that minimize total flight loads, that is, that reduce weight as far as possible. It may also be that the importance of moult is relatively emphasized owing to the unique avian adaptation of a feathered integument, which brings maintenance requirements. In birds two other periods of comparable physiological and aerodynamic demand are breeding (and raising young), and migrating. It is not surprising that in birds cycles of moult, breeding and migration are closely linked at every level from the endocrine system to behaviour and biomechanics, and that there is considerable diversity in these patterns between species in association with lifestyle, habitats and flight capabilities.

Most birds enter moult after breeding, when their body reserves of lipid and protein are often depleted (Austin and Fredrickson, 1987; Chilgren, 1975; Dhondt and Smith, 1980). In many cases, any loss of body mass will help to offset the increased costs of flying with moulting wings (Swaddle and Witter, 1997). Body mass is generally lower during moult, but often rises towards the end of moult as lipid, protein and water content of the body increase. Mass increases are especially pronounced if birds need to store fat for migration (which generally occurs immediately after post-nuptial moult) (Jehl, 1987; Morton and Morton, 1990). Protein composition of the body varies little during moult, except in cases where birds become flightless (as a result of the shedding of many flight feathers at one time) and flight muscles are atrophied (review by Murphy (1996)). In these latter cases, protein content is commonly shifted to leg muscles and the digestive organs (Ankney, 1979; Piersma, 1988) so that temporarily flightless waterfowl maintain their swimming, diving and foraging ability.

To optimize flight performance, birds hypertrophy flight muscle but down-regulate digestive tissue mass before long migration flights, and in some cases consume protein tissues during migration (Biebach, 1998; Piersma, 1998). It has been suggested that birds can down-regulate muscle mass during moult as an adaptation to reduce flight costs (Brown and Saunders, 1998). There is recent experimental evidence for this hypothesis, as European starlings *Sturnus vulgaris* exposed to endurance flight exercise training lose pectoralis mass and size, but show no decrease in take-off performance (J.P. Swaddle and A.A. Biewener, unpublished data).

Moult is extremely inefficient, and can incur substantial energetic and nutritional costs. It has long been recognized that consideration of the direct physiological costs of moult are insufficient to explain fully the common separation of moult from periods of breeding and migration, and also the vast array of moult parameters, sequences and tactics employed by different avian taxa (Earnst, 1992; Jenni and Winkler, 1994; King, 1980). To interpret the life-history implications of moult we must also consider the indirect consequences of feather replacement and its associated physiological responses. The most dramatic consequence of moult is the short-term partial or complete replacement of the flight feathers. There is therefore a pressing need to study and quantify the behavioural, biomechanical and aerodynamic consequences of moult. In the following sections we consider what is known about each of these topics in birds, and then we present recent results exploring the mechanisms by which aerodynamic performance is constrained during the moult period.

2.3 *Behaviour and moult*

Most birds alter behaviour during moult, and many reduce their level of activity (Francis *et al.*, 1991; Haukioja, 1971a; Newton, 1966; Sullivan, 1965); some species become flightless (Haukioja, 1971b; Sullivan, 1965). In birds such as waterfowl this is because their wings are already rather small and they are unable to accommodate the impact on flight speed (already high) and energy budgets (already higher power output than average for birds) from a temporary reduction in wing area (Rayner, 1988). Flightlessness may also be related to the increased physiological and energetic demands of moult: some birds may simply have insufficient energy available for aerial locomotion at the same time as replacing tissues. Naturally moulting birds reduce or alter their activity during moult, spending less time flying and preferentially seeking areas of protective cover with lower predation risk and thermal neutrality (Haukioja, 1971b; Newton, 1966; Stresemann and Stresemann, 1966; Sullivan, 1965). As it has been shown that similar responses can be induced by artificial reduction of feather lengths simulating the wing geometry observed during moult (Swaddle and Witter, 1997), we know that this behavioural response is due to flight biomechanics and not to the physiological changes occurring during moult. Birds may shift the relative timing of behavioural routines during wing moult, especially if they become flightless, to avoid increased exposure to predation (Kahlert *et al.*, 1996). Pied flycatchers *Ficedula hypoleuca* exposed to experimentally simulated moult are more susceptible to predation than are controls (Slagsvold and Dale, 1996). For all of these reasons the physiological and biomechanical costs of moult can affect behavioural routines to a large degree, resulting, for example, in birds spending less time foraging because of an increased perceived predation risk; this will have a profound influence on individual survival and fitness (Swaddle and Witter, 1997).

2.4 *Variation in moult pattern with flight ecology*

The importance of flight to moult (and vice versa) is also indicated by a brief survey of the relations between moult and flight ecology. For example, relatively slow moulting birds, such as the starling *Sturnus vulgaris*, remain capable of flight throughout moult (Jenni and Winkler, 1994; Swaddle and Witter, 1997). The moulting pattern of this bird is typical of most passerines in that it sheds one primary flight feather at a time from the wing in sequential order (proximal to distal) (Bährmann, 1964; Jenni and Winkler, 1994). This results in relatively small gaps in the wing and a maximal loss of wing area of only approximately 10% during the most intense period of moult (Swaddle and Witter, 1997). By maintaining flight capability these birds can continue to occupy similar niches as during non-moult periods, although they appear to reduce the amount of time spent flying (Feare, 1984; Swaddle and Witter, 1997).

Variation in moult among passerines is mostly the result of differences in the rate of moult (rather than in its timing, sequence or extent), and this appears to be intimately linked to their ecology (Jenni and Winkler, 1994). Species that migrate after moult often moult faster, and periods of breeding and moult generally do not often overlap (Ginn and Melville, 1983; Hemborg and Lundberg, 1998; Holmgren and Hedenström, 1995). In some cases, moult is suspended while migration occurs and then resumed once migration has finished. Alternatively, moult and migration can co-occur if few feathers are missing from the wing at any one time (Holmgren and Hedenström, 1995; Holmgren *et al.*, 1993).

In large birds with extended breeding cycles, such as albatrosses and eagle owls, it is imperative to maintain flight year round. These birds moult extremely slowly, and commonly extend their flight feather moult over a number of years (see, e.g., Prince *et al.*, 1993, 1997). Conversely, some passerines and a number of waterfowl moult very quickly and have many flight feathers missing from the wing at one time (Haukioja, 1971b; Stresemann and Stresemann, 1966) so that they become flightlessness and may hide in dense vegetation, spend a greater proportion of time than normal on the water surface (presumably to aid predator avoidance), or adopt a 'moult migration' to deep-water locations free from terrestrial predators (Salomonsen, 1968). The issue of variation in timing of moult is an important one, which may hold important clues to the diversity of moult patterns among birds. As in most such phenomena, we expect it to be a trade-off, ultimately between the need to divert increasing metabolism to tissue turnover and to any enhanced survival costs during moult, in a 'fast' moult, and a longer period during which flight patterns and behaviour are disrupted compared with normal, with consequences for other seasonal change in behaviour, in a 'slow' moult.

2.5 *Aerodynamics of moult*

It is—at least at first sight—evident that the change in wing planform during moult should have an effect on aerodynamic performance. Substantial proportions of the flight feathers, which form the lifting surface of the wings or tail, or of the covert feathers, which form the smooth surface to the body and wings, may be missing (*Figure 1*). A wing with a reduced wing area can be expected to have a reduced capacity to generate aerodynamic lift compared with the intact wing. However, little is known of the aerodynamic effect of moult in birds in flapping flight, and the change in lift may not simply be proportional to the change in area.

The aerodynamic performance of a wing is normally described by the aerofoil *polar* curve (*Figure 2*), which shows how lift and drag vary as a function of the angle of incidence of the wing section. Polar curves have a characteristic shape, which is related

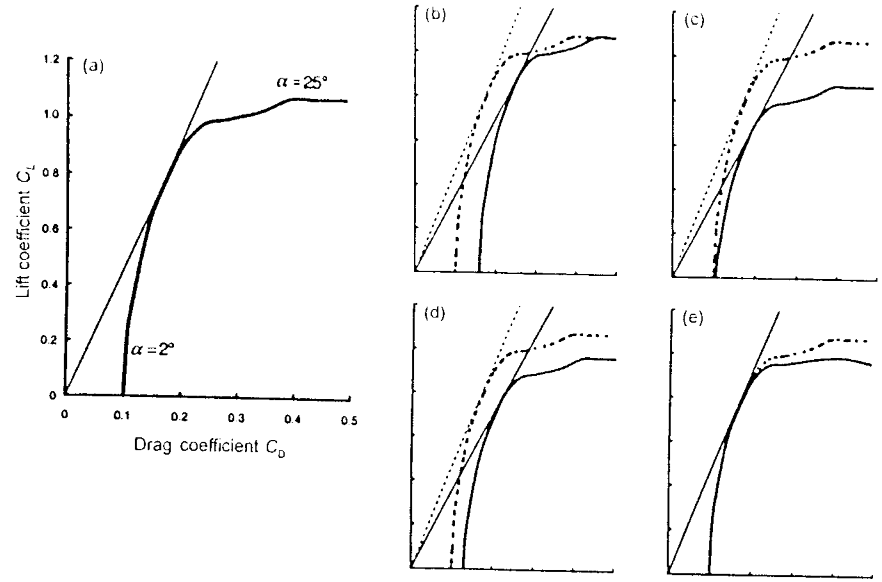


Figure 2. Hypothetical effect of moult on wing aerodynamics. (a) Stylized polar curve for an intact wing, showing the relationship of lift and drag coefficients C_L and C_D; angle of incidence α increases moving from bottom left to top right of the curve. This curve is based on measurements on the body and wings of a swift by Nayler and Simmons (1921); the wing stalls at incidence about 30°. (b)–(e) show the possible effects of moult on the polar curve; in each case the dashed curve is the supposed polar for the intact wing. (b) Moult reduces lift with no change in drag. (c) Moult increases drag but does not affect lift. (d) Moult reduces lift and increases drag. (e) Moult reduces maximum lift coefficient but does not affect normal flight. In each of (b)–(d), the minimum lift–drag ratio, shown by the gradient of the tangent from the origin to the polar, is decreased. From measurements of gliding performance alone it may not be possible to isolate the aerodynamic mechanism for the influence of moult.

directly to the glide polar (Tucker, 1991, 1993) and indirectly to the flapping flight power curve (Rayner and Ward, 1999). At any speed V, lift L and drag D are related to the lift and drag coefficients C_L and C_D by

$$L = \frac{1}{2}\rho S V^2 C_L \quad (1)$$

and

$$D = \frac{1}{2}\rho S V^2 C_D \quad (2)$$

where ρ is air density and S is wing area. If moult does not alter the force coefficients, lift and drag at a given speed should vary proportionally to the change in area. The force coefficients are likely to vary according to the morphology of the wing and feathers, the topography of the moulting feathers, and the bird's ability to compensate for their absence. We expect there will be considerable interspecific variation associated with morphology and with moult patterns, and we see potential for significant temporal variation in an individual as moult proceeds. If, for instance, just one of the wingtip primary feathers is missing, the aerodynamic load (the bound vortex circulation) normally carried by that feather may be redistributed to other wingtip feathers, with little effect on the vortex wake, and therefore little or no change in lift or induced drag, as these quantities are determined primarily by wingspan (Rayner, 1993); this might correspond to the case in *Figure 2(e)*. In a bird in which a single feather determines the wingtip and the maximum wingspan, loss of that feather may have a marked effect on lift and wake momentum: this would represent a loss of lift, with little change in drag (*Figure 2(c)*). Alternatively, when a missing secondary feather causes a gap in the trailing edge, the lift on that section of the wing is impaired; wake vortices may be shed proximally to the gap rather than more distally towards the wingtip, and either or both induced drag will rise or maximum lift will reduce (*Figure 2(b)*-(*d*)). A bird may compensate by adjusting the extent of overlap of the feathers, by increasing the relative speed of the wing (i.e. increasing wingbeat frequency or amplitude) or by increasing the local angle of incidence of the wing (which is very difficult to measure).

