

Bird Maneuvering Flight: Blurred Bodies, Clear Heads¹

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SYNOPSIS. While useful in describing the efficiency of maneuvering flight, steady-state (*i.e.*, fixed wing) models of maneuvering performance cannot provide insight to the efficacy of maneuvering, particularly during low-speed flapping flight. Contrasted with airplane-analogous gliding/high speed maneuvering, the aerodynamic and biomechanical mechanisms employed by birds at low flight speeds are violent, with rapidly alternating forces routinely being developed. The saltatory nature of this type of flight results in extreme linear and angular displacements of the bird's body; however, birds isolate their heads from these accelerations with cervical reflexes. Experiments with pigeons suggest this ability to isolate the visual and vestibular systems is critical to controlled flapping flight: birds wearing collars that prohibited the neck from isolating the head from the angular accelerations of induced rolls frequently exhibited (50% of flights) a loss of vestibular and/or visual horizon and were unable to maintain controlled flight.

INTRODUCTION

Studies and discussions of avian maneuvering performance have long been narrowed by steady-state (*i.e.*, fixed-wing) assumptions, and our views of its morphological correlates, ecological significance, and evolutionary history have been correspondingly limited. Recent information on the behavior and aerodynamic mechanisms of bird maneuvering flight have expanded the scope of discussions beyond wing planform, into specific and highly specialized musculoskeletal flight structures. Our purpose here is to examine the utility and limits of fixed-wing models of maneuvering flight, and suggest new directions investigations into maneuvering flight should take given recent revelations. In addition, we discuss the aerodynamic mechanisms birds use to maintain stable flight, and provide preliminary data on the function and importance of the cervical musculoskeletal mechanisms birds use to isolate their heads from the often violent kinetic energy of flapping and maneuvering flight.

MANEUVERING FLIGHT DEFINED

The maneuverability of a bird (or any flying animal or machine) is traditionally defined by the radius of turn (r); that is, the smaller the radius of turn the more maneuverable the bird (*e.g.*, Pennycuick, 1975, 1989; Norberg and Rayner, 1987). These authors derive this definition by equating the centripetal force needed to produce the curved flight path with the lift force; maneuverability has been defined strictly by wing loading (mS^{-1})

$$mU_b^2 r^{-1} = (1/2)U_w^2 S \rho C_L \sin \theta$$

$$r = 2m / \sin \theta S \rho C_L$$

$$r \propto mS^{-1}$$

where θ is the bank angle, ρ is the density of air, C_L is the dimensionless lift coefficient, S is the area of the wing, m is the mass of the bird, U_w is the velocity of the incident air over the wings and U_b is the velocity of the entire bird. While this equation accurately represents the turning radius of an airplane or a gliding bird when they meet the assumption that $U_w = U_b$, birds are notorious for frequently violating this assumption.

In their extensive analysis of bat flight morphology, Norberg and Rayner (1987) distinguish between *agility* and *maneuverability*, and point out the conflicting requirements for high performance in each: Large, long wings are needed to maintain efficiency and low wing loading (and therefore high maneuverability), but have high inertia and therefore an impediment to agility, defined as the ability to roll into a bank quickly. Yet another type of maneuvering performance that has been defined is *linear maneuverability* (as distinguished from *turning maneuverability*; Warrick, 1998). Whereas turning maneuvering involves a force changing the vector of a mass (*i.e.*, an angular acceleration), linear maneuvering is a change in magnitude of the vector. Data gathered on the acceleration of swifts and swallows illustrate another compromise: Birds with low wing loading and high aspect ratio suffer from lower acceleration performance (Warrick, 1998). Thus, species that forage by capturing insects during short, burst flights from a perch (“sallyers,” or “hawkers”) have, on average, lower aspect ratios than birds that fly continuously in search of prey (“screeners” or “coursers”; Moermond, 1990; Warrick, 1998).

