**REVIEW**

# Effects of wing damage and moult gaps on vertebrate flight performance

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## ABSTRACT

Vertebrates capable of powered flight rely on wings, muscles that drive their flapping and sensory inputs to the brain allowing for control of the motor output. In birds, the wings are formed of arrangements of adjacent flight feathers (remiges), whereas the wings of bats consist of double-layered skin membrane stretched out between the forelimb skeleton, body and legs. Bird feathers become worn from use and brittle from UV exposure, which leads to loss of function; to compensate, they are renewed (moulted) at regular intervals. Bird feathers and the wings of bats can be damaged by accident. Wing damage and loss of wing surface due to moult almost invariably cause reduced flight performance in measures such as take-off angle and speed. During moult in birds, this is partially counteracted by concurrent mass loss and enlarged flight muscles. Bats have sensory hairs covering their wing surface that provide feedback information about flow; thus, wing damage affects flight speed and turning ability. Bats also have thin, thread-like muscles, distributed within the wing membrane and, if these are damaged, the control of wing camber is lost. Here, I review the effects of wing damage and moult on flight performance in birds, and the consequences of wing damage in bats. I also discuss studies of life-history trade-offs that make use of experimental trimming of flight feathers as a way to handicap parent birds feeding their young.

KEY WORDS: Bird flight, Bat flight, Wing wear, Aerodynamics, Kinematics, Drag

## Introduction

Supported by aerodynamic theory, the wings and flight performance of vertebrates are often provided as examples of the efficacy of natural selection to achieve near-optimal functional design. Vertebrates have evolved powered flight three times, i.e. in birds, bats and the extinct pterosaurs. Because of their ability to fly at relatively low cost of transport compared with animals that walk or run (Schmidt-Nielsen, 1992), birds and bats have been very successful in colonizing all continents and biomes (except Antarctica in the case of bats), using flight in their everyday life and performing seasonal migrations between continents. However, the wings of birds and bats can be damaged from accidental interaction with environmental structures and as a result of predator attacks, leading to the loss or breakage of feathers or ruptures in the skin membrane. Feather deformations can have pathological or developmental causes compromising their function. In birds, natural wing gaps occur temporarily during the seasonally recurring moult, which is the periodic replacement of old and worn feathers that

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would otherwise compromise functionality with time. During the moult period, the synthesis of new feathers and the missing wing area are likely to affect the birds' performance in different ways, which in turn may affect the actual moult strategy (timing, intensity and sequence) itself. Because wings are used to fly in situations that are essential for survival, such as during seasonal migrations, when searching for and transporting food to young and during display, we may expect compensatory mechanisms to alleviate the negative effects of wing damage and moult.

Moult gaps are near symmetric, and their effect will mainly be loss of flight performance; in contrast, wing damage often leads to an asymmetric effect. Damage to the wings of flying vertebrates is likely to be associated with reduced function, where the position and extent of damage alter the effect. However, as accidental damage usually occurs at unpredictable times, it is difficult to conduct systematic studies of its effects. More subtle damage, as experienced through the continuous wear and tear of flight feathers and UV-light exposure, may cause a more predictable functional decline that eventually leads to necessary feather renewal (moult). There are only a few studies on the continuous progression of wear of feather properties in birds and how this continuous process influences flight performance (Hedenström, 2003; Williams and Swaddle, 2003). Regarding the effects of moult on flight performance, there are a lot more studies published, probably because moult occurs at predictable times of the year (Ginn and Melville, 1983; Svensson and Hedenström, 1999). To complement studies on natural moult gaps, researchers have used experimentally created wing gaps in combination with flight performance assays (e.g. Swaddle et al., 1996; Swaddle and Witter, 1997, Lind, 2001, Bridge, 2003; Tomotani et al., 2017).

Bats differ from birds in the sense that they do not undergo periodic moults, but instead commit to continuous maintenance and repair of the skin membranes. There are therefore fewer studies available on the effects of wing gaps and damage on bat flight, but considering the superficial similarity of wing planform and body size between birds and bats (Hedenström et al., 2009), any major effects found in birds should also apply to bats. In this Review, I define 'wing damage' as such states that arise from accidental loss of feathers (birds) or holes/ruptures in skin membranes (bats). I do not consider wing damage, as often referred to by veterinarians, that arises as a result of a pathological condition or abnormal development (Fig. 1; Ng et al., 2012; Ng and Wen-Hsiung, 2018) because such conditions are rarely observed in wild animals but are of great concern in poultry science. In this Review, I will outline natural causes of wing wear and wing gaps and their effects on flight performance and related ecological consequences in birds and bats, as well as providing an aerodynamic background and considering experimental tests of flight performance when wing morphology is compromised. When reviewing the literature, it became clear that existing knowledge about vertebrate flight performance in relation to wing wear, wing damage and moult gaps is rather limited.

## Glossary

**Actuator disk**
An imaginary disk of diameter equal to the wing span of the flyer, which generates momentum into the downstream wake at a rate that balances the weight.

