

Aerodynamics and Energetics of Intermittent Flight in Birds¹

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SYNOPSIS. Hypotheses explaining the use of intermittent bounding and undulating flight modes in birds are considered. Existing theoretical models of intermittent flight have assumed that the animal flies at a constant speed throughout. They predict that mean mechanical power in undulating (flap-gliding) flight is reduced compared to steady flight over a broad range of speeds, but is reduced in bounding flight only at very high flight speeds. Lift generated by the bird's body or tail has a small effect on power, but is insufficient to explain observations of bounding at intermediate flight speeds. Measurements on starlings *Sturnus vulgaris* in undulating flight in a wind tunnel show that flight speed varies by around ± 1 m/sec during a flap-glide cycle. Dynamic energy is used to quantify flight performance, and reveals that the geometry of the flight path depends upon wingbeat kinematics, and that neither flapping nor gliding phases are at constant speed and angle to the horizontal. The bird gains both kinetic and potential energy during the flapping phases. A new theoretical model indicates that such speed variation can give significant savings in mechanical power in both bounding and undulating flight. Alternative hypotheses for intermittent flight include a gearing mechanism, based on duty factor, mediating muscle power or force output against aerodynamic requirements. This could explain the use of bounding flight in hovering and climbing in small passerines. Both bounding and undulating confer other adaptive benefits; undulating may be primitive in birds, but bounding may have evolved in response to flight performance optimization, or to factors such as unpredictability in response to predation.

INTRODUCTION

Intermittent flight is the characteristic flight pattern of many birds. Rather than using continuous steady level flight, many birds prefer to alter the geometry and kinematics of the wingbeat and the dynamics of the flight path periodically. In some cases these flight patterns are adaptive responses which are the result of evolutionary adaptation and optimize some aspect of flight performance. In many such cases flight behaviour can be rather highly stereotyped. In others, as for instance in a bird which is predominantly gliding but makes occasion-

ally wing flaps for control or to compensate for local air currents, intermittent flight behaviours are more flexible, and represent a proximal behavioural response within the adaptive envelope which the bird has evolved. In this paper we review some intermittent flight patterns, summarize the mathematical models which have been developed to explain them, and discuss the available evidence for the efficacy of such models. We present a new model emphasizing the importance of changes in flight speed in bounding (flap-bounding) flight, and we describe a comprehensive series of measurements of the dynamics of intermittent undulating (flap-gliding) flight in the European starling *Sturnus vulgaris*. These observations and models lead to the conclusion that periodic variations in flight speed during intermittent flight—which have hitherto been ignored—are considerable, and make a major contribution to performance optimization.

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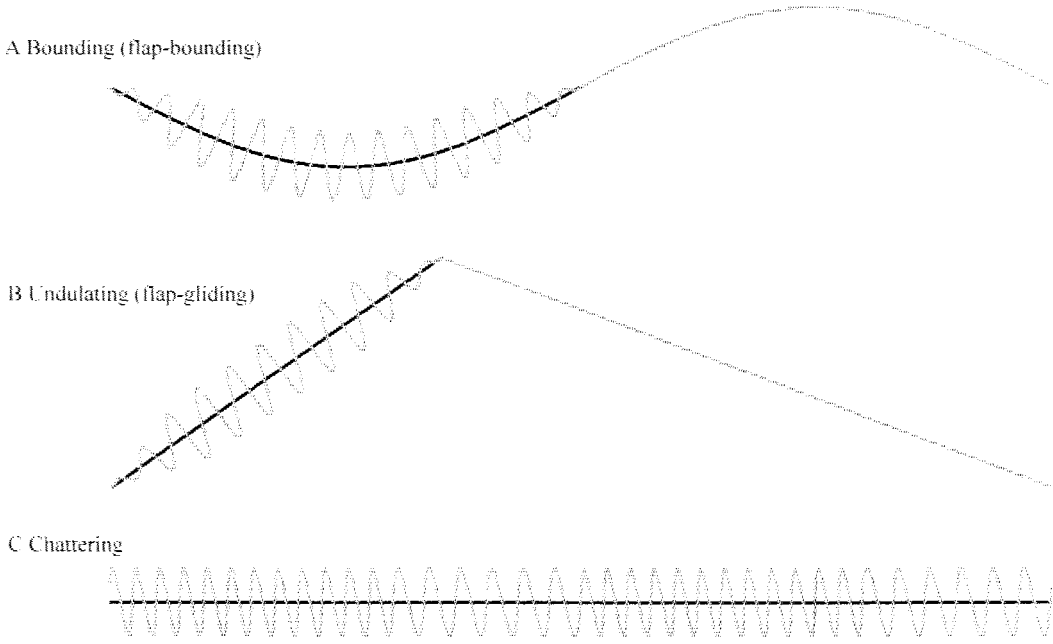


FIG. 1. Intermittent flight patterns. (A) Bounding flight, as modelled by Rayner (1977, 1985), Ward-Smith (1984*b*) and others; the phasing of flapping does not always coincide as shown with flight path geometry. (B) Undulating flight, as modelled by Rayner (1977, 1985) and Ward-Smith (1984*a*); the transition between gliding and flapping may not synchronize with ascending and descending phases. (C) Chattering flight, with alternating wingbeat frequency. In each diagram it has been assumed—unrealistically, as explained in the text—that airspeed is approximately constant.

MODES OF INTERMITTENT FLIGHT

Three modes of intermittent flight typically recognized in birds were reviewed by Rayner (1985): *bounding* flight (also known as flap-bounding; Tobalske and Dial, 1994), in which periods of flapping are interspersed with periods with the wings folded against the body; *undulating* flight (flap-gliding; Tobalske and Dial, 1994), in which periods of flapping are interspersed with periods of gliding; and *chattering* or *alternating flapping*, in which wingbeat frequency varies between two values while in sustained flapping flight (Fig. 1). The last of these three modes is relatively unusual and is best exemplified by the Eurasian Magpie *Pica pica* (Rayner, 1985; Tobalske *et al.*, 1997), but it may occur more widely in birds than has been recognised. It takes its name from the 'chattering control' of aircraft (Houlihan *et al.*, 1982). The main characteristic of all intermittent flight modes is periodic variation in thrust generated by the flapping wings, and therefore

in the dynamics of the body. Bounding and undulating flight are distinguished by the way the bird uses its wings during the resting phase. In chattering flight there is no rest phase.

Bounding flight is confined to small birds, up to a maximum mass about 0.25 kg (the largest species to bound are Piciformes), and is found in almost all of those species in this size range which have wings of relatively low aspect ratio (aspect ratio is defined as wing span squared divided by wing area, and is lowest in species with more rounded wings) (Rayner, 1996). Because the power available from the flight muscles increases with size more slowly than mechanical power required for flight (Rayner, 1977), bounding is expected to be restricted to smaller birds. Bounding is the characteristic flight mode of most small Passeriformes, the main exceptions being longer-winged species such as swallows (Hirundinidae) and wood-swallows (Artamidae) which use brief intermittent glides,

and also in smaller owls (Strigiformes), parrots (Psittaciiformes), woodpeckers and flickers (Piciformes) and most groups of Coraciiformes, and in hummingbirds (Trochiliformes). Because the bird loses mechanical energy to the air during the resting phase and replenishes energy during the flapping phase, bounding flight paths often include substantial cyclic variations in height, and ornithologists often use these characteristic patterns as diagnostic of individual species.