The most obvious aerodynamic effects of moult may be evident only in conditions of maximal aerodynamic performance. In cruising forward flight birds generally fly well below maximum lift coefficient, with comfortable reserves of aerodynamic performance. In slow flight and take-off a bird approaches the limits of aerodynamic force generation (Rayner, 1995; Swaddle *et al.*, 1999; this paper); it may be generating maximum lift, and therefore may be unable to maintain flight performance with even a small reduction in lifting capability. Our hypothesis is that aerodynamic lift generation is a severe constraint on take-off and slow flight, and is a prime mediator of the interaction between flight aerodynamics and behavioural strategies. We therefore expect that this constraint will be most acute at times of high energetic load such as during moult.

There is limited information about how moult affects the aerodynamic performance of a fixed, gliding, wing. Tucker (1991) recorded the change in gliding performance through moult in a Harris hawk *Parabuteo unicinctus* (*Figure 3*). This species has separated primary feathers, which act to reduce induced power compared with an equivalent flat wing by spreading the vortex wake shed by the wingtip both horizontally and vertically (Tucker, 1993). In this species the loss of a distal primary forming part of the wingtip has a marked effect on gliding performance, presumably from the rise in induced drag, which the bird cannot avoid if it is to maintain lift; this corresponds to *Figure 2*(c) or (*d*). There is no information on the effect of moult of a primary feather in species with closed wingtips.

Hedenström and Sunada (1999) showed in a theoretical study of flat wings with rectangular gaps in the trailing edge simulating moult that wing gaps reduced aerodynamic performance in proportion to their size, and that gaps near the tip of the wing had a smaller effect than those created by removing proximal primary feathers. (The effect of a primary feather oriented laterally towards the wingtip was not considered.) Their analysis also indicated that an additional gap in the secondary feathers has little further influence on flight performance added to a gap in the primary feathers alone, and that the effects of wing gaps are dependent on initial aspect ratio of the wing: the effects of gaps are greater in wings of higher aspect ratio, and this may be an explanation for why birds with long, narrow wings (i.e. those with high aspect ratio) often exhibit a slow moult in which only one primary is missing from the wing at a time (Hedenström and Sunada, 1999).

Gaps or irregularity in the trailing edge of the wing during very early stages of wing moult, that is, when the most proximal primaries are being shed, could have an anal-

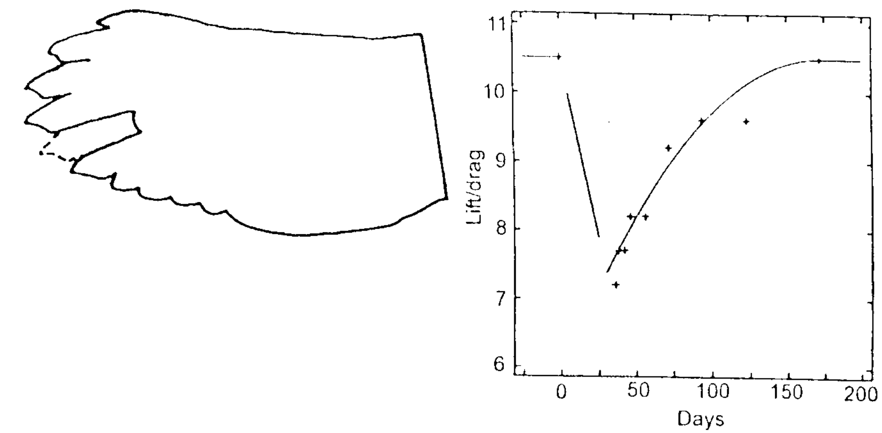


Figure 3. Effect of moult on gliding performance in a Harris hawk Parabuteo unicinctus *measured in a wind tunnel. Left: a fully spread wing, showing the gap left by the missing primary 6; the dotted line shows the outline of the normal feather. Right: lift–drag ratios of a gliding hawk during moulting; moult began on day 0 and was complete before day 172. Lift–drag ratio is the best (i.e. shallowest) gliding performance the bird can achieve. Immediately after moult the ratio drops sharply, and then progressively recovers. This moulting period representing almost half the year is relatively long, as may be expected for a large bird in which the absence of more than one primary at any one time may be detrimental. Adapted from Tucker (1991).*

ogous function to the notches in the trailing edges of the wings of galliforms; in a fixed wing in species with short, rounded wings this secondary notching increases the lift–drag ratio of the wing (Drovetski, 1996). It is not known how these wing gaps influence aerodynamics during flapping flight.

So far there has been less consideration of the effect of moult on the aerodynamics of bird wings during flapping flight. As we have argued above, moult may represent a particularly acute constraint in slow flight and take-off. This topic needs to be addressed before it is possible to assess the aerodynamic and biomechanical costs of moult for most birds. It is difficult to describe aerofoil action in flapping flight by polar curves, as local wing and air velocities vary in time and space, there can be considerable spanwise flow transverse to the aerofoil sections, and the flow is dominated by free vortices on, above and behind the wake; it is preferable to describe wing aerodynamics in terms of bound and trailing vorticity (Rayner 1979, 1993). We hypothesize that moult will have two effects. First, it will reduce the maximal lift that the wing can generate. This would be manifest in a lower maximum lift coefficient, and a lower maximum strength of vortex circulation bound on the wings or trailing in the wake. Second, moult may result in increased induced drag, because wake vortices are not shed as efficiently as in a normal wing; drag may not be directly influenced by reduced wing area because of the possible effects of slotting of the wingtips or of non-planarity in wake of the wingtips, neither of which are well understood in flapping flight, and may not have as marked an effect as Tucker found in a gliding bird. In normal forward flight a bird typically operates well below the maximum lift coefficient or bound circulation (Rayner, 1986, 1993), and we predict that the effect of moult may be confined to a slight increase in wing speed (i.e. wingbeat frequency and/or amplitude), and/or a small increase in local wing pitch. These changes may be so small as to be difficult to measure, or to visualize the effect on the vortex wake strength and geometry. We expect that the effects of moult will be most marked, and therefore most readily measured, during take-off and ascending flight.

2.6 *Empirical studies on moult and flight*

From the arguments above, it is to be expected that—for aerodynamic, and possibly physiological, reasons—moult will have an appreciable effect on flight performance, depending in extent on the species concerned and on their moult habits. There have, however, been relatively few studies exploring this, and most of these have artificially modified feathers to simulate moult. Noguès and Richet (1910) made dramatic mutilations to pigeon wings—far exceeding those occurring during moult—to determine how all flight capacity was lost at a critical wing area. Clement and Chapeaux (1927) showed that removal of the tips of all primary feathers of a pigeon equivalent to 3% of wingspan made all flight impossible, but that 40% of the area of secondaries could be removed with no aerodynamic effect. Wingbeat frequency was increased, and the birds were eventually forced to stop flight through fatigue. Boel (1929) trimmed the emarginated feathers of a vulture slightly, and found that although the bird could not take-off from the ground, it could still fly level; similar modifications had no effect on take-off in a pigeon. As described above, Tucker (1991) showed that the natural loss of one of the separated distal primaries in a Harris hawk depressed lift–drag ratio. Chai (1997) found that hovering flight capacity was reduced during both natural and simulated moult in the ruby-throated hummingbird *Archilochus colubris*; the effect was most marked when primary, rather than secondary, feathers were absent, and this is consistent with the mechanism outlined above by which shortening of the wingtip depresses maximum lift production. Swaddle and Witter (1997) demonstrated that a range of flight performance measures were affected by natural and experimentally simulated moult in starlings. Level flapping flight speed, ability to negotiate an aerial obstacle course and flight speed during take-off were all reduced in response to moult, but there was little indication that this reduction in performance varied through the course of moult: there was no measurable effect of moult stage and response did not depend on the size of wing gaps.

A number of workers have removed or shortened wing feathers in birds in the field, not specifically to study moult, but to explore the response of a bird to energetic stress. The argument has been that, as wings are optimized for flight, reduced wing area will impair flight performance: birds would either require more energy to fly, or would be less effective in finding food for themselves or their young. In the first such study, Harris (1971) found no change in breeding success in gulls; subsequently others have found a range of reactions, including longer foraging trips, reduced clutch sizes, lower chick growth rate, lower rates of delivery of food to young, disappearance (possibly as a result of predation), shorter duration of display, reduced mate acquisition success, and a tendency to seek protected areas (Mather and Robertson, 1993; Mauck and Grubb, 1995; Slagsvold and Dale, 1996; Slagsvold and Lijfeld, 1988, 1990; Verbeek and Morgan, 1980). These studies gave no indication of the biomechanical mechanisms involved in the compensation for modified wing profile, and reported little of changes in flight pattern of the experimental animals. In the light of the results outlined below, that starlings make an abnormal response to simulated moult, it is unlikely that these studies have much biological relevance. They do, however, confirm

that wing shape is closely tuned to aspects of behaviour and ecology, and that during moult flight and foraging efficiency will be impaired, and will have consequences for avian life-history. This confirms our argument that the scheduling of moult alongside other aspects of life-history is influenced by the energetic and aerodynamic consequences of the loss of flight feathers.

2.7 *Wing shape changes and moult*

Wing shape is often used as a cue to interpret relations between flight and ecology (see, e.g. Norberg, 1990; Rayner, 1988). The patterns are complex, reflecting the diversity of trophic strategies in birds, and are overlaid by adaptation of flight muscles and of the legs, and by the phylogenetic history of individual lineages. In short, four main aspects of flight behaviour can be invoked to interpret interspecific patterns of wing design: flight speed is proportional to wing loading (and therefore is related inversely to wing area); cost of transport, or energy consumption for long distance flight, increases with aspect ratio; agility and manoeuvrability (the abilities to control the flight path) are increased by more pointed, and broader, wings (Rayner, 1988); take-off is facilitated by more rounded wings (Lockwood *et al.*, 1998).

These patterns are generally well understood, and have been extensively tested in both cross-order and interspecific studies (e.g. Rayner, 1988). However, wing shape is not stable in any bird, and varies both with growth and seasonally, and also with moult. These changes may represent a further component of phenotypic plasticity, enabling a bird to control wing shape adaptively. Changes as a result of moult may, however, be detrimental. If the most distal primary feathers are shed the wing can become shorter; depending on the change in wing area aspect ratio may also be reduced and as a result a bird may lose turning performance, have an increased cost of transport during flight, and be less able to hover or fly slowly (Lockwood *et al.*, 1998; Norberg, 1990; Rayner, 1988). Even when the feathers that form the wingtip are not moulted, gaps in the wing caused by moult of other feathers can alter the effective aspect ratio and, hence, the performance of the wing (Hedenström and Sunada, 1999).

With these considerations in mind, we feel that it would be useful to have some means of quantifying moult within a biomechanically oriented framework. Two studies have approached this issue, by converting moult scores (a subjective ranking of individual feather regrowth summed across the entire wing (Ginn and Melville, 1983)) to indices of wing raggedness and to estimates of the loss of wing area during moult (Bensch and Grahn, 1993; Hedenström, 1998). However, as indicated above, the aerodynamic influence of moult is more complex than can be assessed simply by loss of wing area. We feel that it may be more fruitful to employ an index of wingtip shape when assessing the mechanical impacts of moult (Lockwood *et al.*, 1998). This is possible with the present methods of moult scoring (Ginn and Melville, 1983) only if species exhibit little heterogeneity in moult parameters. It is more useful to compare the consequences of different moult parameters. Our proposed method takes into account the relative size and position of gaps in the wing, and also the shape of the wingtip in the non-moulting condition; all of which can affect the aerodynamic functioning of the wing. We propose that by plotting changes in the two wingtip shape indices developed by Lockwood *et al.* (1998) (wingtip roundedness and convexity), we can generate a biomechanical moult indicator that could be used to compare the flight consequences of moult among species that vary dramatically in their moult pattern, sequence and duration to explain the evolution of different moult tactics and behaviours.