**Aerodynamic span efficiency**
A correction factor that represents the change in drag with lift of a finite wing as compared with the ideal wing of the same aspect ratio and an elliptic lift distribution associated with a uniform downwash. The ideal span efficiency $e=1$.

**Aerofoil**
A section of a wing (profile) that produces circulation in its vicinity without itself rotating; circulation is a measure of the intensity of an irrotational vortex, defined as the product of the circumference and tangential velocity of the vortex.

**Aspect ratio**
A non-dimensional wing shape index calculated as the wing span divided by the mean wing chord, or wing span squared divided by wing area.

**Downwash**
The downward-deflected airflow caused by the aerodynamic action of an aerofoil or wing.

**Effective aspect ratio**
Geometric aspect ratio multiplied by the span efficiency, $0<e<1$, for non-ideal wings.

**Fault bars**
Impairments of the feather, often caused by periods of malnutrition during feather growth.

**Lift**
The force that is created by the action of an aerofoil normal to the flow; lift is directly proportional to the circulation.

**Lift curve slope**
A measure of how rapidly a wing generates lift with change in the angle of attack; angle of attack is the angle between the chord line, a line from the leading edge to the trailing edge, and the relative flow.

**Lift:drag ratio**
A measure of flight efficiency and calculated as the ratio between lift and drag. For an animal in gliding flight it is identical to the ratio between forward and sink speed.

**Melanin**
A group of natural pigments in keratinous materials such as feathers, responsible for dark coloration.

**Profile drag**
The drag of the wing that arises as a result of the combined effect of pressure and skin friction drag; drag is aligned with the direction of flow.

**Spanwise camber (anhedral)**
The downward angle from the horizontal of the wings; in front view, the wings are held as a shallow inverted 'V'.

**Vorticity**
Calculated as twice the angular velocity of a fluid element at a point in space or, more formally, the circulation around an infinitesimal circuit divided by the area of that circuit.

**Wing tip slots**
In birds, the horizontal and vertical separation of primaries forming the wing tip, akin to the winglets used on the wing tips of aircrafts to reduce the induced drag.
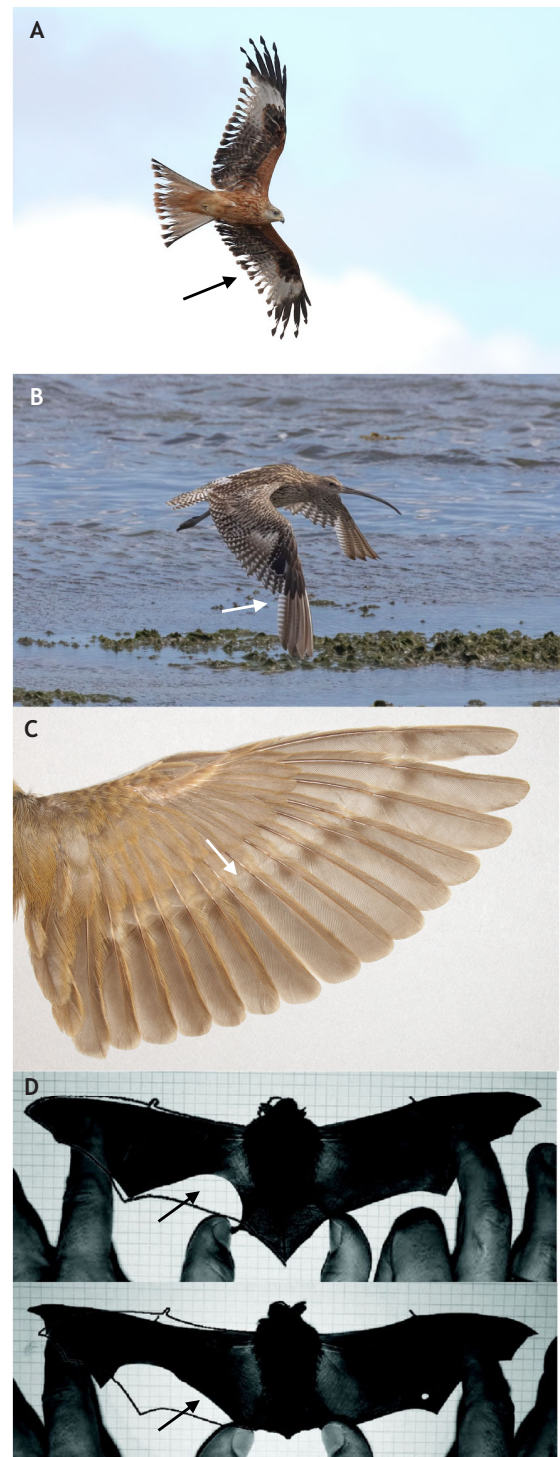


**Fig. 1. Examples of wing deformations, damage and moult in birds and bats.** (A) Deformed flight feathers in red kite (*Milvus milvus*). (B) Moult gap due to the shedding of inner primaries in a curlew (*Numenius arquata*). (C) Fault bars in juvenile marsh warbler (*Acrocephalus palustris*). Feathers are prone to break as a result of fault bars. (D) Asymmetric wing holes in bats, *Myotis albescens* (top) and *Myotis nigricans* (bottom). Structures of interest are indicated by arrows. Image credits: Helen von Holten (A), Clare Slade (B), Yosef Kiat (C), Voigt (2013) (D).