Undulating flight is much more widespread among birds, occurring at least facultatively in almost any of those species which can glide. Regular interleaving of glides between bursts of flapping is the characteristic flight mode of many birds of intermediate size. It is prevalent in species with relatively long wings, including—for example—some petrels, gulls and corvids; undulating flight is also found in starlings *Sturnus vulgaris*, which have become a model species for this pattern. Larger birds with relatively large wings rely on gliding; owing to their size, those larger birds with relatively small wings are confined to fast and direct flight. Many smaller birds—including typical passeriforms—have rounded wings with a low lift-drag ratio and glide rather poorly, so they rarely use undulating flight; instead, they bound.

For further details of these flight patterns and for discussion of the earlier literature on the subject see Rayner, (1985); descriptions of the flight patterns and their neuromuscular correlates in a range of species have been given by Tobalske, and colleagues (Tobalske, 1995, 1996, 2001; Tobalske and Dial, 1994, 1996; Tobalske *et al.*, 1997, 1999).

Although species may be associated with characteristic flight patterns and flight styles, these intermittent behaviours are rarely exclusive. Some species can be very flexible in flight behaviour, selecting from a range of modes according to flight pattern (*e.g.*, speed, acceleration, manoeuvres); others are more constrained. Many small passerines apparently use bounding flight invariably, even while hovering (Scholey, 1983; Rayner, 1985). Some species vary between bounding and undulating flight, ac-

ording to flight speed (Tobalske and Dial, 1994; Tobalske, 1995, 2001), and some woodpeckers unusually resort to “glide-bounding” during a steep descent (Tobalske, 1996). On the other hand, some birds never use intermittent modes in sustained level flight: this includes many species which fly fast and direct and have relatively small wings, such as auks (Alcidae), many ducks (Anseriformes), and many shorebirds or waders (Charadriiformes). It would appear that the aerodynamic constraints imposed by their low wing area (Rayner, 1998, 1995) deny these species the flexibility they might obtain from intermittent flight.

Intermittent flight patterns are predominantly confined to birds. Some butterflies use a form of undulating flight (Gibo and Pallett, 1979), but this tends to be erratic, and does not give an impression of aerodynamic efficiency. It may be associated more with confusing predators than with performance optimization. Among bats, larger species among the Pteropodidae (Old World fruit bats with mass in the range 0.2–1.5 kg) often glide or soar, and use undulating flight facultatively. The only smaller insectivorous species in which undulating flight has been reported is the European pipistrelle *Pipistrellus pipistrellus*, which intersperses brief glides in relatively long periods of sustained flapping (Thomas *et al.*, 1990). (Other microchiropterans may behave similarly, but this is not evident from patterns of repetition of echolocation calls in flight.) One evident reason for the absence of any form of bounding flight in bats is the difficulty of folding their membranous wings to save wing drag. An additional explanation for the absence of either mode in Microchiroptera is their reliance on echolocation, and their need to maintain regular sensory input. Echolocation is correlated with wing movements, and if the animal omits wingbeats it reduces the effectiveness with which it can sense its environment (Speakman and Racey, 1991; Thomas *et al.*, 1990).

A characteristic of all of the three intermittent flight modes is a periodic variation in the mean aerodynamic thrust force produced as the bird flies. As a result the dy-

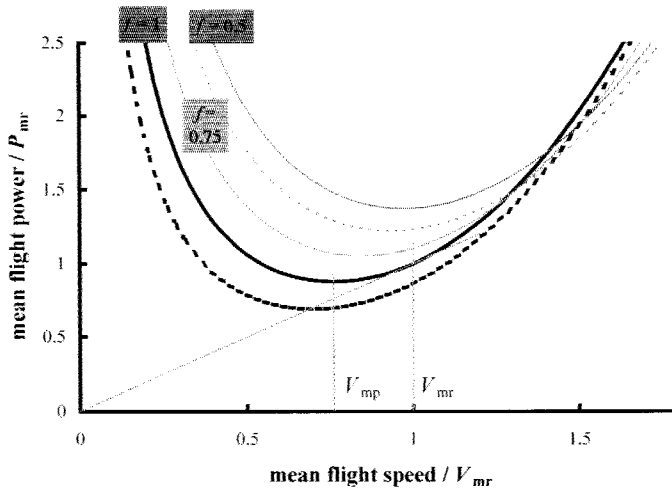


FIG. 2. Estimated mean mechanical flight power in bounding flight showing also definitions of the characteristic flight speeds V_{mp} (minimum power) and V_{mr} (maximum range, where tangent from origin meets the curve). Speed and power are shown normalized by maximum range speed V_{mr} and power $P_{mr} = P(V_{mr})$, respectively. Heavy lines: steady flapping with no body lift (continuous) and with body lift contributing 15% of weight support (dashed). Light lines: bounding flight with duty factor $f = 0.75$ and 0.5 , calculated from equation (8) (after Rayner, 1985); the dashed line is for bounding flight with duty factor $f = 0.5$ and body lift 15% of the weight. This model assumes that the bird generates thrust only during flapping phases, and that airspeed is constant throughout a bound cycle, 15% body lift reduces total mechanical power by around 20%, but whether with or without body lift, bounding is only optimal to continuous flight at speeds well above the steady flight V_{mr} .

dynamic energy (DE) of the bird also varies periodically, Dynamic energy, which is the sum of the instantaneous kinetic and potential energies of the bird, is given by

$$DE = \frac{1}{2}MV^2 + Mgz, \quad (1)$$

where M is body mass, V is the airspeed (both horizontal and vertical movement), g is the acceleration due to gravity, and z is the height. (DE values reported in this paper are specific to body mass, and can be computed directly from the geometry of the flight path.) DE is distinct from, although closely interrelated to, the mechanical energy output by the flight muscles which is transferred to the air during flight. This mechanical energy is normally quantified by the mechanical power–speed curve $P_{mech}(V)$ (see, for example, Rayner and Ward, 1999; Rayner, 1999, 2001a); a component of mechanical power output is the energy used to accelerate and gain height, and it is this which is closely associated with changes in DE; the greater component of P_{mech} (and the only component in sustained level flight) represents work done by thrust

which acts against aerodynamic drag. DE was used by Rayner, (1985) to model undulating flight patterns, and has recently been applied by Rayner and Swaddle (2000) to quantify take-off behaviour. When applied in the form of the change in dynamic energy over a wingbeat, it is a valuable measure of what a bird is able to achieve in flight beyond the performance required for sustained level flight. DE is also convenient as a means of summarizing the geometry of the flight path over a bounding or undulating flight cycle. We use it in this form in this paper.