To illustrate the possible application of wingtip shape as a moult indicator, we have calculated wingtip shape index scores for starlings during their complete annual moult (*Figure 4*). The two shape indices are derived from the lengths of the eight most distal primary feathers by the following equations:

$$C_2=\log_e(3.332\,Q_1^{-3.490}Q_2^{-1.816}Q_3^{-0.893}Q_4^{-0.003}Q_5^{0.829}Q_6^{1.351}Q_7^{1.661}Q_8^{2.361}) \quad (3)$$

and

$$C_3=\log_e(0.0879\,Q_1^{-6.231}Q_2^{1.683}Q_3^{4.033}Q_4^{4.721}Q_5^{3.955}Q_6^{1.349}Q_7^{-3.185}Q_8^{-6.326}) \quad (4)$$

where $Q_1 - Q_8$ are the lengths (mm) of primary feathers 1–8, respectively, numbered in ascending order from distal (i.e. nearest wingtip) to proximal on the wing. Vestigial most distal primary feathers are ignored. This unconventional numbering of primary feathers allows comparison of wingtip shapes among species with differing numbers of primary feathers (Lockwood *et al.*, 1998). In a comparative analysis of feather sizes in birds, C_2 and C_3 were shown to be effective measures of the roundedness and convexity of the wingtip, respectively, which correlated well with aspects of flight behaviour and aerodynamics (Lockwood *et al.*, 1998). When applied to moult, these two wingtip shape indices allow a quantifiable comparison of the position and size of wing gaps among species. By concentrating on the handwing (i.e. the lengths of primary feathers), this method focuses on the part of the wing that should have the largest aerodynamic effect during moult.

Although, at this stage, we do not know the aerodynamic consequences of the exaggerated values of roundedness and convexity during moult rendered by this analysis, they are useful in comparing wing geometry among species. Future experimental analyses will include simulation of these moult wing forms and study of their aerodynamic effect, both theoretically and quantitatively, on models and live birds. Exploration of the mechanical consequences of these wing forms will contribute greatly to our understanding of the flight costs of moult and so help to illuminate the selection pressures acting on both wing design and moult parameters in volant avian species.

The second way in which moult and wing shape can interact is through changes in wing shape brought about by a complete moult. Wing shape alters systematically from juvenile to adult plumage in some passerine species (Alatalo *et al.*, 1984), and as explained above these changes are clearly adaptive. Moult has the capacity to alter wing shape in a long-term manner (i.e. for the duration between successive moults). For species that show two complete moults per year, this could mean an alteration of wing shape between reproductive and migratory periods of the calendar, with the possibility of effective adaptation for differing wintering and breeding habitats. We are not aware of any studies that have explicitly explored this possibility, but it seems likely, as subtle changes in wingtip shape are associated with predictable changes in flight performance. Within-individual changes in wingtip shape in starlings are related to changes in take-off performance (Swaddle and Lockwood, unpublished): birds whose wings become more rounded because of a complete moult (i.e. comparing post-moult and pre-moult wingtip shape) take-off from the ground at a steeper angle of ascent. It is also relevant that this same measure of wingtip roundedness is related to relative predation risk, in that small passerine species with rounded wings appear to suffer less predation by sparrowhawks *Accipiter nisus* than those with relatively pointed wings (Swaddle and Lockwood, 1998).

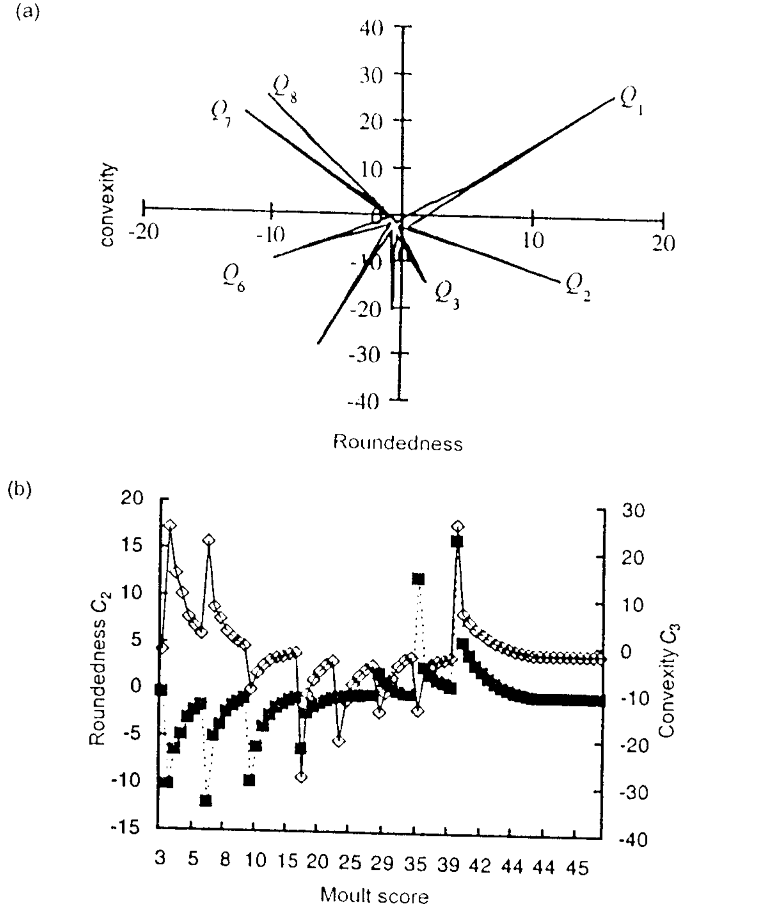


Figure 4. (a) *Wingtip roundedness and convexity through a complete primary feather moult in a adult European starling* Sturnus vulgaris. Q_1 *to* Q_8 *refer to the occasions when these primary feathers are shed from the wing (see text for further description). This description of moult commences with the shedding of* Q_8 *in the upper left-hand part of the graph and follows an anti-clockwise trajectory around an eight-pointed star, finishing after* Q_1 *has been replaced. Each point on the star represents the shedding of a particular primary, which results in a large gap in the wing.* (b) *Wingtip roundedness (■) and convexity (◊) versus moult score (Ginn and Melville, 1983) for the same individual over a single moult cycle, as above. A moult score of 45 indicates that primary feather moult has finished.*

3. Take-off in birds

Take-off is widely described as the most costly or demanding form of flight. It is generally accepted that take-off performance constrains birds, particularly in the maximum size they can reach and the loads they can carry, and that these constraints become more acute in larger birds (see, e.g., Rayner, 1995); direct experimental evidence explaining the mechanisms involved is, however, sparse (see Marden, 1987). Take-off involves high short-term energy rates associated with dynamic height gain and acceleration, and the aerodynamic lift on the wing is expected to approach maximum values. Other possible constraints on take-off performance include the contraction strain rate of the flight muscles, which may limit how much a bird can increase wing speed, the force the muscles can generate, and the power the muscles can deliver. An integrated hypothesis would explore the idea that the limits to performance set by independent aerodynamic, musculo-mechanical and physiological constraints coincide through *symmorphosis* (Weibel, 1984). In this paper we concentrate on aerodynamics, and review evidence that aerodynamic factors limit dynamic energy gain in take-off.

In a typical take-off or other extreme behaviour it may therefore not be possible to identify any one dominating constraint. Evidence of high levels of muscle activity in take-off is convincing: in pigeons, pectoralis (*pars thoracobrachialis*) EMG intensity (Dial, 1992), tail muscle activity (Gatesy and Dial, 1993) and stress developed in the pectoralis muscle (Dial and Biewener, 1993) are much higher than in normal forward flight. There are, to our knowledge, no measurements of metabolic energy consumption in take-off, but this may not be a material constraint as metabolism during brief take-off exertion is likely to be glycolytic.

The ability to take-off is vital to most birds in a trivial sense as a means of initiating flight, but it is also a major contributor to survival: many bird species escape from predators by employing short, fast flights to areas of cover (Grubb and Greenwald, 1982; Lazarus and Symonds, 1992). In particular, improved ability to take-off from the ground will reduce the risk from terrestrial-based predators (Lima, 1993), and there is considerable evidence to indicate that the speed and trajectory of escape take-off are important determinants of predation (Cresswell, 1993; Kullberg *et al.*, 1998; Page and Whitacre, 1975; Witter *et al.*, 1994). In this way maximized take-off performance will directly influence the probability of survival and, hence, will increase individual fitness.

Size has a marked influence on take-off performance, and it has been argued (e.g. Rayner, 1995) that take-off sets the upper limit to viable size for flying birds (but see Marden (1994)). As size increases, the margins between the power required to fly and the power available from the flight muscles, and between lift on the wing and maximum force from the flight muscles, both become narrower, and birds tend to have less scope for rapid or steep take-offs. A range of highly specialized adaptations have evolved to maintain take-off performance in relatively large species, including clap-and-fling wingbeats (in pigeons, Nachtigall and Rothe (1982)), enlarged supracoracoideus muscles associated with short, rounded and highly cambered wings (in galliforms, Rayner (1988)), or the use of extended accelerating flights often over a water surface (in gaviiforms, Norberg and Norberg (1971); in swans, Prior (1984)). Many species can take off only by running into the wind, or by dropping from a high point to convert potential into kinetic energy until speed is sufficient for aerodynamic thrust generation to be effective. Take-off has been identified as one of the major selective constraints to be overcome in the course of the evolution of flying birds from cursorial theropod dinosaurs (Rayner, 1991).

Theoretical modelling of take-off so far has been limited, possibly owing to the relative scarcity of adequate experimental information, and the practical difficulty of controlling a bird's behaviour when it is close to biomechanical or physiological limits. Norberg and Norberg (1971) modelled the generation of thrust by flapping wings during running take-offs in divers (Gaviidae), and Rayner's (1979) vortex models are applicable to take-off provided flight path dynamics are known (see below). The major limitation to formalizing such an approach has been that neither the dominant constraints on take-off performance nor the appropriate selective currency are well known.

A wing is limited in the maximum aerodynamic lift it can produce. Lift is proportional to the product of the square of the local speed of the wing and the lift coefficient (Equation (1)), which depends on the geometry of the wing cross-section and on the local angle of incidence (or pitch) of the wing section. Equivalently, lift is proportional to the strength (or circulation) of the vortices bound on the wing and trailing in the wake. Beyond a maximum pitch, the airflow over the upper surface of the wing breaks away from the wing, the wing is said to stall, and lift drops away. Stall (occurring in *Figure 2(a)* at angle of incidence of around 25°) is a major problem for fixed-wing aircraft, but is less serious for birds, for two reasons. First, stall is a dynamic pheonomenon: in flapping flight the local pitch and the magnitude of the lift force vary continuously, and instantaneous values of lift well above steady-state stall can be attained. Second, even if the wing were held still in gliding flight, a bird can readily flap to recover from a stall. In forward cruising flapping flight, the lift coefficient is well below its maximum, and a bird has considerable scope to control lift and thrust by adjusting local wing pitch and wingbeat kinematics. However, in slow flight and take-off, lift coefficient and vortex circulation are relatively high compared with forward flight, and approach the maximal levels that the wings can generate, even in flapping flight. Pigeons flying at 2–3 m s^{-1} (Spedding *et al.*, 1984) are unable to generate sufficient wake vortex momentum to support their weight (Rayner, 1993). Mean lift coefficients as high as around five—and sometimes higher—are typical in slow flight and hovering in small birds (e.g. Norberg, 1975; Scholey, 1983), whereas lift coefficient rarely exceeds 1.5 in forward flight. In take-off flight the bird must provide additional force to gain height and to accelerate, and lift coefficient is likely to be even closer to maximal values. We hypothesize that this is the dominant constraint on take-off flight dynamics.