Therefore, by pointing out some of the deficiencies in our knowledge, I hope that this Review will inspire students of biomechanics and ecology to fill those gaps.

## Natural wing wear in birds

After a feather has been formed, it is not maintained other than being preened and having preen wax/oil from the uropygial gland applied. Feathers are exposed to mechanical wear and UV-light, as well as being attacked by feather-eating mites and bacteria. All these factors result in the loss of feather mass (Dawson and Carey, 1976). Feather parts rich in melanin (see Glossary) resist wear better than non-melanic parts, which probably explains why wing tips of, for example, gulls are often dark/black (Bergman, 1982). By filling the space between keratin

strands, melanin granules make feathers harder and therefore also more resistant to mechanical wear from airborne particles and contact with vegetation (Bonser, 1995; Schreiber et al., 2006). Melanic feathers also seem to resist degradation by feather-eating bacteria better than non-melanic feathers (Burtt and Ichida, 2004). In particular, the edges of feather tips become ragged from wear and exposure to UV-light, which – apart from reducing the area – is also likely to compromise overall aerodynamic efficiency because some air will slip through. However, the continuous process of wear and abrasion reduces the quality and functional properties of flight feathers and is ultimately the reason why feathers are replaced during a period of moult (Jenni and Winkler, 2020).

The flexural stiffness of the feather shaft is reduced over time as a consequence of mechanical bending, which occurs in response to the aerodynamic load during each wingbeat cycle; this has been experimentally demonstrated for flight feathers in two species of warblers (Weber et al., 2005). The shaft properties, e.g. the cross-sectional second moment of area, are related to flexural stiffness of single feathers (Weber et al., 2010), but how a worn, yet intact, bird wing performs in relation to the fresh wing is difficult to quantify (but see below).

### Wing damage in birds

Feathers may break from accidental interaction with thorny vegetation or from a successful escape from a close predator encounter. The result is usually loss of a few wing or tail flight feathers; sometimes they break off at fault bars (see Glossary) where they are already weakened (Fig. 1C; Jenni and Winkler, 2020). Feathers that are accidentally lost and replaced outside the usual moult period may be of lower quality than those replaced during moult (de la Hera et al., 2010). Wing damage typically results in asymmetric loss of wing area. When attacked by a predator, birds may eject feathers as an adaptive strategy to create confusion for the attacker, akin to the octopus ejecting ink, but such 'fright moult' usually involves mainly body feathers (Lindström and Nilsson, 1988) and therefore has little effect on subsequent flight performance. There are more subtle forms of wing damage, such as the holes that occur in the vanes of flight feathers that are caused by grazing feather lice (e.g. Möller, 1991a; Stenkewitz et al., 2017) or other agents such as keratinolytic microorganisms (Vágási, 2014). The presence of feather holes affects both acceleration and velocity in barn swallows, *Hirundo rustica*, challenged to fly through a maze (Matyjasiak et al., 2018).

### Wing gaps due to moult in birds

Birds replace feathers periodically by a process called moult, where body and flight feathers are shed and regrown according to a certain sequence. The regrowth of new feathers is an energy-demanding process (Lindström et al., 1993; Buttemer et al., 2020), which therefore rarely overlaps with other energy-demanding periods of the annual cycle, i.e. breeding and migration (Wingfield, 2008). In passerines, the flight feather moult typically starts with the innermost primary and proceeds sequentially towards the wing tip (Stresemann and Stresemann, 1966). Usually, 3–4 feathers are affected simultaneously, which causes a gap whose position slowly moves distally along the wing. When primary moult has reached ~P6–7 (P1 is the innermost feather, P10 is the outermost), the outermost secondary (S1) is shed and moult moves towards the body (S1–S6, S7–S9 being tertials) (Ginn and Melville, 1983). Therefore, at later stages of moult there are two gaps in the wing, one proximal and one distal, and when the outermost primaries forming the wing tip are affected, the wing span becomes temporarily

shortened, and the shape of the wing tip is changed. The wing area lost during moult can be so large that flight capacity is temporarily lost, a common feature in ducks and geese (Owen and Ogilvie, 1979; Sjöberg, 1988; Guillemette et al., 2007). Some species undergo a so-called 'moult migration' to certain moulting areas, where the birds can be flightless relatively safely when moulting (Salomonsen, 1968; Kjellén, 1994). Moult migrations in wildfowl may even be in a different direction to that between the breeding and wintering sites (Salomonsen, 1968), while some passerines may interrupt post-breeding migration to conduct moult (Vigants et al., 2023). Furthermore, some sub-alpine passerines drop so many flight feathers simultaneously that they become near-flightless (Haukioja, 1971). During more 'normal' moult, passerines lose a maximum 10–12% of wing area (Hedenström, 1998), whereas hummingbirds may lose up to 30% (Chai, 1997).