Perhaps surprisingly, there are circumstances in which mean mechanical power consumption can be lower for an intermittent flight pattern than for steady level flight (Rayner, 1985; see below for summary of models). This is predicted to be the case for bounding flight at high speeds above the maximum range speed V_{mr} (Fig. 2), and for undulating flight speeds above the minimum power speed V_{mp} (Fig. 2). In these circumstances the advantages of an intermittent flight pattern are clear. It is more challenging to explain why birds do not fly

steadily in other conditions: no mechanical or aerodynamic explanation has yet been advanced for the use of bounding flight by small passerines while hovering.

Mechanical power P_{mech} is a component of the total metabolic power consumption P_{met} (V) (see Rayner, 1999 and Rayner and Ward, 1999 for recent reviews, and for discussion of methods of measuring or estimating both quantities). The much greater metabolic power is the total energy output by the bird, including energy radiated as heat; it is this quantity that is supposed to determine a bird's choice of performance optimization during flight. Although there have been many individual measurements of total metabolic power in birds (for reviews see Masman and Klaassen, 1987; Rayner, 1990; Butler and Bishop, 2000), relatively few (reviews by Rayner, 1993, 1999; Rayner and Ward, 1999; Butler and Bishop, 2000) have measured it as a function of speed P_{met} (V). Instead, P_{met} (V) is normally estimated by extrapolation from theoretical estimates of P_{mech} (V). However, available measurements are not sufficient to justify the many assumptions involved in deriving these estimates. In particular, we know little of the efficiency with which a bird converts metabolic energy into mechanical work. We know that efficiency increases with increasing body size (Rayner, 1990, 1995), but the mechanisms involved are not fully understood. Efficiency appears also to vary with speed (Rayner and Ward, 1999) (because wingbeat frequency and amplitude vary with speed for aerodynamic force equilibrium).

One hypothetical purpose of intermittent flight (Rayner, 1985) is to mediate the total power consumption or the power output from the flight muscles against the mechanical power required to fly. Effectively, variation of the time of flapping in bounding and undulating flight provides a bird with a simple gear. If—hypothetically—efficiency is tightly tuned to a particular combination of wingbeat kinematics, then it may be optimal (or in extreme cases even obligatory) for a bird to use those kinematics at all speeds. If the aerodynamic thrust and lift associated with that kinematic pattern exceed the drag and weight in steady level

flight then a bird may be forced to use an intermittent mode. Rayner (1985) proposed this mechanism as an explanation for the use of bounding flight in small birds at relatively low flight speeds, hypothesizing that a correlate of this constraint on efficiency would be uniformity of wingbeat kinematics and constant work output on all wingbeats. Despite some evidence to the contrary from speed-related changes in kinematics and from muscle activity (Tobalske and Dial, 1994; Tobalske *et al.*, 1999), this remains an attractive hypothesis. Unfortunately there have so far been no measurements of mechanical power output in birds in bounding flight with which to test this hypothesis directly (and very few measurements of P_{met} (V)), and it remains hypothetical whether efficiency acts as a constraint in this way. It may be that limits to efficiency or a related factor constrain the range of wingbeat kinematics or flight patterns that a bird might adopt, and that for speeds or flight modes outside these constraints a bird adopts intermittent flight.

MODELS AND HYPOTHESES FOR INTERMITTENT FLIGHT

Mechanical flight power

A bird in flight experiences a mean drag force D which may be modelled in outline by the equation

$$D = \frac{\alpha L^2}{V^2} + (\beta + \gamma)V^2, \quad (2)$$

where V is flight speed, L is the lift force generated by the wings (which is normally equated to the weight Mg), and α , β and γ are morphological parameters determined by air density and the bird's morphology. The terms in equation (2) correspond respectively to the induced or vortex drag ($\alpha L^2/V^2$), the profile drag of the wings (βV^2), and the parasite drag of the body (γV^2). This model is founded on lifting-line theory, and is consistent with the known vortex dynamics of a flying bird, and all theoretical models of mechanical power are basically of this form (Rayner, 1993, 1999, 2001a; Rayner and Ward, 1999). For the purposes of the present model discrepancies between this formulation and slightly dif-

ferent power models (*e.g.*, Pennycuick, 1989) are unimportant. We present our modelling results in non-dimensional form and do not use absolute values of the morphological parameters.

In flight, a bird flaps its wings to generate a mean thrust force T . In steady level flight T is in equilibrium with D , and mechanical power is given by

$$P_{\text{mech}} = TV = DV. \quad (3)$$

This is the equation of the familiar U-shaped power curve (Rayner, 1999, 2001a; Rayner and Ward, 1999). In intermittent flight the bird generates a greater thrust T during a burst of flapping, and then rests. Some of the additional thrust is used to gain dynamic energy. In the right circumstances the resulting P_{mech} is less than that for steady flight at the same speed. The model above and this concept of intermittent thrust is the basis of existing models of intermittent flight.

Undulating flight

Undulating flight was modelled by Rayner (1977); the optimal flight strategy, offering savings in power compared to steady flight, was presented graphically in terms of dynamic energy by Rayner (1985). The model is similar to that originally used for negatively buoyant fish by Weihs (1973). During the flapping phase, climbing at angle θ and airspeed V , power output is

$$P_{\text{mech}}(V, \theta) = \frac{\alpha(Mg \cos \theta)^2}{V} + (\beta + \gamma)V^3 + MgV \sin \theta. \quad (4)$$

During the gliding phase the bird supports its weight with its wings, but does no mechanical work; it loses height as potential energy is converted into work against drag. Glide angle θ_g is <0 , depends on V , and satisfies

$$P_{\text{mech}}(V, \theta_g) = 0. \quad (5)$$

Climbing angle θ and the relative duration f of the flapping phase (the *duty factor*, termed *flapping ratio* by Rayner [1985]) are determined by the condition that the mean flight path is level, and must satisfy

$$\tan \theta = -\frac{1-f}{f} \tan \theta_g. \quad (6)$$

Since no mechanical work is done while gliding, mean power in undulating flight is

$$\bar{P}_{\text{mech}} = fP_{\text{mech}}(V, \theta), \quad (7)$$

which by appropriate choice of θ can be less than $P_{\text{mech}}(V, 0)$ for speeds V above the minimum power speed V_{mp} (Rayner, 1977, 1985).

Ward-Smith (1984a) developed a similar linearized theory, treating all angles as small, and concluded that there were no power savings available.

Bounding flight

Models of bounding flight (Lighthill, 1977; Rayner, 1977; Alexander, 1982; Ward-Smith, 1984b; Azuma, 1992) are similar to the above model for undulating. They differ because the bird generates no useful aerodynamic force during the resting phase, and must generate sufficient lift and thrust to support its weight and overcome drag in the flapping phase alone; it will accelerate upwards in order to “drive” the subsequent bound. With duty factor f , drag during this phase is

$$D_{\text{flap}} = \frac{\alpha}{V^2} \left(\frac{L}{f} \right)^2 + (\beta + \gamma)V^2, \quad (8)$$

while during the resting phase drag is simply

$$D_{\text{bound}} = \gamma V^2, \quad (9)$$

since the only force acting is body parasite drag and the bird moves as a projectile. Mean power is therefore

$$\begin{aligned} \bar{P}(V, f) &= [fD_{\text{flap}} + (1-f)D_{\text{bound}}]V \\ &= \frac{\alpha L^2}{fV} + (f\beta + \gamma)V^3. \end{aligned} \quad (10)$$

Bounding should be more expensive than continuous flapping at all but the very highest speeds. There are values of f which are <1 and for which $\bar{P}(V, f)$ is less than the power for steady flight $\bar{P}(V, 1)$ only if V is relatively high, exceeding maximum range speed V_{mr} (Fig. 2). For lower speeds, including the minimum power and maximum

range speeds, the model predicts that bounding flight is more expensive than steady flight. The paradox arising from this conclusion is that many birds are observed to bound, with relatively low duty factors, at much lower speeds than this, and even in hovering or climbing flight (Kipp, 1950; Rayner, 1985; Tobalske *et al.*, 1999).