Physiological constraints have independently been considered to limit flight performance. Pennycuick (1969) proposed that upper limits to oxygen delivery by the respiratory and circulatory systems and to the rate of conversion of oxygen and fuel to mechanical work in the flight muscles would act as a constant upper limit to power output in any bird, independent of flight speed or behaviour, and that this power output would impose upper *and lower* limits to flight speed in steady flight. Power delivery is undoubtedly limiting, but there is little information on the magnitude of such constraints. Recent aerodynamic and mechanical evidence (Rayner, 1999; Rayner and Ward, 1999) suggests that power output at higher speeds does not rise to limiting levels, and therefore other, possibly mechanical, factors determine maximum flight speeds. It appears to us that physiological constraints setting an upper level to power output from the flight muscles are unlikely to be acute, as take-off and short slow flights are associated with glycolytic metabolism, with high bursts of power for limited duration. Indirectly, aerodynamic and physiological factors may interact to constrain take-off: to generate sufficient lift, a bird in slow flight and take-off will normally increase wingbeat kinematics and wing amplitude to maximize wing section speed during the downstroke. Force and power output from the muscles will vary with contraction rate and strain, and therefore with wingbeat kinematics, in a manner not well understood. A bird's scope for achieving high levels of performance in take-off might therefore be associated with the diversity of contractile properties of flight muscles. So far there have been no studies demonstrating substrate use or depletion in an anaerobic take-off or short-term flight in birds, and there is insufficient information to develop realistic estimates of the maximum performance.

4. Moult and take-off

In the previous sections we have described mechanisms by which moult may have an influence on flight, and have shown why take-off, climbing and accelerating flight are likely to be constrained by aerodynamic force generation. We have argued that the influence of moult will be most obvious when these two effects are combined. Indeed, it is probable that the rigorous aerodynamic constraints imposed on take-off in moulting birds are responsible for some of the changes observed in behaviour or habitat use that are commonly reported. In the following sections we report two experimental studies that have started investigation of the interaction of moult and take-off flight in starlings.

4.1 *Take-off during simulated moult*

Swaddle and Witter (1997) developed an experimental method by which the direct physiological effects of moult can be separated from the indirect effects by trimming feathers of non-moulting birds to simulate moult. A more recent experiment has expanded on these experiments (Swaddle *et al.*, 1999). In this study, manipulated starlings had their primary feathers trimmed with scissors to simulate feather lengths of a bird in mid-moult (*Figure 5*). Manipulated moult birds and control groups were filmed during take-off with a high-speed video camera (at 100 Hz) to study the changes in wingbeat kinematics during simulated moult. To quantify aerodynamic performance of the birds, Swaddle *et al.*, (1999) computed aerodynamic performance (mean wing lift coefficient by blade element theory; vortex momentum and induced power by vortex ring models (Rayner, 1979)) from measured wingbeat kinematics, and they combined measures of potential and kinematic energy gain during take-off to assess instantaneous dynamic 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). This quantity has the advantage of combining a bird's take-off performance into a single parameter that should be independent of the bird's behavioural decisions to trade-off a gain in height (i.e. ascent angle) against a gain in speed; both are important aspects of predator avoidance, but a bird is unlikely to be able to maximize both speed and height gain.

As in the previous simulated moult study (Swaddle and Witter, 1997), birds reduced take-off speed immediately after the feather manipulations, but feather trimming had no influence on the climb angle of the take-off trajectory. Six days after the manipulations birds had regained their previous flight speed, as was also reported by Swaddle and Witter (1997). Most other measures of flight performance and kinematics (*Table 1*), including dynamic energy gain and acceleration, were significantly impaired by the manipulations, and had not recovered at least 6 days after the manipulations were performed.

Swaddle *et al.* (1999) explored possible mechanisms by which this adjustment arose. Wingbeat frequency did not change through the experiments, but wingbeat amplitude increased significantly after manipulations, although it reduced subsequently.

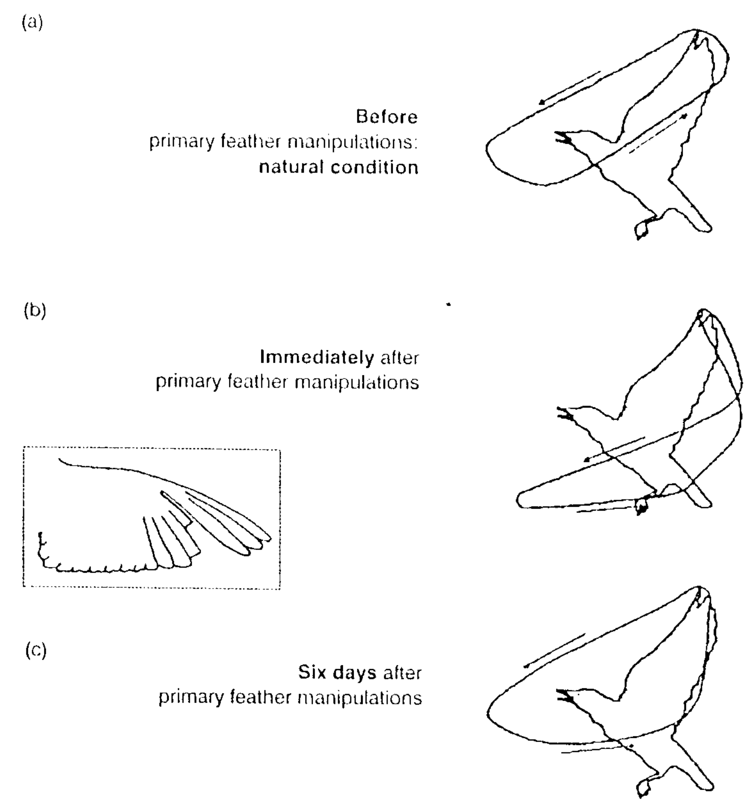


Figure 5. Wingbeat kinematics in European starlings Sturnus vulgaris *during simulated moult (from Swaddle* et al. *(1999). The inset shows how feathers were modified to simulate an intermediate stage of a natural moult with one primary slightly shortened and the adjacent primary almost removed. All birds from this treatment group showed this consistent pattern of wingtip reversals during phase 2. Kinematics for two control groups, which experienced the same handling either with no manipulation or with trimming of the same feathers to remove less than 1% of wing area, remained similar to phase 1 throughout.*

The consequence of these changes was that the wingtip speed was increased, but because acceleration is lower the birds operated at a lower mean lift coefficient. It is expected that this was the maximum lift coefficient they were able to achieve, and this value was insufficient to maintain acceleration and rates of energy gain (= dynamic power). Immediately after manipulations there were dramatic changes in movement of the wingtip during the wingbeat (*Figure 5*). Before the manipulations the kinematics and posture are characteristic of passerines in take-off flight: the body is steeply inclined, and 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 (*Figure 5(a)*). Immediately after the feather manipulation birds exhibited an abnormal wing movement not known from any bird in natural flight. The wingtip path followed a looping movement at the top of the trace, indicating the presence of a wingtip reversal during the latter phase of the upstroke, and during most of the downstroke the leading edge is at an obtuse angle to the body axis (*Figure 5(b)*). Six days after the manipulations the wingtip pattern displayed less of this disruption, but was still dissimilar to that observed during session 1 or in control birds. Wingtip reversals have been associated with lift production in the upstroke of pigeons (Brown, 1963) although flow visualization experiments do not support this interpretation (Rayner, 1995; Spedding *et al.*, 1984), and it is inconsistent with the backward-slanted orientation of the upstroke wingtip path. Upstroke lift is equally unlikely to occur in these starlings, which—like pigeons—employ a vortex ring gait during take-off (*Figure 6*). The estimated reduction in lift production during the downstroke, with parallel reductions in wake momentum, vortex ring circulation and induced power, is consistent with the decline in dynamic energy gain and acceleration (*Table 1*). Although the low value of induced power may seem advantageous, this is in practice the symptom of the birds' inability to generate more lift.

In these experiments, moult was simulated by cutting the distal portions of individual feathers (*Figure 5*). That the abnormal kinematic response arose simply from unfamiliarity with the unexpected low lift coefficient is evident from the birds' adjustment over the following 6 days. The difference from behaviour in natural moult (below) emphasizes the need for caution in employing such experimental techniques to simulate morphological variation. The 'tips' of the trimmed feathers are distinct from the true tips of a regrowing feather during moult: the shaft and vane will have different mechanical properties, and will probably be stiffer. This, in addition to the unexpected change in wing planform, are apparently responsible for the reduction in maximum lift coefficient.

There was no indication that birds generated extra lift with their tails, as tail feathers were held at similar angles among treatment groups. It does not seem that birds are exploiting novel sources of lift immediately after manipulations. Upstroke wingtip reversals are more likely to be used as a means of accelerating the wing rapidly before the downstroke, and thereby of developing lift more quickly. This mechanism is likely to be important to a starling with an impaired wing, and we propose that the increase in wingbeat amplitude and the deformation of the wingtip pattern are the immediate mechanisms of compensation for removal of feathers and loss of integrity of the distal parts of the wing. We suspect that this pattern entails some, perhaps significant, extra costs, although we have not been able to confirm this: induced power appears to decline (*Table 1*), but there may be demands on unfamiliar muscle groups associated with this flight pattern.

Subsequently, perhaps associated with adjustments to the flight muscles or simply with familiarity, the bird accommodates its wingbeat to a pattern more similar to normal, and is able to some extent to compensate for the immediate cut in lift coefficient.

4.2 *Take-off during natural moult*

Experiments with simulated moult have the advantage of separating biomechanical changes to the wing from the physiological changes to body composition, total weight and flight muscle contraction physiology, which are an essential component of the natural moult cycle. In the absence of this accommodation it is perhaps not surprising that the aerodynamic performance of birds in simulated moult is sharply depressed.