Highly aerial species tend to replace flight feathers slowly, one at a time, to minimize the moult gap and maintain a high flight capacity even during the periods of feather replacement. In common swifts, *Apus apus*, a species that remains airborne continuously throughout the 9–10 month non-breeding period (Hedenström et al., 2016), the moult lasts for about 6 months (De Roo, 1966), which is the entire period spent in the wintering range.

Larger birds such as raptors, albatrosses, storks and vultures also replace flight feathers slowly, even at such a slow rate that one complete moult cycle takes more than a year to complete (Stresemann and Stresemann, 1966; Prince et al., 1993; Langston and Rohwer, 1996; Jenni and Winkler, 2020). In albatrosses, the moult is interrupted to allow breeding, and then resumed the next year to replace the remaining flight feathers, with an apparent interaction between moult and breeding attempts (Langston and Rohwer, 1996).

### Aerodynamics of holey wings

An aerofoil (see Glossary) exposed to a flow at speed $U$ will generate lift, $L$ (see Glossary), according to the formula:

$$L = \frac{1}{2}\rho S U^2 C_L, \tag{1}$$

where $\rho$ is air density, $S$ is wing area and $C_L$ is the lift coefficient. From this equation, it is clear that if wing area is reduced and all other parameters remain equal, there will be a reduction of lift proportional to the loss of wing area. The position of a wing gap also affects the shape of the wing and thereby the lift coefficient, in most cases negatively. An ideal actuator disk (see Glossary) will generate a uniform downwash (see Glossary) to generate lift, where the associated induced drag, $D_{ind}$, is:

$$D_{ind} = \frac{k(m\boldsymbol{g})^2}{q\pi b^2}, \tag{2}$$

where $m$ is body mass, $\boldsymbol{g}$ is acceleration due to gravity, $q$ is dynamic pressure ($0.5U^2$), $b$ is wing span and $k$ is the induced drag factor (Spedding and McArthur, 2010). If moult or damage affects the wings such that the wing span is reduced, as when losing the outermost (longest) primary, the induced drag increases and, consequently, so does the cost of generating lift. The induced drag factor $k=1/e$, where $e$ is the aerodynamic span efficiency (see Glossary) of a finite wing, is 1 for the ideal elliptic lift distribution along the span (Fig. 2A). Any departure from an elliptic lift distribution is associated with reduced $e$ (and increased $k$) and should be reflected in the wake as deviations from a uniform downwash along the span (Fig. 2B).
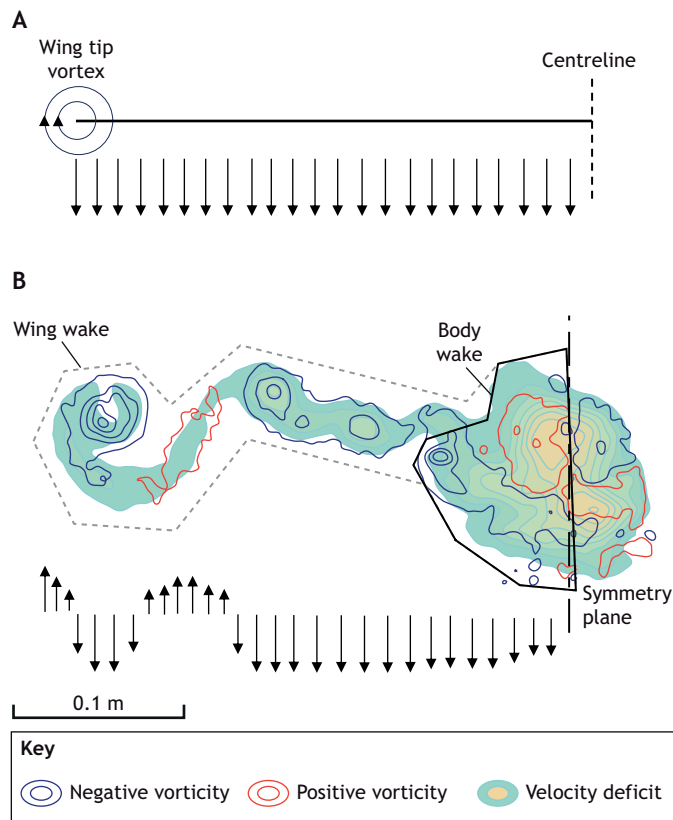
**Fig. 2. Downwash and vortex distributions of ideal and real wings with moult gap.** (A) An ideal wing with elliptic lift distribution generates a uniform downwash distribution (arrows) and a wing tip vortex. The vertical dashed line indicates the centreline through the body. (B) The streamwise vorticity in the wake of a jackdaw (*Corvus monedula*) gliding in a wind tunnel at 7.8 m s$^{-1}$, where moult has been initiated by dropping the four innermost primaries. Left wing and body are shown. The dashed line encircles the region of interest containing all vorticity and streamwise perturbations; the solid black line encircles streamwise perturbations attributed to the body and tail, and the dash-dot vertical line indicates the symmetry plane of the body. Below the vorticity map, arrows indicate the associated downwash distribution, which clearly deviates from the ideal uniform distribution of a planar wing (A). Modified from Klein Heerenbrink and Hedenström (2017).