Ward-Smith (1984*b*) extended the above model to allow for vertical curvature of the flight path, and reached essentially the same conclusions. Rayner (1985) also considered the effect of body and tail lift during the bound phase, and showed that if this quantity exceeded about half the body weight, then the critical speed above which bounding flight is optimal could be depressed to around V_{mp} . However, Tobalske *et al.* (1999) have estimated body lift as around 15% of weight in zebra finches, and similar (maximum) magnitudes of body lift have been determined for starlings (unpublished data, W. J. Maybury and JMVR). Values of lift with this order of magnitude are plausible, but are insufficient to force the critical speed down to below V_{mr} (Fig. 2). Moreover, the implicit comparison with steady flight with no body lift may be unreasonable since body lift may equally be present in the flapping phase. Although body lift can provide an appreciable saving in power requirement at intermediate speeds (Fig. 2), it cannot explain the use of bounding at lower speeds. The paradox remains that some birds bound at speeds well below V_{mp} .

Bounding and undulating with variation in flight speed

The two models set out above assume that the bird flies at a constant horizontal speed throughout. In the bounding flight model vertical kinetic energy is exchanged for potential energy; in the undulating flight model, kinetic energy remains constant but potential energy varies. Analysis of video recordings of undulating flight patterns in starlings (see below), and of high-speed film of bounding flight in small passerines (unpublished results, JMVR) reveals that potential energy cycles are accompanied by substantial variations in mean flight speed, and therefore in kinetic energy. Although this speed variation has been noted before

(Rayner, 1985; Tobalske, 1995), it has been ignored in previous theoretical models (above). It contributes a new dimension to the intermittent flight problem, with the potential for providing a hypothetical mechanical explanation for some of the flight patterns which may be observed.

Currently rather little information is available about speed variation in bounding flight, and there have been no field observations. This makes it difficult to model this situation, and without guidance from observations a general model has too many parameters to be informative. However, the following simple model based on level flight in bounding with varying thrust gives a clear indication that significant energy savings may be achieved. This model is similar to a model of burst and coast swimming in neutrally buoyant fish (Weihs, 1974; Videler and Weihs, 1982), but with the addition of a term for the induced drag associated with lift generation.

Suppose that the cycle period is τ , and that duty cycle is f . Suppose also that during the flapping phase (which has duration $f\tau$) a bird generates a constant thrust T which is greater than the drag D , and that it uses the excess thrust to accelerate. Then during this phase the equation of motion of the bird is:

$$\begin{aligned} M\dot{V} &= T - D(V) \\ &= T - \left[\frac{\alpha(M^2g^2 + T^2)}{V^2} + \left(\beta \frac{T}{D} + \gamma \right) V^2 \right]. \end{aligned} \quad (11)$$

The T^2 term in induced drag emphasizes that thrust is generated by the flapping wings (Rayner, 1993, 2001*a*). The factor T/D in profile power is included to model the cost of the faster and/or larger amplitude wing movements associated with thrust generation; no information is available about the dependency of this term, but it is plausible that profile power will increase in proportion to thrust.

During the bounding phase—of duration $(1-f)\tau$ —the only force acting is body parasite drag, and therefore

$$M\dot{V} = -\gamma V^2; \quad (12)$$

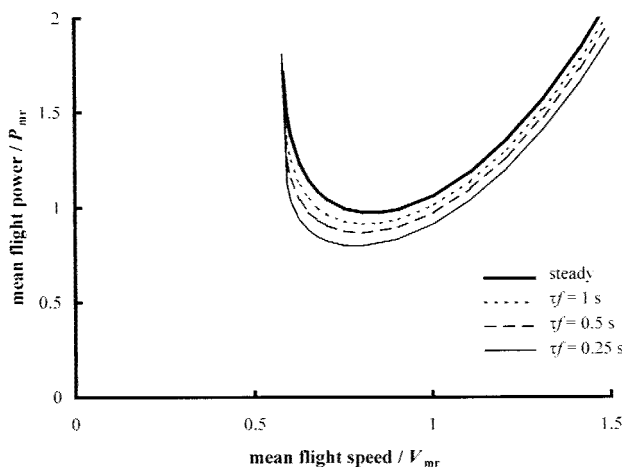


FIG. 3. Estimated mean mechanical flight power in bounding flight allowing for periodic variation in flight speed as well as in thrust, for different durations of the flapping burst, computed from equations (11)–(13). Shorter flapping bursts are more economic, because potential energy loss increases non-linearly with time; however, the model ignores the duration of the changeover phase from bounding to flapping, which makes short burst durations less attractive.

again, body lift and induced drag are neglected. The minimum and maximum speeds (at the start and finish of the flapping phase) and the durations of the flapping and bounding phases are determined by the requirement for a constant mean speed, and this imposes a constraint on f . The mean power is

$$\bar{P} = \left(\int_0^T TV dt + Mg\Delta z \right) / \tau, \quad (13)$$

where the second (and relatively small) term is included to allow for loss of height Δz in the absence of lift during the bounding phase. Results of simulations with this model for a bird of the morphology of a typical medium-sized passeriform are shown in non-dimensional form in Figure 3. At each speed there is an optimum T which minimizes \bar{P} . This thrust, and the associated power saving, depends on flapping duration $f\tau$. Generally, shorter flapping phases are preferred; however, there is a lower limit on this duration since the bird must be able to make a sufficient number of wingbeats, and the model ignores any costs which would be associated with starting to flap; thus low flapping durations may not be feasible. \bar{P} is less than mechanical power for steady flight over a wide range of speeds, including V_{mp} and V_{mr} . Flight is not possible for this model below a critical

speed, owing to two factors. First, drag at low speeds is predicted to increase rapidly and to exceed any thrust which might be generated. Second, the lifting line theory used here is not applicable at low speeds. Unlike the constant speed model above, the solution depends on bird morphology, and in particular on a parameter related to cost of transport (energy per unit flight distance), or equivalently to aspect ratio and to body drag. Savings available by this model are greater for birds with lower aspect ratio.

Similar computations (not shown here) indicate that, under certain conditions, comparable savings can be obtained for high aspect ratio birds in level undulating flight with short decelerating glides, and also in bounding flight if thrust varies during the burst phase.