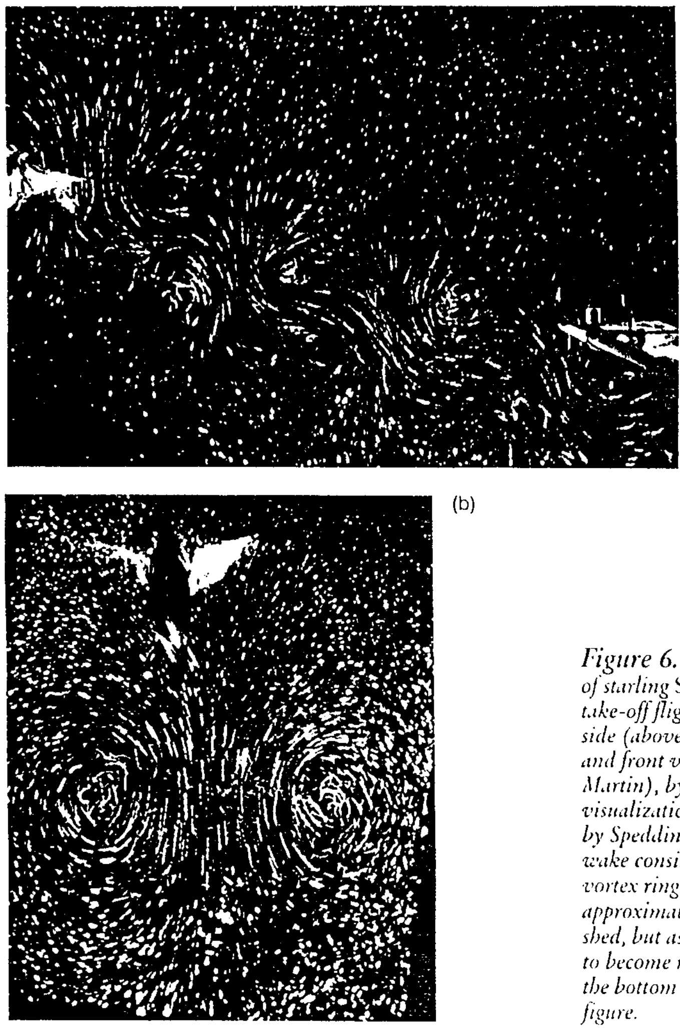
Table 1. Mean morphology, wingbeat kinematics, flight path dynamics and computed aerodynamic performance for European starlings Sturnus vulgaris *undergoing natural (left columns) and simulated (right columns) moult.*

	Natural moult			Simulated moult		
	2 weeks before moult	Mid-moult	2 weeks after moult	Before manipulation	Immediately after manipulation	6 days after manipulation
Morphology						
Body mass (kg)	0.074	0.074	0.077	0.073	0.072	0.072
Wing area (m^2)	0.0188	0.0174	0.0187	0.0191	0.0176	0.0176
Wingspan (m)	0.350	0.350	0.370	0.393	0.393	0.393
Flight Path						
Speed ($m\ s^{-1}$)	2.6	2.7	3.1	2.7	2.5	2.6
Take-off angle (°)	22.8	17.4	13.8	25.4	26.0	27.9
Acceleration (g)	0.77	0.69	1.35	1.12	0.74	0.75
Dynamic energy gain in second wingbeat ($J\ kg^{-1}$)	2.0	1.7	3.3	2.5	1.7	1.8
Kinematics and aerodynamics						
Wingbeat frequency (Hz)	14.8	15.2	14.9	16.1	16.3	16.8
Wingbeat amplitude (°)	90.2	125.9	120.1	136.3	144.2	127.1
Mean downstroke wingtip speed ($m\ s^{-1}$)	8.2	11.6	11.5	15.0	16.1*	14.7
Mean lift coefficient C_L	6.6	3.7	4.9	2.9	2.3*	2.7
Wake momentum ($kg\ m\ s^{-1}$)	0.49	0.47	0.76	0.60	0.47	0.46
Wake vortex ring circulation ($m^2\ s^{-1}$)	1.42	1.07	1.37	1.01	0.79	0.83
Power output						
Induced power (W)	4.6	3.0†	5.1	3.4	2.2†	2.4†
Dynamic power (W)	2.2	1.9	3.8	3.0	2.0	2.2
Total mechanical power (W)	6.8	4.9	8.8	6.35	4.2	4.6

Aerodynamic parameters relate to the second wingbeat after take-off ($n = 7$ for natural moult, $n = 7$ for simulated moult experiments). (For details of experiments see text.) Simulated moult from Swaddle *et al.* (1999), natural moult from Williams *et al.* (unpublished). Full details of experimental design, control groups, and statistical comparisons within and between groups are given in those papers.

* Assumes linear wingtip path in downstroke, and ignores wingtip reversal in upstroke; this will increase downstroke wingtip speed and reduce lift coefficient, will possibly depress induced power, but will not significantly affect wake momentum.

† Neglects change (?reduction) in aerodynamic wing efficiency (spanwise distribution of circulation) as a result of change in wing planform during moult; this might increase induced power.



(a)

(b)

Figure 6. The vortex ring wake of starling Sturnus vulgaris *in take-off flight from a perch, seen in side (above: photo E.V. Williams) and front views (below; photo J. Martin), by helium-bubble flow visualization (methods described by Spedding* et al. *(1984)). The wake consists of a sequence of vortex rings. The rings are approximately horizontal when shed, but as they evolve they rotate to become more tilted, as seen to the bottom right of the upper figure.*

Recent observations of seven adult starlings experiencing natural moult have unveiled interesting patterns suggesting that the biomechanical consequences of moult are more complex than the simulated moult experiments indicate (Williams *et al.*, unpublished material). Take-off was filmed with a high-speed cine-camera (at 185 Hz) on three occasions: 2 weeks before moult, at mid-moult and 2 weeks after moult was completed. Wingbeat kinematics, take-off speed, angle, acceleration and dynamic energy were determined from the films, and, as described above, aerodynamic performance was estimated by vortex ring theory (*Table 1*). Morphological measures indicate that body mass was low at the beginning of moult, remained depressed during moult, and rose when moult was completed. Swaddle and Witter (1997) have previously indicated significant mass reduction in starlings during moult. Wing area decreased during moult. Interestingly, wing length after moult was completed (16.7cm) was longer than

before moult began (15.9cm), indicating the benefit of regrowing worn or abraded primary flight feathers.

During moult birds decreased their angle of ascent compared with before moult, but did not alter their speed of take-off. This is consistent with previous analyses of take-off behaviour in moulting captive starlings (Swaddle and Witter, 1997), and with aerodynamic theory, which indicates that the faster a bird takes off, the lower the total aerodynamic work done to accelerate it. 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 birds in mid-moult in the present study remained unchanged compared with the wingspan pre-moult. Any decrease in mechanical power or aerodynamic force output may compromise ascent angle and/or acceleration, in preference to a reduction in speed, because ascent angle and acceleration are probably linearly related to energy input (Hedenström and Alerstam, 1992; Rayner, 1986), unlike take-off speed or speed in forward flight (review by Rayner and Ward (1999)). Therefore, a decrease in angle or acceleration would lead to a direct power saving, whereas a decrease in take-off speed, assuming no change in ascent angle or acceleration, would incur an increase in power requirement during take-off. We would therefore expect a bird to maintain flight speed as much as possible in an impaired take-off.

Kinematic analysis revealed that all birds exhibited uniform wingtip movements, similar to those commonly observed in this species (compare *Figure 5* pre-moult pattern), and there was no indication of the wingtip reversals observed in the simulated moult experiments (above). As in the experiments with simulated moult, wingbeat frequency remained constant, but wingbeat amplitude increased sharply in mid-moult and remaining elevated after moult had been completed, so that the wingtip was moving markedly faster. The birds were able to maintain speed, climbing angle, dynamic energy and acceleration (all fell slightly but non-significantly) with a lower lift coefficient on the wing. From this evidence we can determine that birds altered wingbeat kinematics in response to moult to maintain lift; they were not physiologically or structurally constrained in their wingbeat amplitude before moult began, but during moult the maximum lift coefficient they could obtain was sharply depressed. Experiments (above) simulating moult reached the same conclusion. As birds in nature commonly enter moult in a 'physiologically challenged' state, it is possible that there are limits to the functioning of muscles involved in flight and to the ability of worn feathers to generate aerodynamic force. After moult is under way and has finished it is possible that these constraints are less severe. *In vivo* measurement of muscle and tendon performance of birds in varying physiological and photoperiodic states may shed light on these hypotheses. Birds attempting to improve take-off performance through manipulating their wingbeat kinematics may not have been able to increase downstroke wingtip speed any further owing to physiological and energetic constraints imposed by muscles and tendons, which become exacerbated by the increased demands of moult.

Because of the low lift coefficients during moult, the wake vortex circulation and the induced power were also low. It is tempting to suggest that this is an adaptive response, in reducing the costs of flight during moult, and therefore permitting energy resources to be diverted to tissue and feather synthesis. However, three points should be set against this hypothesis. First, the energy reduction is a consequence largely of the reduced acceleration rates during take-off, and any reduction in power in steady forward flight is likely to be small or absent. Second, the reduced take-off performance increases exposure of the bird to predation risk, and this is likely to outweigh any small energetic benefits. Third, if small wings with moult gaps are adaptive during moult, they should be even more beneficial at other stages of the life cycle.

The most marked evidence of accommodation of flight performance to moult comes, perhaps surprisingly, from the period after moult. Speed, acceleration, dynamic energy gain and vortex wake parameters all increase significantly, and rise to performance significantly better than that before moult. This is in contrast to the experimentally simulated moult experiment described above, in which these values did not recover. The reduction in take-off angle in response to new plumage confounds the relationship between wingtip speed and take-off speed, but this is offset by the dramatic increase in acceleration. We interpret these results to mean that before and during moult birds are constrained in lift generation by the condition of their wings (worn or abraded feathers) and by the wingbeat kinematics they can achieve. After moult, they can achieve better rates of energy gain with a lower lift coefficient than before. This may mean that the generation of aerodynamic force is a significant constraint before and during moult, but is not a constraint subsequently.

The comparison of pre-manipulation performance with that 1 week post-manipulation is probably more relevant to the effects of the mid-moult stage in the present natural moult study; that is, birds had time to adapt take-off performance to their moult plumage. Therefore, the evidence from both the natural and experimentally simulated moult experiments indicates that starlings do not experience significant decreased take-off performance as a result of prolonged exposure to a moult plumage (as happens in nature). This is a surprising finding, and has important implications for the survival and behaviour of starlings during moult. It may also help to explain why starlings (and similar passerines) have a relatively prolonged moult and shed feathers sequentially rather than simultaneously. Further experimental investigations to examine the flight costs of different moult patterns and strategies in the starling and other species may further help to explain why avian species vary so much in the timing, duration and patterns of moult. However, as our kinematic data indicated that birds increased wingbeat amplitude (and to some extent frequency) during moult, there may be a physiological and energetic cost to maintaining flight performance during moult at pre-moult levels. Therefore alteration of kinematics to minimize the apparent (to the observer) influence of moult on overall flight performance may, in itself, impose costs that could impinge on the birds' energy budget and behaviour. Hence, we advocate a life-history approach to studying moult.

There was a significant increase in dynamic energy gained per wingbeat associated with new plumage. These data further indicate the benefits of moulting into new plumage, which are important to consider when explaining the factors that give rise to the evolutionary radiation of moult parameters. Although Williams *et al.* (unpublished material) selected individuals with apparently undamaged plumage for their study, the data appear to indicate that the renewed plumage after moult was functionally more efficient than the year-old plumage that each bird possessed before moult. An increase in the functional efficiency of new feathers may also have important implications for other possible indirect costs and benefits of moult, such as water repellence, thermal insulation and visual appearance of display plumage. Future studies of the costs of moult could also incorporate studies of these additional indirect consequences of renewed plumage.

4.3 *Comparison of simulated and natural moult*

The mechanical realization of changes in wingform as a result of simulated and natural moult are different. The disruption of the ability of the wing to generate lift force appears comparable when feathers are physically altered to match the pattern observed in moult, or when feathers are naturally at these lengths during moult (Swaddle and Witter, 1997; Swaddle *et al.*, 1999; Williams *et al.*, unpublished). It is not possible to identify the aerodynamic mechanism, but the observed response is consistent with a sharp reduction in maximum lift coefficient C_L, and a probable reduction in lift–drag ratio (cf. *Figure 2(c)* and *(d)*). Different aerodynamic mechanisms might apply in forward cruising flight, as outlined above. The difference between natural and simulated flight feather moult is accentuated by the longer-term changes in flight performance in the simulated moult experiments (Swaddle and Witter, 1997; Swaddle *et al.*, 1999). In both cases, wingtip kinematics altered immediately after moult or plumage manipulations, but in the simulated moult there were dramatic changes in the geometry of the wingtip path, which represent an extreme attempt by the bird to adjust to unexpected changes. Within 1–2 weeks after the feathers had been trimmed the birds had partially regained some of their flight ability. This clearly demonstrates that birds are capable of compensating or adjusting the behavioural response of flight to a new wing geometry. As birds can do this in response to a wholly artificial manipulation of feather lengths, it is more than likely that they can do the same during natural moult (as the data above indicate). Possible adaptive mechanisms could include alteration of wingbeat amplitude, wingbeat frequency, angle of attack of the wings, altering the shape of the wing and feather overlap, increasing maximal extension of the wing during the downstroke and tighter furling of the wings to the body during the upstroke. These all deserve further investigation to help explain how birds maintain flight performance during moult.