Using a computational approach, Hedenström and Sunada (1999) evaluated the effect of moult gaps on the aerodynamic properties of wings in relation to wing shape, gap position and size, including two gaps at different positions that may occur at advanced stages of moult. Both gap position and size had negative effects on the lift curve slope (see Glossary), effective aspect ratio (see Glossary) and aerodynamic efficiency. The detrimental effect of moult gaps increased with increasing aspect ratio (see Glossary) when compared with the baseline intact wing (Hedenström and Sunada, 1999).

Strictly, the aerodynamic relationships above apply to steady gliding wings, whereas models of flapping flight are modified versions of fixed wing theory (Pennycuick, 1975; Klein Heerenbrink et al., 2015). Flapping flight involving flexible surface–fluid interaction still defies analytic solution, but with modern experimental approaches, the effects of wing wear, moult gaps and wing damage can provide useful information (Spedding et al., 2003; Klein Heerenbrink and Hedenström, 2017). It is, however, likely that the effects of adjusted wing shapes due to moult and wing damage on flapping flight performance will parallel those

predicted for gliding flight, because gaps due to moult appear to generate similar vortex structures and downwash distribution in flapping flight to that observed in gliding flight (see below).

When it comes to accidental damage of wings, the additional effect of asymmetric force generation occurs, which requires compensatory motor output control. Unilateral wing damage will cause a roll torque; to avoid roll, fruit flies maintain zero roll torque by increasing the stroke amplitude and advancing the timing of span-wise wing rotations at stroke turns, with opposite adjustments to the intact wing, as well as maintaining a constant roll angle towards the damaged wing (Muijres et al., 2017). Birds and bats have more degrees of freedom when it comes to changing the wing planform than insects, such that unilateral wing damage could be compensated for by flexing the intact wing (Thomas, 1993). Hambly et al. (2004) measured the effect of symmetric and asymmetric wing span/area reduction in zebra finches (*Taeniopygia guttata*) by trimming the primaries by 0.5 cm on one wing or by 0.25 cm on both wings. The flight metabolic rate was measured during short flights between perches in an aviary before and after manipulation using the $^{13}$C-labelled bicarbonate technique, and wing-beat frequency was obtained from high-speed video. Wing-beat frequency increased after both manipulations, whereas flight energy cost increased significantly only in birds with symmetric span/area reduction (Hambly et al., 2004; Table 1). How birds and bats adjust for asymmetric wing damage is, however, still little known (but see below about bats).

### Flight performance assays
The effect of variables such as fuel load and wing gaps due to moult or experimentally manipulated gaps on flight performance has been assessed by recording take-off flights. Birds are put on a perch and encouraged to take off by a play-back startle sound or the sudden appearance of a model predator, and the take-off flight trajectory is recorded by high-speed video cameras. Typically, the bird is flying away at an angle, although some experimental set-ups force the bird to make a vertical exit (Tomotani et al., 2018). The results of take-off assays for birds in moult are shown in Table 1 (extended data in Table S1). Generally, the take-off speed, measured as instantaneous speed at some fixed distance away from the perch, is reduced when wing area is reduced, as is the escape flight angle (Table 1; Table S1). For both experimentally inflicted wing gaps and those due to natural moult, measures of flight performance were reduced (Swaddle and Witter, 1997; Lind, 2001), although – after some time – flight performance was restored as a result of adaptive mass loss (Swaddle and Witter, 1997) or compensatory growth of flight muscles (Lind and Jacobsson, 2002). Birds may also partially alleviate the negative effects of wing gaps by changing the angle of attack and by adjusting the feathers neighbouring the gap to minimize the 'holey' area of missing feathers (Tomotani and Muijres, 2019).

### Effects of moult on steady flight performance in birds
Birds that moult all their flight feathers simultaneously lose their flight capacity altogether until the new feathers have regrown, but the majority of birds replace flight feathers sequentially and remain flight capable throughout moult. The question then is to what extent do wing gaps affect flight performance? The available information comes from a few studies opportunistically undertaken with birds trained to fly in wind tunnels that underwent moult (Tucker, 1995; Klein Heerenbrink and Hedenström, 2017).

A study using a moulting Harris's hawk, *Parabuteo unicinctus*, trained to glide in a tiltable wind tunnel before, during and after