This model is preliminary and tentative, and probably fails fully to account for the cost of offsetting height loss during the bounding phase. Nonetheless the conclusions are robust. If combined with the cyclic height variation characteristic of bounding and undulating flight, a bird may obtain improvements in flight performance of the order of a 15% saving in mechanical power requirement compared to steady level flight.

UNDULATING FLIGHT DYNAMICS

Starling flight in a wind tunnel

As part of a comprehensive experimental study of flight energetics (Ward *et al.*, 1998, 1999), Hi-8 video films were taken of European starlings *Sturnus vulgaris* flying in a wind tunnel. This was a recirculating tunnel at the Universität des Saarlandes, Saarbrücken, with a 1 m³ working section (Nachtigall, 1998). Full results of the analysis of these video sequences will be presented elsewhere. Here we discuss variation with flight speed of aspects of flight path dynamics and wingbeat kinematics for a single bird (Bird, 19), flying at a range of speeds between 6 and 14 m/sec. This bird flew readily in the wind tunnel, and used a regular undulating flight pattern at speeds above about 7.5 m/sec. At 6 m/sec the bird flew continuously, but erratically; none of the birds would fly at lower speeds.

Video fields (50 Hz) were digitized on an Apple PowerMac 8100AV microcomputer fitted with a Data Translation DT2225 QuickCapture image capture card, and were analysed in the public domain NIH Image v1.62 (<http://rsb.info.nih.gov/nih-image/>) and Microsoft Excel97®, with algorithms from Rayner and Aldridge (1985). Wingbeat frequency was determined by counting wingbeats from the mid point of the downstroke when the wingtip passed below the beak.

Flight kinematics and path dynamics

At 6.2 m/sec the bird usually flapped continuously and did not adopt the regular undulating movements of higher speed. However, flight was not steady. A typical flight pattern was for the bird to flap with a slight thrust deficit so that it drifted backwards relative to the air; as it reached the rear of the working section it executed two or three rapid wingbeats to recover position. At this speed below the minimum power speed V_{mp} drag was high. We hypothesize that this behaviour is a form of *chattering* flight, with the bird using a preferred wingbeat for much of the time although this is mechanically inappropriate wingbeat for the particular flight speed. We do not know if this pattern is characteristic of slow-flying

starlings in the wild, or if as an alternative they choose to fly only at certain speeds.

At all speeds, birds using undulating flight moved around substantially within the working section, although they showed a strong preference for the top third of the tunnel. Horizontal position (of the beak) varied by up to 55 cm, increasing with increasing mean airspeed (Table 1; Fig. 4a). Vertical position varied by up to 25 cm. Horizontal speed ranged about mean airspeed by around ± 1 m/sec at all speeds, but the range of vertical speeds decreased as airspeed increased.

Flight path geometry within the working section was relatively consistent (Fig. 4b). The bird tended to flap up, gaining speed, until it was close to the tunnel roof; it then switched to gliding, with wings flexed, and decelerated and descended towards the rear of the working section. It then began to flap to accelerate forwards, repeating the cycle. The maximum angle of ascent and the maximum glide angle both decreased markedly with increasing speed. At higher speeds, the gliding phase was confined to a small part of the cycle, when the bird was close to the roof of the wind tunnel. Neither ascent angle nor glide angle were constant during the flapping and gliding phases (Fig. 4b); the constant-speed model of undulating flight with linear ascending flapping and descending gliding phases (Fig. 1) is unrealistic and oversimplified, at least for these flights in the wind tunnel.

During the greater part of the flapping phase, the bird gained both speed and height. Both kinetic energy and potential energy components of dynamic energy DE increase in phase with one-another (Fig. 4c). Contrary to some hypotheses for intermittent flight, and unlike some other animals using intermittent locomotion strategies (Rayner, 1985), the bird did not act as a pendulum, interchanging energy between kinetic and potential. Variation in dynamic energy over a flap-glide cycle was considerable (Fig. 4), and the range of this variation was of the order of one-quarter or one-third of the (estimated) work done against aerodynamic drag during a flapping burst (Fig. 5).

During flapping bursts, wingbeat fre-

TABLE 1. *Undulating flight kinematics in European starling (bird #19) flying in a wind tunnel at various speeds.**

| Mean wind tunnel airspeed (m/s) | 6.2 | 8.5 | 10.2 | 12.4 | 14.1 |
|-------------------------------------|------------|------------|------------|------------|------------|
| Duty factor | — | 0.65 | 0.55 | 0.70 | 0.83 |
| Mean flapping duration (s) | — | 1.14 | 1.05 | 1.35 | 2.06 |
| Mean gliding duration (s) | — | 0.64 | 1.01 | 0.58 | 0.23 |
| Mean cycle period (for DE) (s) | — | 1.78 | 2.06 | 1.93 | 2.29 |
| Phase of onset of flapping | — | 0.49 | 0.58 | 0.40 | 0.37 |
| Phase of onset of gliding | — | 0.17 | 0.11 | 0.09 | 0.20 |
| Wingbeat frequency (Hz) | 10.3 ± 0.8 | 10.7 ± 1.7 | 11.2 ± 2.4 | 11.1 ± 2.0 | 11.1 ± 1.7 |
| Wingbeat vertical displacement (cm) | 25.9 | 29.8 | 33.2 | 33.9 | 31.6 |
| Number wing flaps per burst | — | 10–12 | 10–12 | 9–16 | 22** |
| Horizontal displacement (cm) | 68.2 | 41.8 | 47.4 | 52.6 | 54.9 |
| Vertical displacement (cm) | 28.2 | 25.3 | 23.3 | 21.5 | 16.047 |
| Maximum flight path angle (°) | 3.9 | 6.0 | 4.3 | 2.4 | 2.1 |
| Minimum flight path angle (°) | -3.7 | -5.4 | -3.4 | -3.6 | -2.8 |
| (steepest observed glide angle) | | | | | |
| Horizontal speed range (m/s) | 6.1–6.7 | 7.5–9.3 | 9.4–11.4 | 11.4–13.3 | 13.0–15.0 |
| Vertical speed range (m/s) | -0.7–0.6 | -1–0.7 | -1–0.8 | -1–0.9 | -0.6–0.7 |
| Specific DE variation (J/kg) | — | 13.1 | 18.4 | 21.0 | 25.9 |

* Phases of onset of flapping and of gliding are defined relative to the cycle of specific dynamic energy (DE), with maximum energy as phase 0 (see Figs. 4 and 6). Mean cycle period is determined as average time between maxima of the DE-time trace. Wingbeat vertical displacement is the maximum vertical movement of the wingtip during flapping bursts; this is closely related to wingbeat amplitude. Horizontal and vertical displacement are the range of movement of the bird (the base of the beak) relative to the air in the wind tunnel during a cycle. At 6.2 m/s the bird flies continuously but erratically, with brief bursts of acceleration but no glides. At other speeds the bird uses undulating flight.