As natural moult entails significant physiological changes, it is also possible that the physiological alterations during moult could account for the differences between the natural and simulated moult experiments. It seems at first glance counter-intuitive that despite the additional physiological and energetic demands of moult, birds in natural moult appear to retain a greater flight performance than those that have had their feathers trimmed to simulate moult. This may simply be due to the disruption by the manipulations. We hypothesize that birds are able to reap some biomechanical benefits from the physiological changes that occur during moult. Perhaps wing weight and, hence, inertia are significantly reduced during moult: this could sharply reduce the maximum force required to move the wings (Rayner, 1986, 1993). Additionally, a loss of feathers (primaries, secondaries and coverts) from the wing may help with furling the wings tighter to the body during the upstroke, hence giving a slight reduction in profile drag (and also inertia). The expanded blood volumes during moult could increase aerobic supply to the flight muscles. The most important physiological effect on biomechanical performance may be the reduction in body mass commonly observed during moult. This will help the bird to achieve more with the reduced lift force from the wing. This loss of mass can even comprise loss of flight muscle mass without a detrimental effect on flight (J.P. Swaddle and A.A. Biewener, unpublished data). In simulated moult, birds are immediately exposed to a sub-optimal wing geometry and lower wing area without any alteration of body mass or other aspects of body composition. In natural moult, birds have often lost mass before wing moult commences, and therefore their wing loading is preserved at a lower, less costly, level. The experimental data we have presented in this chapter suggest that this mass loss is the primary mechanism by which starlings can reduce flight costs or compensate for reduced aerodynamic performance during natural moult. However, this does not preclude the action of alternative and additional mechanisms, nor can it explain flight performance in species that do not lose mass. In further investigations it will be necessary to take account of the physiological state of birds before moult begins, as the data presented in this chapter indicate that these initial conditions are vital in determining the influence of the wing geometry of moult on biomechanical performance.

5. Discussion

Moult frequently occurs between periods of breeding and migration (or overwintering for non-migratory species) and there tends to be little overlap among these periods for most avian species (Ginn and Melville, 1983; Hemborg and Lundberg, 1998; Holmgren and Hedenström, 1995; Langston and Rohwer, 1996; Slagsvold and Lifjeld, 1989). Hence, moult (especially in those species that moult once per year) often delimits the end of breeding and also the beginning of migration, and we must adopt a broad, life-history view of the factors that influence and drive the evolutionary radiation of moult parameters. These factors (i.e. the relative costs and benefits of moult as well as evolutionary and developmental constraints) are not only important in shaping 'moult' as a life-history trait, but they will also have indirect influences on breeding, migration and overwintering strategies. Therefore, quantification of cost–benefit trade-offs and identification of developmental and evolutionary constraints acting on moult parameters are essential in assessing many life-history elements of bird species. The review and presentation of novel data in this chapter further indicate the importance of biomechanical considerations to such analyses. We cannot obtain a full understanding of the factors that shape the evolution of moult without empirical and theoretical studies of biomechanical costs, benefits and constraints.

A life-history approach to the study of moult has often indicated the interplay between moult parameters and features of the ecology and behaviour of particular species (e.g. Ashmole, 1963, 1965; Furness, 1988; Langston and Rohwer, 1996; Slagsvold and Lifjeld, 1989). An intriguing example is that of Laysan and black-footed albatrosses (*Diomedea immutabilis* and *D. nigripes*, respectively), which appear to display trade-offs between the time available for moult versus breeding (Langston and Rohwer, 1996). Because of their extended breeding period and the lack of overlap between moult and breeding, there is often insufficient time available to complete a full moult every year; hence Laysan and black-footed albatrosses exhibit various patterns of incomplete moult. In years when breeding starts earlier or when the breeding period is shorter or abandoned, individuals are able to moult more feathers after their breeding attempt. In addition, when feathers become too abraded (as they may not be replaced every year), breeding may be sacrificed so that birds have time available to complete a full moult and renew their worn feathers (see discussion by Langston and Rohwer (1996)). Hence, moult not only influences breeding during the same year, but can also influence future breeding attempts, as albatrosses may be able to trade-off long-term investment in moult versus breeding. Ultimately, these birds are constrained in their rate of moult by the cost of regrowing many primary feathers at one time (as feather growth rates are very conservative in these species (Langston and Rohwer, 1996)). This may entail energetic and physiological costs of feather replacement (as indicated earlier in this chapter), but will also incur significant biomechanical cost, as having more feathers missing from the wing will increase the size and number of wing gaps (these birds show split sequences of primary moult in which the outer primaries are shed proximal to distal, but the inner primaries are shed distal to proximal). Therefore, the biomechanical consequences of moult can have profound influences on the breeding tactics of individuals.

These forms of life-history trade-offs are not particular to slow moulting seabirds with prolonged breeding periods, such as albatrosses. Other large birds have extended moult cycles, sometimes taking more than 1 year to complete a full wing moult. Similar observations have also been reported in many passerine species. For example, breeding pairs that invest more during the breeding season (i.e. raise a larger brood, or raise more broods) tend to start their post-nuptial moult later (e.g. Dhondt, 1973; Newton, 1966; Slagsvold and Lifjeld, 1989). Additionally, in cases where the male tends to expend less parental effort than the female, the male will often moult earlier than the female (e.g. Hemborg and Merilä, 1998; Orell and Ojanen, 1980; Slagsvold and Lifjeld, 1989). Hence, breeding, migration and moult strategies can be intimately linked in many avian species.

Biomechanical considerations are intrinsic in determining the relative costs of these different strategies, and so are important in mediating life-history trade-offs. For example, moult could overlap with breeding (or migration) in species that have short rounded wings, as the aerodynamic cost of wing gaps may be relatively small for species with low aspect ratio (Hedenström and Sunada, 1999). Also, wing gaps may be smaller in species with short, rounded wings, as there is more overlap among neighbouring feathers than in species with longer, more pointed wings. Slow moulting species with short rounded wings may be able to minimize the costs of moult and, therefore, have more flexibility to overlap moult with periods of breeding or migration. These observations could explain why species such as the dunlin *Calidris alpina* moult during their migration (Holmgren *et al.*, 1993).

Many large soaring or gliding birds have wingtips with separated primary feathers. The geometry of these wingtips is critical in determining the structure of the wing's vortex wake, and therefore the drag. It is to be expected that loss of primaries in species with separated wingtips could be aerodynamically more costly than for birds with closed wingtips. Not only will the gaps in the wing be larger for birds with separated primaries, but these species will also lose (to some degree) the benefit of possessing wingtip slots, which will result in a relative increase in induced drag (Tucker, 1993). In addition, mechanical aerodynamic loads must be redistributed over the remaining feathers, increasing the incidence of abrasion and wear. Hence, biomechanical factors may constrain such species to slow moult in which only one feather is missing from the wingtip at any one time: Harris hawks display this form of slow moult sequence (Tucker, 1991), which is typical of raptors. Vultures are commonly observed flying with primaries missing (*Figure 1(a)*), indicating a very slow moult (Fischer, 1962).

Biomechanically derived hypotheses may also help explain natural variation in moult patterns. For example, Laysan albatrosses show an incomplete primary feather moult, but the most commonly replaced feathers are the outer primaries (Langston and Rohwer, 1995). These are the longest primaries and, hence, are the most energetically costly feathers to regrow (there is more feather to replace). So why moult the longest feathers in preference to shorter inner primaries? There are three mechanical explanations. First, distal feathers may be more likely to become abraded or damaged than proximal feathers, as the distal feathers form the wingtip. Hence, these feathers may need to be replaced more often. Second, loss of aerodynamic function of outer primaries during non-moult periods may be more costly than loss of function in inner primaries. So even if abrasion rates were the same across the wing, it may be more important to replace distal feathers than proximal feathers for flight mechanics reasons. Third, a gap created during moult at the wingtip (i.e. by shedding of distal feathers) may be aerodynamically less costly than a gap at a more proximal section of the wing (Hedenström and Sunada, 1999). For this reason replacing outer primaries may be mechanically less costly than replacing inner primaries.

The data that we have presented and reviewed in this chapter further support the life-history perspective that we advocate. In natural moult, birds appear to undergo several adaptations that reduce the flight costs of missing feathers from the wing. The most notable of these is a loss of body mass. Regulating a lower body mass during moult will impose its own suite of costs and benefits (see Witter and Cuthill, 1993). Two of the most obvious costs of reduced mass may be an increased probability of starvation (which has obvious fitness consequences) and also increased nutritional stress during moult, which is known to increase the occurrence of deformities and abnormalities in regrowing feathers (e.g. Swaddle and Witter, 1994; see below), which are also likely to have fitness consequences. Hence, although birds appear to reap flight benefits from a reduced mass during moult, there will also be costs and, ultimately, constraints to this mass loss, all of which can only be fully interpreted by adopting a life-history approach. Experiments in which moult is simulated may appear to isolate specific biomechanical or behavioural aspects of the problem; our comparison of aerodynamic responses to simulated and natural moult in starlings indicates that the response to simulation of moult for which the bird is unprepared induces abnormal behaviour, approaching the limits of aerodynamic performance. We advocate caution in experiments employing artificial manipulation of wing or tail feathers to simulate natural inter- or intra-individual morphological variation.

A possible integrated approach to study many of the costs and benefits associated with moult is in terms of energetics (as described earlier). The increase in wingbeat amplitude and wingbeat frequency observed during natural moult are bound to impose an increased physiological and energetic burden on the birds. Not only is the wingtip moving faster, but it is also moving further. In terms of flight, these responses help to maintain take-off performance at pre-moult levels, but the costs of these kinematic changes may be difficult to ascertain without measuring energetics. This form of study also needs to be integrated with knowledge of physiological and anatomical constraints of muscle, tendon and joint operation during moult. It is possible that these are altered by moult, or that birds do not perform maximally when outside moult periods. Once we have gained a more complete understanding of the energetic costs and constraints imposed by both the direct physiological implications and also the indirect biomechanical and behavioural consequences of moult, these elements can be combined with existing models of moult energetics. Without incorporating such elements we will not be able to fully explain the adaptive radiation of moult parameters or the interaction of moult with other important periods of the avian annual cycle, such as breeding and migration.

Studying the energetic cost of various elements of moult could create a number of methodological difficulties. Implicit throughout our discussion we have assumed that birds trade-off costs with benefits, and there is no reason to think that birds would not do this in experimental conditions, and would even alter the dynamics of these trade-offs among experimental protocols. Studies using free-flying birds could be limited as birds could compensate, energetically, by shifting behavioural patterns and reducing energy expended in particular behaviours (as was indicated explicitly by Swaddle and Witter (1997)). Hence, we would need to know the energetic implications of all behaviours exhibited by birds during the experiment and also the amount of time spent performing each of these behaviours. In most cases this would be an onerous (and probably unfeasible) task. Conversely, bringing birds into captive conditions in which their behaviour can be monitored more closely or their environment controlled to reduce confounding environmental factors, also poses problems. The studies reported here are limited in that we do not know, ultimately, if birds can trade-off any loss of take-off performance with any other part of their behavioural repertoire. We also do not know whether birds' motivation to escape from an experimenter in an enclosed aviary is the same as the performance birds would show in a real predatory event. What we suggest is the explicit integration of field observations and controlled laboratory experimentation. This is something that many behavioural ecologists are used to but appears less prevalent in the biomechanical literature, as birds often have to be in controlled conditions to give accurate data. Hence, not only can biomechanics make substantial contributions to the study of behaviour, but also behavioural ecological approaches can be incorporated into biomechanical studies to increase the ecological and evolutionary relevance of any data that are collected.