**Table 1. The effect of moult and wing damage on flight performance**

| Species | Manipulation | Flight performance | Kinematics | Lift coeff. | Power | Source |
|---|---|---|---|---|---|---|
| *Sturnus vulgaris* | Natural wing damage | Reduced | | | | Swaddle et al., 1996; Williams and Swaddle, 2003 |
| *Sturnus vulgaris* | Simulated moult | Reduced | | | | Swaddle et al., 1996; Swaddle and Witter, 1997 |
| *Hirundo rustica* | Natural wing holes | Reduced | | | | Matyjasiak et al., 2018 |
| *Passer montanus* | Natural moult | No effect | | | | Lind, 2001; Lind and Jacobsson, 2002 |
| *Passer montanus* | Simulated moult | Reduced | | | | Lind, 2001 |
| *Ficedula hypoleuca* | Simulated moult | Reduced | Changed | | | Tomotani et al., 2018; Tomotani and Muijres, 2019 |
| *Taeniopygia guttata* | Simulated span/ area asymmetry | | Changed | | Increased power | Hambly et al., 2004 |
| *Taeniopygia guttata* | Simulated symmetric span/ area reduction | | Changed | | Increased power | Hambly et al., 2004 |
| *Corvus monedula* | Natural moult | | | | $P_{ind}$ increased | Klein Heerenbrink and Hedenström, 2017 |
| *Archilochus colubris* | Natural moult | Reduced | Changed | Reduced | Increased power, reduced efficiency | Chai, 1997; Chai and Dudley, 1999 |
| *Calypte anna* | Natural moult | | | Reduced | Increased power | Achache et al., 2018 |
| *Archilochus alexandri* | Damage | | | | $P_{met}$ increased | Epting, 1980 |
| *Selasphorus sasin* | Moult | | | | $P_{met}$ increased | Epting, 1980 |
| *Selasphorus sasin* | Damage, broken primary | | | | $P_{met}$ increased | Epting, 1980 |
| *Columba livia* | Simulated moult | Increased | Changed | | | Bridge, 2003 |
| *Parabuteo unicinctus* | Natural moult | | | Reduced | $P_{ind}$ increased | Tucker, 1991 |

Flight performance was measured as escape velocity ($U_{esc}$), maximum velocity ($U_{max}$), acceleration, take-off angle and manoeuvrability. Power was measured as induced power ($P_{ind}$), profile power ($P_{pro,et}$), metabolic power ($P_{met}$) and efficiency. Most studies refer to escape flight assays, although a few are from measurements of aerodynamic performance or energy consumption. For detailed information about the various studies, see Table S1.

moult completion showed that the lift:drag ratio (see Glossary), an alternative measure of aerodynamic efficiency, dropped from 10.5 before moult to a minimum 7.2 at peak moult (P5–8 dropped; Tucker, 1991). When moult was completed, the lift:drag ratio was 10.5 again. The lowest lift:drag ratio occurred when the primaries forming the wing tip were missing. In a similar study of a jackdaw (*Corvus monedula*) in gilding flight at different stages of moult, flow visualization showed that the presence of moult gaps affected the vortex wake, so that induced and profile drag (see Glossary) increased, with the result of reduced span efficiency (Klein Heerenbrink and Hedenström, 2017). The position of the wing gap was reflected in the wake as vorticity (see Glossary) of opposite sense to that of the wing tip vortex, hence affecting the downwash distribution. A gap at the inner wing likewise resulted in a shedding of vorticity that reduced efficiency. To partially mitigate the negative effects of moult gaps, the jackdaw reduced the spanwise camber (anhedral; see Glossary), which effectively increased span at the cost of reduced stability (Klein Heerenbrink and Hedenström, 2017). Moult of the primaries forming the wing tip not only reduces the wing span but also compromises their function as 'slots' (see Glossary). Separated wing tips, as seen in many raptors, storks and large passerines, help spread the vorticity shed at the wing tip to reduce drag (Tucker, 1995; Klein Heerenbrink and Hedenström, 2017). Wind tunnel experiments of a pied flycatcher (*Ficedula hypoleuca*) during moult in flapping flight showed gap-related shedding of vorticity similar to that of the jackdaw (Bowlin et al., 2011). Although our knowledge is based on only a few studies, the presence of symmetric moult gaps appears to compromise steady fight efficiency of birds, mainly by modifying the downwash when the gap is in the mid-wing, and the span and wing tip shape when the outermost primaries are missing. However, there is still a need for further study of the aerodynamic mechanisms of wing gaps,

especially those due to accidental damage causing asymmetric loss of wing area.

### Ecological consequences in birds

As discussed above, the loss or damage of flight feathers in birds leads to reduced performance of a number of metrics (Table 1; Table S1). During moult, reduced flight performance can partially be compensated for by enlarged flight muscles, but birds also tend to change their behaviour, becoming more secretive (for example, by avoiding exposure in the open; e.g. Haukioja, 1971). In a field experiment where flight feathers were plucked to simulate moult during the breeding season in female pied flycatchers, those birds with inflicted wing gaps experienced elevated mortality rate (Slagsvold and Dale, 1996). In a similar study of pied flycatchers, where both members of the pair had their two innermost primaries removed 5 days after the clutch had hatched, thus simulating moult–breeding overlap, manipulated males showed reduced survival (as measured by return rate the following season; Hemborg and Lundberg, 1998). Moreover, the young from manipulated pairs were less likely to be recruited as breeders in comparison with control birds (Hemborg and Lundberg, 1998). In contrast, in male pied flycatchers, birds with experimental wing gaps reduced their food provisioning to the nest, but survival until the following year was not reduced (Tomotani et al., 2017). The reduced feeding rate by males was compensated for by a corresponding increase in feeding rate by their female partners, and so the survival of the nestlings was unaffected by the manipulation, but the increased feeding efforts by females may lead to reduced survival on their part (Tomotani et al., 2017). In birds feeding their young, an increased flight cost will also impact foraging efficiency, with reduced net energy delivered to their young (Hedenström and Alerstam, 1995). This echoes the observations in male pied flycatchers whose flight feathers were