** At 14.1 m/s flapping phases are 22 wingbeats long, formed of two bursts of 11 wingbeats interspersed with either a very brief glide or bound, or one or two wingbeats of low amplitude.

quency was not constant. The bird began flapping while it was still travelling backwards relative to the working section, and used two or three rapid but low amplitude wingbeats (frequency ~13 Hz) for the initial acceleration out of the decelerating glide; then frequency decreased to around 8–10 Hz as amplitude and speed increased. At the end of the flapping burst, as it approached the tunnel roof, the bird often made one or two low frequency wingbeats (~4 Hz), possibly stabilizing itself for the ensuing glide. Variation of wingbeat frequency was an important mechanism of controlling thrust: the gain in dynamic energy over a wingbeat increased significantly with wingbeat frequency (Fig. 5), and the gradient of the slope between DE and frequency in turn increased with speed.

While the wings flap, the inertial force due to the weight of the wings and the aerodynamic lift force both vary. As a result there is a periodic recoil movement in the position of the body. Our video images do not have sufficient temporal or spatial resolution to measure this recoil with any ac-

curacy, but it is clearly visible in the vertical speed trace and in small variations in glide angle during the climbing phase (Fig. 4).

Mechanisms for controlling thrust

A bird in sustained flight controls flight speed by manipulating wingbeat kinematics—mainly frequency and amplitude—so that horizontal thrust from lift on the flapping wings balances drag (Rayner, 1993, 2001a). At any speed, a combination of kinematics generating thrust in excess of drag will permit a bird to accelerate. The rules governing kinematics in relation to speed or thrust requirements in birds are not well understood: the results in Figure 5 provide an important clue to these processes. However, presently we know little of how drag varies during a cycle in undulating flight, and therefore cannot partition the total work done by thrust into components to overcome aerodynamic drag (which can only be estimated, for example by equation (11)) and to increase DE (which we have measured from flight path dynamics). For this

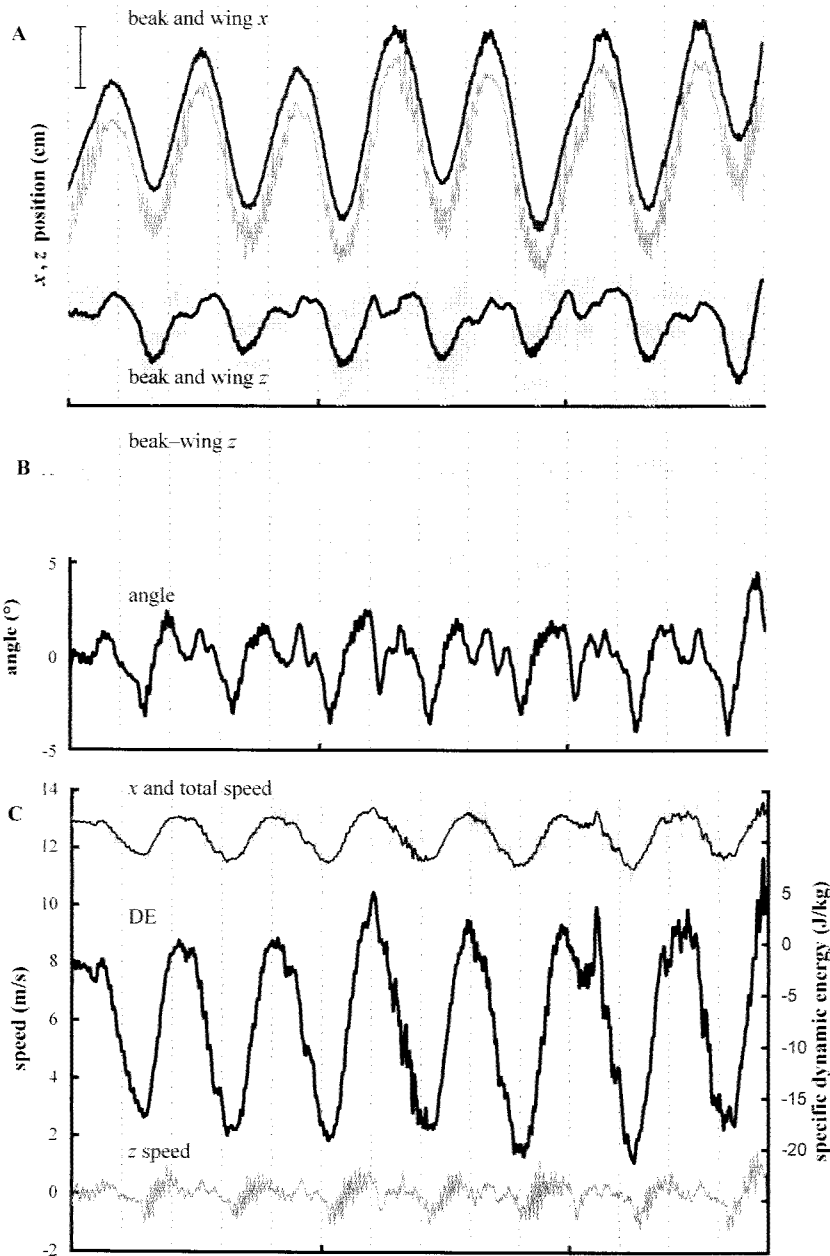


FIG. 4. Flight path dynamics for a European starling *Sturnus vulgaris* in undulating flight in a wind tunnel at a mean flight speed of 12.4 m/sec. (A) Variation of horizontal (upper) and vertical (lower) positions of beak and wingtip against time. Scale bar 20 cm. (B) Angle of flight path relative to the air, showing vertical position of wingtip relative to body to identify flapping and gliding phases. Oscillations in angle following each flapping phase represent glides very close to the roof of the wind tunnel. (C) Variation of horizontal (upper; 11.3–13.2 m/sec) and vertical (lower; -1–0.9 m/sec) flight speeds and of dynamic energy (solid curve). The value of specific DE is arbitrary; it is the variations in DE which are critical. Note that despite the relatively low temporal resolution of the video the vertical body recoil associated with each wingbeat during the flapping phases is evident in both flight path angle and vertical body speed.

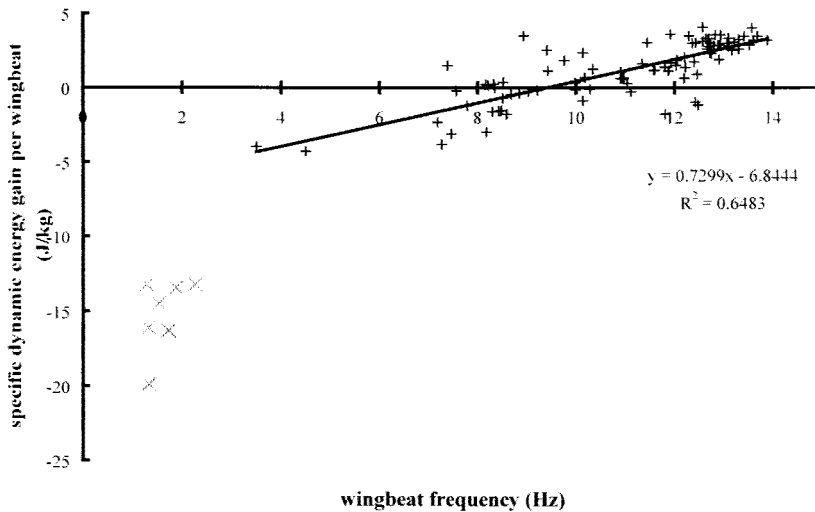


FIG. 5. Specific dynamic energy gain increases significantly ($n = 92$, $r = 0.805$) with wingbeat frequency during the flapping phases of undulating flight, as shown here for European starling *Sturnus vulgaris* at a mean speed of 12.4 m/sec. +, dynamic energy gain in flapping wingbeats; ×, dynamic energy gain during gliding phases (this quantity is negative during gliding phases, which had a period of approximately 0.5 sec (Fig. 4a), and are therefore shown here with a notional frequency of around 2 Hz). For comparison, mechanical work done against aerodynamic drag in a typical steady flight wingbeat in starlings is estimated at around 6–8 J/kg (unpublished results, JMVR).

reason we do not present estimates of mean or instantaneous mechanical power in undulating flight here, although we assert on the basis of the models discussed above that this mean power is lower than the mechanical power for sustained steady level flight. For a duty factor of 0.50 a starling should obtain a saving in mechanical power of approximately 10%: the saving could be increased by variations in flight speed.