In this chapter we hope to have provided some initial ideas and empirical evidence for the importance of biomechanics to the moult tactics and behaviour of birds. Crucial to our arguments are identification of biomechanical constraints acting during moult, and also quantification of the mechanical costs and benefits of moult. We have discussed the aerodynamic consequences of moult at length, but there may be additional costs that should also be incorporated. These include assessment of the thermoregulatory costs of feather loss. This should be studied not only in terms of feather loss, but also in terms of the physiological alterations and demands of natural moult. As water requirements are greatly elevated during moult, there may be significant thermoregulatory consequences independent of the insulatory effects of plumage loss. Other factors to be considered are water repellence (which will affect not only thermoregulation but also buoyancy) and also alteration of the appearance of the plumage in terms of visual communication. The appearance of plumage colours that are derived from dietary sources (e.g. coloration produced by carotenoids (Gray, 1996)) is mediated by moult, and the coloration of such plumage areas can have profound influences on natural and sexual selection processes (e.g. Hill, 1990). This latter issue does not solely apply to gross colour or morphological changes observed in birds that switch between nuptial and overwintering plumage, but also to more subtle changes in structural colours, which could be influenced by feather wear and ultrastructural properties of feathers. There are also numerous studies that could be performed to assess biomechanical constraints acting during moult. It is possible that muscle, tendon and joint functional limits are different during moult because of the gross physiological changes that birds experience during this period.

A life-history approach also demands that we consider the long-term effects of moult. These could include annual alteration of wing form, such as changes in wing dimensions (e.g. aspect ratio and wingtip shape). These are factors that are known to influence flight costs (Lockwood *et al.*, 1998; Norberg, 1990; Pennycuick, 1975; Rayner, 1988), and so will impinge on numerous behavioural, energetic and physiological traits. Conditions during moult have also been demonstrated to affect the left–right symmetry of growing feathers (i.e. fluctuating asymmetry (Swaddle and Witter, 1994, 1998)). Changes in asymmetry of feathers have been demonstrated to influence a range of important behaviours, such as angle of escape take-off (Swaddle, 1997), speed of take-off (Swaddle *et al.*, 1996), aerial manoeuvrability and agility (Evans *et al.*, 1994; Swaddle and Witter, 1998; Thomas, 1993), level-flight speed (Swaddle, 1997; Thomas, 1993) and mate preferences (Swaddle and Cuthill, 1994). All of these behaviours are likely to have a direct influence on fitness and survival. Environmental conditions during moult may also influence the overall condition and performance of feathers, hence influencing flight, abrasion and breakage resistance, thermoregulation and water repellence.

It is important also to take account of the condition of birds before moult. For example, Laysan albatrosses with a higher parasitic load of oesophageal nematodes replaced fewer feathers in their moult than those with a relatively lower number of parasites (Langston and Hillgarth, 1995). Hence, pre-moult condition may place constraints on moult, which may in turn influence behaviour and survival. Condition of feathers before moult is also an important consideration. Williams *et al.*, (unpublished) explicitly demonstrated that the flight costs of bearing year-old feathers can be as significant as the flight costs of moult itself. Future studies could include assessment of pre-moult feather condition in terms of a range of physical and mechanical properties (e.g. abrasion, hardness, stiffness, thermoregulation, water repellence, visual appearance). These properties may vary among species and within individuals, and may help explain the timing of feather replacement. For example, species occupying harsh environments and that experience high levels of feather abrasion may have to moult more than once a year.

The preceding discussion has indicated the importance of moult to most birds and, in particular, that moult can have profound life-history influences, including indirect influences on other life-history traits (such as breeding, migration and overwintering). Biomechanical costs and constraints are important elements of the factors that shape moult and so will have life-history implications. Therefore, we urge evolutionary biologists to consider and quantify the mechanical effects of moult so we can achieve a better understanding of the vast array of moult parameters observed in nature.

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References

Alatalo, R.V., Gustafsson, L. and Lundberg, A. (1984) Why do young passerine birds have shorter wings than older birds? *Ibis* 126: 410–415.

Ankney, C.D. (1979) Does the wing molt cause nutritional stress in Lesser Snow Geese? *Auk* 96: 68–72.

Ashmole, N.P. (1963) Molt and breeding in populations of the Sooty Tern *Sterna fuscata*. *Postilla Yale Peabody Mus.* 76: 1–18.

Ashmole, N.P. (1965) Adaptive variation in the breeding regime of a tropical sea bird. *Proc. Natl Acad. Sci. USA* 53: 311–318.

Austin, J.E. and Fredrickson, L.H. (1987) Body and organ mass and body composition of post-breeding female Lesser Scaup. *Auk* 104: 694–699.

Bährmann, U. (1964) Über die Mauser des europäischen Stars *Sturnus vulgaris*. *Zool. Abh. Dresden* 27: 1–9.

Bensch, S. and Grahn, M. (1993) A new method for estimating individual speed of molt. *Condor* 95: 305–315.

Biebach, H. (1998) Phenotypic organ flexibility in Garden Warblers *Sylvia borin* during long-distance migration. *J. Avian Biol.* 29: 529–535.

Blackmore, F.H. (1969) The effect of temperature, photoperiod and molt on the energy requirements of the House Sparrow, *Passer domesticus*. *Comp. Biochem. Physiol.* 30: 433–444.

Boel, M. (1929) Scientific studies of natural flight. *Trans. Am. Soc. Mech. Engrs* 51: 217–242.

Brown, R.E. and Saunders, D.K. (1998) Regulated changes in body mass and muscle mass in molting Blue-winged Teal for an early return to flight. *Can. J. Zool.* 76: 26–32.

Brown, R.H.J. (1963) The flight of birds. *Biol. Rev. Cambridge Philos. Soc.* 38: 460–489.

Chai, P. (1997) Hummingbird hovering energetics during moult of primary flight feathers. *J. Exp. Biol.* 200: 1527–1536.

Chilgren, J.D. (1975) Dynamics and bioenergetics of postnuptial molt in captive White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). PhD thesis, Washington State University, Pullman.

Clement, H. and Chapeaux, E. (1927) Quelques modifications expérimentales des surfaces portantes du pigeon et leurs effets sur le vol. *C. R. Assoc. Fr. Avanc. Sci.* 50: 415–416.

Cresswell, W. (1993) Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. *Anim. Behav.* 46: 609–611.

DeGraw, W.A., Kern, M.D. and King, J.R. (1979) Seasonal changes in the blood composition of captive and free-living White-crowned Sparrows. *J. Comp. Physiol.* 129: 151–162.

Dhondt, A.A. (1973) Postjuvenile and postnuptial moult in a Belgian population of Great Tits, *Parus major*, with some data on captive birds. *Gerfaut* 63: 187–209.

Dhondt, A.A. & Smith, J.N.M. (1980) Postnuptial molt of the Song Sparrow on Mandarte Island in relation to breeding. *Can. J. Zool.* 58: 513–520.

Dial, K.P. (1992) Activity patterns of the wing muscles of the pigeon (*Columba livia*) during different modes of flight. *J. Exp. Zool.* 262: 357–373.

Dial, K.P. and Biewener, A.A. (1993) Pectoralis muscle force and power output during different modes of flight in pigeons (*Columba livia*). *J. Exp. Biol.* 176: 31–54.

Dietz, M.W., Dann, S. and Masman, D. (1992) Energy requirements for molt in the Kestrel, *Falco tinnunculus*. *Physiol. Zool.* 65: 1217–1235.

Dol'nik, V.R. (1965) Bioenergetics of the molts of fringillids as adaptations to migration. *Nov. Ornithol.* 4: 124–126 [In Russian].

Dol'nik, V.R. (1967) Annual cycles of the bioenergetical adaptations for life condition in some passerines. *Dokl. Akad. Nauk SSSR* 40: 115–163 [In Russian].

Driver, E.A. (1981) Hematological and blood chemical values of Mallard, *Anas p. platyrhynchos*, drakes before, during and after remige [sic] moult. *J. Wildl. Dis.* 17: 413–421.

Drovetski, S.V. (1996) Influence of the trailing-edge notch on flight performance of galliforms. *Auk* 113: 802–810.

Earnst, S.L. (1992) The timing of wing molt in Tundra Swans: energetic and non-energetic constraints. *Condor* 94: 847–856.

Evans, M.R., Martins, T.L.F. and Haley, M. (1994) The asymmetrical cost of tail elongation in red-billed streamertails. *Proc. R. Soc. Lond. Ser. B* 256: 97–103.

Feare, C. (1984) *The Starling*. Oxford University Press, Oxford.

Fischer, W. (1962) *Die Geier*. Franckh'sche Verlag, Stuttgart.

Francis, I.S., Fox, A.D., McCarthy, J.P. and McKay, C.R. (1991) Measurement and moult of the Lapland Bunting *Calcarius lapponicus* in West Greenland. *Ringing Migr.* 12: 28–37.

Furness, R.W. (1988) Influences of status and recent breeding experience on the moult strategy of the yellow-nosed albatross *Diomedea chlororhynchos*. *J. Zool.* 215: 719–727.

Gatesy, S.M. and Dial, K.P. (1993) Tail muscle activity patterns in walking and flying pigeons (*Columba livia*). *J. Exp. Biol.* 176: 55–76.

Ginn, H.B. and Melville, D.S. (1983) *Moult in Birds*. British Trust for Ornithology, Tring.

Gray, D.A. (1996) Carotenoids and sexual dichromatism in North American passerine birds. *Am. Nat.* 148: 453–480.

Grubb, T.C. and Greenwald, L. (1982) Sparrows and a bushpile: foraging responses to different combinations of predation risk and energy costs. *Anim. Behav.* 30: 637–640.

Harris, M.P. (1971) Ecological adaptations to moult in some British gulls. *Bird Study* 18: 113–118.

Haukioja, E. (1971a) Summer schedule of some subarctic passerine birds with reference to post-nuptial moult. *Rep. Kevo. Subarctic Res. Stat.* 7: 60–69.

Haukioja, E. (1971b) Flightlessness in some moulting passerines in Northern Europe. *Ornis fennica* 48: 13–21.

Hedenström, A. (1998) The relationship between wing area and raggedness during moult in the willow warbler and other passerines. *J. Field Ornithol.* 69: 103–108.

Hedenström, A. and Alerstam, T. (1992) Climbing performance of migratory birds as a basis for estimating limits for fuel carrying capacity and muscle work. *J. Exp. Biol.* 164: 19–38.

Hedenström, A. and Sunada, S. (1999) On the aerodynamics of moult gaps in birds. *J. Exp. Biol.* 202: 67–76.

Hemborg, C. and Lundberg, A. (1998) Costs of overlapping reproduction and moult in passerine birds: an experiment with the pied flycatcher. *Behav. Ecol. Sociobiol.* 43: 19–23.

Hemborg, C. and Merilä, J. (1998) A sexual conflict in collared flycatchers, *Ficedula albicollis*: early male moult reduces female fitness. *Proc. R. Soc. Lond. Ser. B* 265: 2003–2007.

Hill, G.E. (1990) Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Anim. Behav.* 40: 563–572.

Holmgren, N. and Hedenström, A. (1995) The scheduling of moult in migratory birds. *Evol. Ecol.* 9: 354–368.

Holmgren, N., Ellgren, H. and Pettersson, J. (1993) The adaptation of moult pattern in migratory Dunlins *Calidris alpina*. *Ornis Scand.* 24: 21–27.

Jehl, J.R. (1987) Moult and moult migration in a transequatorial migrating shorebird: Wilson's phalarope. *Ornis Scand.* 18: 173–178.

Jenni, L. and Winkler, R. (1994) *Moult and Ageing of European Passerines*. Academic Press, London.