removed (Tomotani et al., 2017), presumably because the bird must spend more time foraging for itself to cover the elevated locomotion costs. Female tree swallows (*Tachycineta bicolor*) that had a third of their flight feathers removed during nest building to increase flight/ foraging costs laid smaller clutches later, fed their young at a lower frequency and were less likely to return the next season than unmanipulated control birds (Winkler and Allen, 1995). In an experiment on Leach's storm petrel (*Oceanodroma leucorhoa*), both parents of breeding pairs had their wing span reduced by 3 cm (6%), which resulted in fewer feeding visits by the parents and a reduced rate of mass gain by the chicks compared with control pairs/ nests (Mauck and Grubb, 1995). The condition of the adult birds remained unaffected by the elevated flight costs, implying they allocated time to feed themselves and shunted the cost to their offspring. Very similar results were obtained for Cory's shearwater (*Calonectris diomedea*), where primaries were trimmed to reduce the wing span by 5% (males) and 4% (females) in one member of each breeding pair to incur an estimated 5% increase in power required to fly (Navarro and González-Solís, 2007), after which the foraging effort and several condition measures in the parent birds and the chick were monitored. The manipulated birds extended their foraging range and stayed away for longer periods, but they maintained their physical condition while transferring the cost to their partner and the chick (Navarro and González-Solís, 2007). In female blue-footed boobies (*Sula nebouxii*) whose wing span was experimentally reduced by 4%, the handicapped birds were in poorer condition, measured as the residuals of a linear regression between body mass and wing length, than controls at the end of the incubation period, and female chicks showed reduced growth rate (Velando, 2002). Furthermore, removing two inner primaries in thin-billed prions (*Pachyptila belcheri*), creating a wing gap without affecting the span, caused a body mass decline and changed foraging routines by the adult bird (Weimerskirch et al., 1995). In addition, the load of feather-chewing parasites (which cause holes in the flight feathers) is related to the arrival date of barn swallows (*Hirundo rustica*) at the breeding area following their spring migration: heavily loaded birds arrive late (Möller et al., 2004). By challenging barn swallows using a flight maze, Matyjasiak et al. (2018) found a link between flight feather parasite load, feather holes and flight performance. It is possible that parasite-induced reduction of flight efficiency could be the proximate reason for a bird's late arrival from its spring migration, explaining the link between arrival time and parasite load.

Many open-habitat birds use various types of aerial displays (or song flight) to attract mates. Male skylarks (*Alauda arvensis*) with experimentally trimmed flight feathers reduce the duration of their song flights (Möller, 1991b), presumably with negative fitness consequences. Male bobolinks (*Dolichonyx oryzivorus*) in which the outer primaries are experimentally clipped likewise shorten the duration of their song flight display and also acquire fewer mates than control males (Mather and Robertson, 1992). Hence, there are many situations where reduced flight performance due to wing damage or moult negatively affect a bird's performance, such as food provisioning to young or performing flight displays. Wing damage can also increase mortality risk. This may explain why in highly aerial species, such as members of the swift family (Liechti et al., 2013; Hedenström et al., 2016), moult takes place during the non-breeding season at a very slow rate with minimal effects on flight performance (De Roo, 1966).

### Bats

In contrast to birds, bats do not undergo periods of moult, but their wing membranes, consisting of two layers of skin stretched between the elongated finger bones and the legs, are continuously maintained. Damage to the wings may arise as ruptures or holes caused by collision with thorny vegetation, or as a result of predator attacks, fighting with conspecifics or pathogens. In a study surveying 1327 big brown bats (*Eptesicus fuscus*), as many as 25% showed moderate to severe wing damage (Powers et al., 2013); in a sample of 63 pallid bats (*Antrozous pallidus*), 28 showed some type of wing defect (Davis, 1968). In healthy bats, small wounds of wing or tail membranes usually heal in a month or less (Pollock et al., 2016; Greville et al., 2018). The wing damage that arises due to infection by the fungus causing white nose syndrome can result in discoloration, tears, necrosis and receded wing margins (Reichard and Kunz, 2009), but these can heal during the following summer season (Fuller et al., 2011). In common pipistrelles (*Pipistrellus pipistrellus*), tears/holes most often occur in the plagiopatagium (the membrane closest to the body), suggesting they are the result of predator attacks aiming for the body (Khayat et al., 2019).