To be able to fly at different mean flight speeds. Bird 19 varied a number of parameters relating to both kinematics (*e.g.*, wingbeat frequency and amplitude) and dynamics (*e.g.*, flight path geometry; flapping and gliding phase schedules). Of these parameters the one with the greatest impact on performance was probably duty factor, which follows a U-shaped curve with speed (Fig. 6). If it is accepted that total mean mechanical power output during the flapping phases is broadly independent of speed (as Rayner (1985) hypothesized for bounding, and Ward-Smith (1984a) for undulating flight), then mean power in flapping will be proportional to duty factor; then this U-shaped curve will correspond quite closely to mean mechanical power in steady

flight. On this basis, the minimum power speed would be between 9 and 10 m/sec; this is consistent with other estimates for starlings (Ward *et al.*, 1998, 1999). Duration of flapping bursts and wingbeat amplitude both increase with speed (the latter largely because the stroke plane becomes closer to vertical at higher speeds), but wingbeat frequency does not change (Table 1).

The results of these kinematic changes are a decrease in climb speed and climb rate, and a shallower glide angle, at higher airspeeds. Most marked is the sharp increase in the range of variation in DE (Table 1, Fig. 7). At higher speeds the bird tends to spend longer gliding close to the top of the tunnel. The decrease in glide angle with increasing speed is unexpected: glide angle should steepen at higher speeds. However, the bird rarely glided with wings fully extended, and moreover geometry of decelerating glides cannot readily be deduced from a constant-speed glide polar curve.

Wind tunnel effects

Flight in some of our birds was highly stereotyped, but others were more erratic.

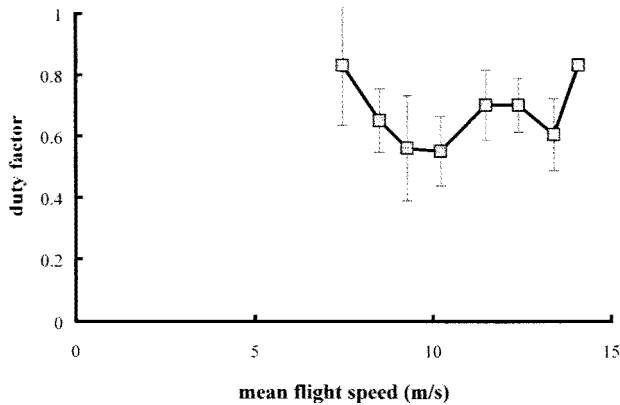


FIG. 6. Variation in mean flapping duty factor (\pm SD) with mean flight speed in European starling *Sturnus vulgaris* using undulating flight in a wind tunnel at a range of speeds. At 7.4 m/sec the bird uses only brief glides: at lower speeds it flaps continuously with changing (chattering) frequency. Duty factor follows an approximately U-shaped variation with flight speed: if, as seems plausible, this variation follows mean mechanical power output, then the minimum power speed V_{mp} for this bird would be approximately 10 m/sec. Tobalske (1995, 2001, fig. 9) reported similar results for starlings and other species.

This indicates a range of responses to conditions in the wind tunnel. We have no data on undulating flight dynamics in starlings in the field, although analysis of video films indicates that the birds use comparable duty factors (unpublished results, SW and JMVR). In the wind tunnel birds exploit

much of the available volume, particularly in the upper portion of the working section. The geometry of the flight path (in both speed and position) may be dictated by the confines of the tunnel. Birds appear to benefit aerodynamically from proximity to the tunnel roof by the 'inverse ground effect'

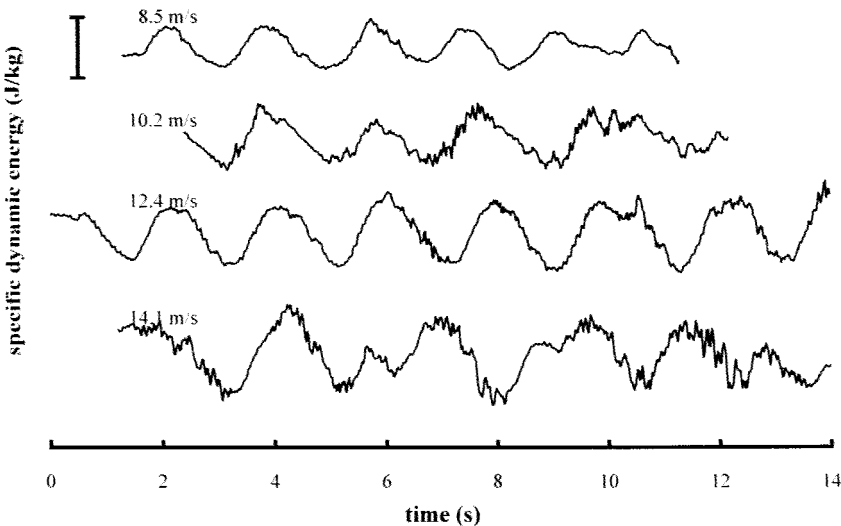


FIG. 7. Cyclic variation in specific dynamic energy (J/kg) for European starling *Sturnus vulgaris* using undulating flight in a wind tunnel at various speeds. Scale bar 20 J/kg. At speeds lower than about 8 m/sec the bird does not use undulating flight. Note the regularity of variation in energy: at all speeds gains in kinetic energy (equivalently the square of airspeed) and in potential energy or height are synchronized. Note also the increasing amplitude of variation of DE with mean flight speed, and the tendency for cycle period to increase with speed (see also Table 1). At 10.2 m/sec the rise and fall of dynamic energy are close to linear during the cycle; at other speeds variation is more sinusoidal, and is most regular at 12.4 m/sec.

mechanism described by Rayner (1994). This means that wind tunnel flight may differ appreciably from flight in starlings in the wild. Estimates of mechanical energy consumption in undulating flight in the tunnel are valuable for comparison with our direct measurements of metabolic power and heat radiation in flight (Ward *et al.*, 1998, 1999), but may not be representative of mechanical power in free-flying and unconstrained starlings.

DISCUSSION

Why fly intermittently?