Kahlert, H., Fox, A.D. and Ettrup, H. (1996) Nocturnal feeding in moulting Greylag Geese *Anser anser*—an anti-predator response? *Ardea* 84: 15–22.

King, J.R. (1980) Energetics of avian moult. *Acta Int. Ornithol. Congr.*, 27: 312–317.

Kullberg, C., Jakobsson, S. and Fransson, T. (1998) Predator-induced take-off strategy in Great Tits (*Parus major*). *Proc. R. Soc. Lond. Ser. B* 265: 1659–1664.

Langston, N. and Hillgarth, N. (1995) Molt varies with parasites in Laysan albatrosses. *Proc. R. Soc. Lond. Ser. B* 261: 239–243.

Langston, N.E. and Rohwer, S. (1995) Unusual patterns of incomplete primary molt in Laysan and black-footed albatrosses. *Condor* 97: 1–19.

Langston, N.E. and Rohwer, S. (1996) Molt-breeding tradeoffs in albatrosses: life history implications for big birds. *Oikos* 76: 498–510.

Lazarus, J. and Symonds, M. (1992) Contrasting effects of protective and obstructive cover on avian vigilance. *Anim. Behav.* 43: 519–521.

Lima, S. (1993) Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bull.* 105: 1–47.

Lindström, Å., Visser, G.H. and Daan, S. (1993) The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiol. Zool.* 66: 490–510.

Lockwood, R., Swaddle, J.P. and Rayner, J.M.V. (1998) Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *J. Avian Biol.* 29: 273–292.

Marden, J.H. (1987) Maximum lift production during take-off in flying animals. *J. Exp. Biol.* 130: 235–258.

Marden, J.H. (1994) From damselflies to pterosaurs: how burst and sustainable flight performance scale with size. *Am. J. Physiol.* 266: R1077–R1084.

Mather, M.H. and Robertson, R.J. (1993) Honest advertisement in flight displays of bobolinks (*Dolichonyx oryzivorus*). *Auk* 109: 869–873.

Mauck, R.A. and Grubb, T.C.J. (1995) Petrel parents shunt all experimentally increased reproductive costs to their offspring. *Anim. Behav.* 49: 999–1008.

Morton, G.A. and Morton, M.L. (1990) Dynamics of postnuptial molt in free-living mountain White-crowned Sparrows. *Condor* 92: 813–828.

Murphy, M.E. (1996) Energetics and nutrition of molt. In: *Avian Energetics and Nutritional Ecology* (ed. C. Carey). Chapman and Hall, New York, pp. 158–198.

Murphy, M.E. and King, J.R. (1992) Energy and nutrient use during moult by White-crowned sparrows *Zonotrichia leucophrys gambelii*. *Ornis scand.* 23: 304–313.

Murphy, M.E., King, J.R. and Taruscio, T.G. (1990) Amino acid composition of feather barbs and rachises in three species of pygoscelid penguins: nutritional implications. *Condor* 92: 913–921.

Murphy, M.E., Taruscio, T.G., King, J.R. and Truitt, S.G. (1992) Do molting birds renovate their skeletons as well as their plumages—osteoporosis during the annual molt in sparrows. *Can. J. Zool.* 70: 1109–1113.

Murton, R.K. and Westwood, N.J. (1977) *Avian Breeding Cycles*. Clarendon Press, Oxford.

Nachtigall, W. and Rothe, H.J. (1982) Nachweis eines 'clap-and-fling-Mechanismus' bei der im Windkanal fliegenden Haustaube. *J. Ornithol* 123: 439–443.

Nayler, J.L. and Simmons, L.F.G. (1921) A note relating to experiments in a wind channel with an alsatian swift. *ARC Rep. Memo.* 708.

Newton, I. (1966) The moult of the bullfinch *Pyrrhula pyrrhula*. *Ibis* 108: 41–67.

Noguès, P. and Richet, C.R. (1910) Expériences sur le vol des pigeons à ailes rognées. *Trav. Inst. E.J. Marey* 2: 217–224.

Norberg, R.Å. and Norberg, U.M. (1971) Take-off, landing, and flight speed during fishing flights of *Gavia stellata* (Pont.). *Ornis Scand.* 2: 55–67.

Norberg, U.M. (1975) Hovering flight in the pied flycatcher. In: *Swimming and Flying in Nature* (eds T.Y.-T. Wu, C.J. Brokaw and C. Brennen). Plenum, New York, pp. 869–880.

Norberg, U.M. (1990) *Vertebrate Flight*. Springer, Heidelberg.

Orell, M. and Ojanen, M. (1983) Overlap between breeding and moulting in the great tit *Parus major* and willow tit *P. montanus* in northern Finland. *Ornis Scand.* 11: 43–49.

Page, G. and Whitacre, D.F. (1975) Raptor predation on wintering shorebirds. *Condor* 77: 73–83.

Payne, R.B. (1972) Mechanics and control of moult. In: *Avian Biology*, Vol. 2 (eds D.S. Farner & J.R. King). Academic Press, New York, pp. 103–155.

Pennycuick, C.J. (1969) The mechanics of bird migration. *Ibis* 111: 525–556.

Pennycuick, C.J. (1975) Mechanics of flight. In: *Avian Biology*, Vol. 5 (eds D.S. Farner & J.R. King). Academic Press, New York, pp. 1–75.

Piersma, T. (1988) Breast muscle atrophy and constraints on foraging during flightless periods of wing moulting in the great crested grebes. *Ardea* 76: 96–106.

Piersma, T. (1998) Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight? *J. Avian Biol.* 29: 511–520.

Prince, P.A., Rodwell, S., Jones, M. and Rothery, P. (1993) Moult in Black-browed and Grey-headed Albatrosses *Diomedea melanophris* and *D. chrysostoma*. *Ibis* 135: 121–131.

Prince, P.A., Weimerskirch, H., Huin, N. and Rodwell, S. (1997) Molt, maturation of plumage and ageing in the wandering albatross. *Condor* 99: 58–72.

Prior, N.C. (1984) Flight energetics and migration performance in swans. Ph.D. Thesis, University of Bristol.

Rayner, J.M.V. (1979) A new approach to animal flight mechanics. *J. Exp. Biol.* 80: 17–54.

Rayner, J.M.V. (1986) Vertebrate flapping flight mechanics and aerodynamics, and the evolution of flight in bats. In: *Biona Report 5, Bat Flight—Fledermausflug* (ed. W. Nachtigall), Gustav Fischer, Stuttgart, pp. 27–74.

Rayner, J.M.V. (1988) Form and function in avian flight. *Curr. Ornithol.* 5: 1–66.

Rayner, J.M.V. (1991) Avian flight evolution and the problem of *Archaeopteryx*. In: *Biomechanics in Evolution. Seminar Series of the Society for Experimental Biology*, Vol. 36. (eds J.M.V. Rayner and R.J. Wootton). Cambridge University Press, Cambridge, pp. 183–212.

Rayner, J.M.V. (1993) On aerodynamics and the energetics of vertebrate flapping flight. In: *Fluid Dynamics in Biology. Contemporary Maths*, Vol. 141 (eds A.Y. Cheer and C.P. van Dam). American Mathematical Society, Providence, RI, pp. 351–400.

Rayner, J.M.V. (1995) Flight mechanics and constraints on flight performance. *Israel J. Zool.* 41: 321–342.

Rayner, J.M.V. (1999) Estimating power curves for flying vertebrates. *J. Exp. Biol.* 202: 3449–3461.

Rayner, J.M.V. & Ward, S. (1999) On the power curves of flying birds. In: *Proc. 22nd Int. Ornithol. Congr., Durban* (eds N.J. Adams and R.H. Slotow). Johannesburg: Bird Life South Africa, pp. 1786–1809.

Salomonsen, F. (1968) The moult migration. *Wildfowl* 19: 5–24.

Scholey, K.D. (1983) Developments in vertebrate flight. Ph.D. Thesis, University of Bristol.

Slagsvold, T. and Dale, S. (1996) Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced molt. *Ecology* 77: 462–471.

Slagsvold, T. and Lijfeld, J.T. (1988) Ultimate adjustment of clutch size to parent feeding capacity in a passerine bird. *Ecology* 69: 1918–1922.

Slagsvold, T. and Lifjeld, J.T. (1989) Hatching asynchrony in birds: the hypothesis of sexual conflict over parental investment. *Am. Nat.* 134: 239–253.

Slagsvold, T. & Lijfeld, J.T. (1990) Influence of male and female quality on clutch size in tits (*Parus* spp.). *Ecology* 71: 1258–1266.

Spedding, G.R., Rayner, J.M.V. and Pennycuick, C.J. (1984) Momentum and energy in the wake of a pigeon (*Columba livia*) in slow flight. *J. Exp. Biol.* 111: 81–102.

Stresemann, E. and Stresemann, V. (1966) Die Mauser der Vögel. *J. Ornithol.* 107: 3–448.

Sullivan, J.O. (1965) 'Flightlessness' in the Dipper. *Condor* 67: 535–536.

Swaddle, J.P. (1997) Within-individual changes in developmental stability affect flight performance. *Behav. Ecol.* 8: 601–604.

Swaddle, J.P. and Cuthill, I.C. (1994) Female zebra finches prefer males with symmetric chest plumage. *Proc. R. Soc. Lond. Ser. B* 258: 267–271.

Swaddle, J.P. and Lockwood, R. (1998) Morphological adaptations to predation risk in passerines. *J. Avian Biol.* 29: 172–176.

Swaddle, J.P. and Witter, M.S. (1994) Food, feathers and fluctuating asymmetries. *Proc. R. Soc. Lond. Ser. B* 255: 147–152.

Swaddle, J.P. and Witter, M.S. (1997) The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. *Can. J. Zool.*

Swaddle, J.P. and Witter, M.S. (1998) Cluttered habitats reduce wing asymmetry and increase flight performance in European starlings. *Behav. Ecol. Sociobiol.* 42: 281–287.

Swaddle, J.P., Witter, M.S., Cuthill, I.C., Budden, A. and McCowen, P. (1996) Plumage condition affects flight performance in starlings: implications for developmental homeostasis, abrasion and moult. *J. Avian Biol.* 27: 103–111.

Swaddle, J.P., Williams, E.V. and Rayner, J.M.V. (1999) The effect of simulated flight feather moult on escape take-off performance in starlings. *J. Avian Biol.* 30: 351–358.

Taruscio, T.G. and Murphy, M.E. (1995) 3-Methylhistidine excretion by molting and non-molting sparrows. *Comp. Biochem. Physiol.* 111A: 397–403.

Thomas, A.L.R. (1993) The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners. *Proc. R. Soc. Lond. Serv. B* 254: 181–189.

Tucker, V. A. (1991) The effect of moulting on the gliding performance of a Harris' hawk (*Parabuteo unicinctus*). *Auk* 108: 108–113.

Tucker, V.A. (1993) Gliding birds—reduction of induced drag by wing tip slots between the primary feathers. *J. Exp. Biol.* 180: 285–310.

Verbeek, N.A.M. and Morgan, J.L. (1980) Removal of primary remiges and its effect on the flying ability of the glaucous-winged gull. *Condor* 82: 224–226.

Ward, P. and D'Cruz, D. (1968) Seasonal changes in the thymus gland of a tropical bird. *Ibis* 110: 203–205.

Weibel, E.R. (1984) *The Pathway for Oxygen*. Harvard University Press, Harvard, MA.

Witter, M.S. & Cuthill, I.C. (1993) The ecological costs of avian fat storage. *Philos. Trans. R. Soc. Lond., Ser. B* 340: 73–90.

Witter, M.S., Cuthill, I.C. and Bonser, R.H.C. (1994) Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Anim. Behav.* 48: 201–222.