As for birds, wing damage in bats is likely to introduce asymmetries in the wing surface, which are more costly than asymmetries in the tail membrane (see Thomas, 1993). The reason is that aerodynamic forces are generally larger on the wings than on the tail, and that force asymmetries on the wings apply to a longer moment arm than those on the tail. In accordance with this, common pipistrelles with unilateral wing tears tend to tilt the body towards the intact wing, whereas individuals with bilateral tears tend to reduce the stroke amplitude and increase the wing beat frequency (Khayat et al., 2020). Note that as bats rotate the body towards the intact wing when one wing is damaged, fruit flies rotate the body towards the damaged wing (cf. Muijres et al., 2017). Individuals of two bat species – *Myotis albescens* and *Myotis nigricans* – with wing damage perform fewer manoeuvres when allowed to fly in a circular flight arena compared with individuals with intact wings; bats with damaged wings also have reduced flight metabolic rate, probably because their flight path is straighter (Voigt, 2013).

Bat wings are highly compliant and flexible structures, allowing adaptive 3D-geometric changes in relation to aerodynamic requirements (Waldman and Breuer, 2017). To control membrane stiffness, bats have thin thread-like muscles, plagiopatagiales propria, distributed within the membrane (Swartz et al., 1996). The function of these muscles is to control the camber (curvature) of the plagiopatagium depending on aerodynamic load (Pennycuick, 1973; Cheney et al., 2014). These muscles are contracted at moderate and high flight speeds to reduce camber, and are relaxed at slower speed to increase camber and, hence, the lift coefficient (Cheney et al., 2022). Therefore, any tears or ruptures through these muscles will impact the bat's ability to control its wing shape and will reduce its flight repertoire, which is likely to affect foraging efficiency. The wings of bats are covered with sensory hairs, which provide feedback information about airflow near the wing surface (Sterbing-D'Angelo et al., 2011). Bats with wing hairs removed appear to lose some control of their flight (Sterbing-D'Angelo et al., 2011). The directional sensitivity of these airflow sensors suggests they are involved in the control of the leading-edge vortex, especially in slow manoeuvring flight (Muijres et al., 2014). As with the plagiopatagiales propria, any damage to the wings that affects the sensory hairs, such as is likely to occur as a result of the fungal infection causing white nose syndrome, will affect manoeuvrability and is also likely to affect foraging efficiency.

### Conclusions and future prospects

The combination of physiology and morphology in a species, population or individual contributes to the finely tuned balance of a

complex whole, which is the result of exposure to conflicting demands from the environment. It is therefore not surprising that perturbations in the form of damage to the bird or bat flight apparatus, either permanent or temporary, nearly invariably causes reduced performance in a great number of measures (Table 1). Apparent damage, such as the breakage or loss of feathers, shows clear and expected effects on flight performance. Flight performance of birds and bats can be predicted with some confidence on the basis of flight mechanics (e.g. Pennycuick, 2008), and empirical measurements of aerodynamic efficiency are currently beginning to generate useful results (Klein Heerenbrink and Hedenström, 2017). However, the consequences of more subtle damage or continuous wing wear, and the loss of flexural stiffness of the remiges on flight performance and aerodynamics are still little known. This is mainly because flight mechanical theory does not include elastic and material properties of feathers or wing membranes, and empirical techniques are still too imprecise to detect any effects. There is thus a need to refine both flight mechanical models and empirical techniques to quantify flight efficiency.

A certain class of complex life-history models, so-called 'annual routine models' (Holmgren and Hedenström, 1995; Barta et al., 2008), where the optimal timing of behaviours (breeding, moult and migration) is calculated, rely heavily on a state variable called 'feather quality'. In such models, feather quality is assumed to be a function of time and activity, whose slope can vary depending on activity. For example, feather quality is assumed to decline as a function of energy use. However, there are almost no data on how feather quality actually varies over the year in birds; this may differ between species living in different environments and with different ecology. For example, the willow warbler (*Phylloscopus trochilus*) conducts two complete annual moults of its flight feathers (Underhill et al., 1992), but each set of feathers seems to be of lower quality than in a close relative having one annual moult only (Weber et al., 2005). So far, the feather quality used in annual routine models has simply been assumed to be a linear function of time, but real bird feather quality may follow other trajectories depending on habitat, foraging technique, migration, geographical position and climate, all factors that may affect the rate of feather degradation. Hence, the model output depends on the underlying assumptions, and here we clearly confront a knowledge gap. Until this gap can be filled with empirical data, researchers will continue to rely on their guesswork regarding feather quality.

As is evident from this Review, we still have significant gaps in our knowledge about the effect of wing gaps on flight performance, especially on more long-term fitness effects. The majority of experimental studies are carried out on birds, while relatively few studies examine bats. Experiments on moult gaps usually involve the symmetric removal or trimming of flight feathers; therefore, the consequences of asymmetric wing damage, which is more likely to occur in natural environments through accidents or predator attacks, are less known. The majority of field studies have used different manipulations as a way to study life-history decisions during breeding, where the main effects monitored have been the condition of the manipulated bird(s) and the growth of their chicks. Future studies of this kind could be refined by also deploying GPS and flight activity loggers to understand how different manipulations actually affect flight effort and performance. Additionally, more detailed studies of the aerodynamic effects of gaps at different wing positions in wind tunnels will be welcome, and will benefit attempts to explain the occurrence of different moult patterns in birds.

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