It is inescapable that most intermittent flight patterns convey an adaptive benefit in enhancement of flight performance. Two hypotheses explain how this benefit might be achieved (Rayner, 1985).

The first is direct: intermittent strategies reduce mean mechanical power compared to steady flight. Theoretical models predict that there are modest savings for undulating flight at most speeds, and for bounding flight at higher speeds. If there is significant lift from the body, or if strategies that vary flight speed are as beneficial as estimated above, then bounding flight may be advantageous over a wider range of speeds (Figs. 2, 3). However, these model predictions cannot explain the observation that some small passerine birds “bound” while hovering or during steep climbs. No aerodynamic factor can be responsible for this phenomenon.

The second hypothesis is that intermittent flight is a mechanism to minimize total power output in flight, despite the increase in the aerodynamic component of power which our models show will occur in some circumstances. This may operate because the bird cannot select the wingbeat kinematics at every flight speed that minimize total power, because muscle power or force output is constrained by the physiological properties or the geometry of the muscles. Such a mechanism can potentially explain the presence of intermittent flight phenomena at all flight speeds, as well as variation in intermittent flight behaviour with speed. As originally formulated (Rayner, 1985), the muscle constraint in bounding flight might

be that the force or the quantity of mechanical work output by the flight muscles in any contraction cannot be varied. Tobalske and Dial (1994) and Tobalske *et al.* (1999) used the term “fixed gear” to describe this hypothesis, but this terminology is somewhat misleading. Rather, the variation in kinematics, particularly in duty factor, provides a bird with a *continuous* “gear,” by which it mediates mean power or force output to the requirements of a particular flight pattern. Under the hypothesis as originally stated it is some aspect of muscle output which is fixed. Rayner (1985) suggested that a correlate of this hypothesis could be uniformity in wingbeat kinematics over a range of speeds, and—in small bounding passeriforms—the recruitment of all of the pectoralis muscle during each downstroke. Tobalske and Dial (1994) and Tobalske *et al.* (1999) have shown that these predictions are invalid in bounding flight in zebra finches or budgerigars, and our results show that wingbeat kinematics vary to control force production during the flapping bursts in starlings (Fig. 5). However, these observations do not discount the hypothesis that intermittent flight is associated with constraints arising from muscle performance or with the optimization of overall power consumption in flight. This hypothesis remains attractive. Any or all of a number of physical or physiological quantities—mechanical work, mechanical power output, thrust, or efficiency—associated with performance from the flight musculature may be constrained to a limited range. When the optimum power (or force) output from a bird’s muscles exceeds the power required (or the aerodynamic drag) for flight at a particular speed, then a bird may either use sub-optimal muscle output, or may use the preferred muscle output for a fraction of time. If the latter case is optimal then the bird should fly intermittently.

These two hypotheses are not exclusive. A bird evolving to benefit from reduced mechanical power output can benefit further from being able to develop simpler muscles. Equally, a bird in which physiological factors constrain muscle performance, can find ways to fly which are not excessively

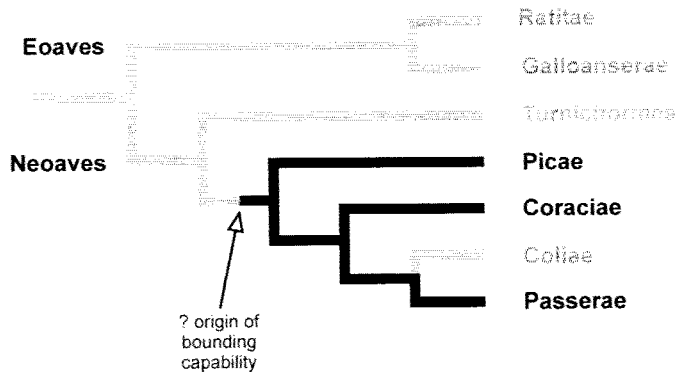


FIG. 8. Phylogeny of avian superorders (after Sibley *et al.*, 1988), showing in bold lineages which include representatives using bounding flight. Passerae is a large group which includes—in addition to Passeriformes—many accipitriform, charadriiform, pelecaniform, gruiform and ciconiiform birds which do not use bounding flight. Bounding has not been reported in mousebirds Coliae, which have highly specialized flight morphology and unusual feathers. The use of bounding flight appears to be a derived adaptation in birds, but may have arisen separately on multiple occasions.

expensive and retain a degree of flexibility. It is not possible to state which came first.

Adaptive value of intermittent flight modes

Beyond these prime reasons for using intermittent flight, additional benefits can ensue. Because it provides a continuous gear (whether or not muscle performance is constrained), it confers considerable flexibility. Undulating flight allows a bird to respond readily to gusts or to changes in air currents. Bounding permits a bird to accommodate substantial variations in body mass or changes in body composition: increased body mass results in increased flight power, and a bird needs simply to increase duty factor to maintain flight speed, albeit with increased mean power output. Increased muscle mass, for instance during migration, can allow a bird to increase available power to compensate. Both factors are consistent with both hypotheses above. Many small passerines increase body mass considerably: fat deposition can represent up to 50% of lean mass prior to migration. We predict that duty factor in the initial phases of migration flight will be high compared to duty factor in a lean bird at the same speeds.

Some waders (Charadriiformes) can double body mass prior to migration. The apparent absence of bounding flight in this group is remarkable, given that many are

relatively small species which might otherwise benefit from its adoption.

Evolution of intermittent flight

Undulating flight is widely distributed in birds, and while relatively few species are obliged to use it in normal flight, species from many lineages can use it facultatively. It requires no special morphological adaptations, although it is most effective in birds with low wing loading. It is plausible to suggest that some form of undulating flight is primitive in birds. Gliding is generally considered to be the precursor to true flapping flight (*e.g.*, Rayner, 2001*b*), although early avian fliers are probably unlikely to have been arboreal (*pace* Feduccia, 1996). Occasional small wing flaps introduced into glides can reduce glide angle and ultimately—as in modern undulating birds—permit level flight. The morphology of *Archaeopteryx*, with large wings and tail, but no sternal keel, and with semi-lunate carpal in the wrist, is consistent with this model.

By comparison, bounding flight is more derived and more restricted in its distribution. It is confined to lineages of the Neoaves (Fig. 8), where it occurs in three of the four superorders defined by Sibley *et al.* (1988). The capability for bounding may have appeared in the course of the neoavine radiation, or may have evolved separately,

and more recently, within some Picae, Coraciidae and Passerae. Some Mesozoic enantiornithine birds had similar size and morphology to modern passerines, and it is tempting to speculate that they too had evolved some form of bounding flight. Hypothetical selective pressures for the origin of bounding include the two adaptive explanations considered above. Its initial appearance may have been due to other factors. Although not confined today to migrants, initial pressure may have come from performance optimization in birds faced with demanding long distance flights. Among other hypotheses for the initial use of bounding flight we list protean behaviour (Driver and Humphries, 1988) to confuse potential predators; display or communication; crypsis or camouflage. Each of these factors may play some part in a modern species' use of bounding flight, but cannot displace the hypothesis that this flight mode is driven primarily by performance optimization in flight.

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