MANIPULATING THE AIR TO MANEUVER

Gliding flight: wing presentation

During gliding flight, birds may manipulate both the lift coefficient and/or the surface area of the wing to create a force asymmetry between the two wings that will result in an angular acceleration around the roll axis. The angles of attack (α), and hence, the lift coefficients C_b of the wings can be independently altered

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by pronation or supination. By pronating the wing on the inside of the intended turn, and supinating the wing on the outside of the turn, the bird respectively decreases and increases the angle of attack of each wing (and hence, the lift coefficients), creating a lift-force asymmetry that rolls the animal into a bank. This is probably the most common mechanism of creating force asymmetry employed by gliding birds (Rüppell, 1977; Warrick and Dial, personal observation); indeed, its obvious use by gliding vultures was the inspiration for the wing-warping mechanism the Wright brothers developed for their first aircraft (Wright, 1900).

Birds may also reduce the surface area of the wing on the inside of the intended turn by simply flexing at the wrist and elbow. In so doing, the bird can not only completely eliminate the aerodynamic force created by the inside wing, but also greatly reduce the inertia of that wing, thus greatly facilitating rolling acceleration. In addition, reducing or eliminating the force produced by the inside wing alters the center of rotation of the roll. If no dorsally directed lift is created by the inside wing, either because of pronation to $\alpha = 0$, or flexion to $S = 0$, the body of the bird undergoes a purely "rotational roll" (Warrick and Dial, 1998), and only the inertia of the cross-section of the body and wings must be overcome to enter a bank. If lift continues to be produced on the inside wing, the center of rotation is shifted laterally toward the inside wing, and the body is lifted against gravity, reducing roll rate.

By whatever means, the elimination of lift on the inside wing is probably an important mechanism for birds with long, high-inertia wings. Observations of swallows maneuvering during gliding flight indicate that strong pronation of the inside wing is routine during hard maneuvering (Warrick, personal observation). Pronation and supination are kinematically compact, and probably quicker than flexion, and certainly more quickly executed than producing a velocity asymmetry by flapping. Further, if the inside wing can be pronated to an angle of attack < 0 , a ventrally directed aerodynamic force could be produced by this wing, which may more than compensate for the inertia of leaving the inside wing extended.

Birds can also use supination of a wing to manipulate drag rather than lift. Here, the wing on the *inside* of the intended turn is strongly supinated to beyond the critical angle of attack, stalling the wing and causing a large increase in drag on that wing. With this aerodynamic 'anchor' in place, the bird yaws strongly to the inside, which in turn, creates a greater velocity and lift on the outside wing, resulting in a bank. This mechanism is reported to be used by slowly flying gulls (Rüppell, 1977), and terns frequently use this pivoting turn as they roll into a dive after fish (Warrick and Dial, personal observation). The need to quickly stall the wing probably restricts the use of this mechanism to low-speed flight, when the wings are at a high angle of attack and more easily stalled.

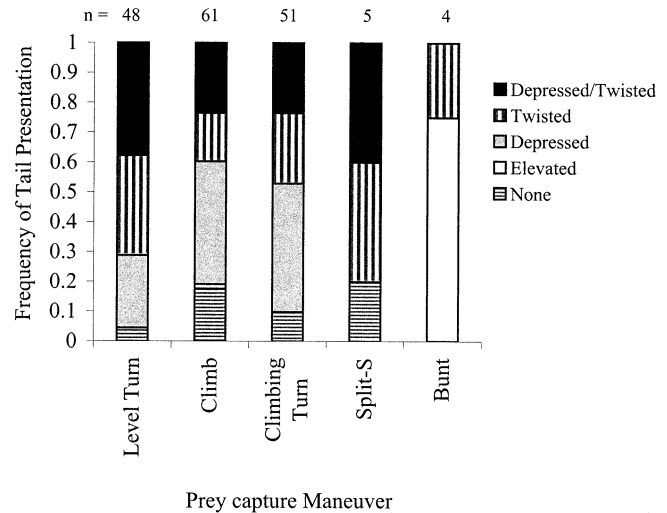


FIG. 1. Observed tail use by swallows during aerial prey capture maneuvers. Note that tail presentation for the pitchup (climbing) and pitch down (bunt) maneuvers are opposite of what would be expected if the tail was being used for pitch control.

Gliding flight: tail presentation

Beyond its theoretical capabilities (Hummel, 1992; Hoey, 1992; Thomas, 1993; Rayner, unpublished), the precise use of the tail in flying birds has not been thoroughly documented. Using models in windtunnels, Hummel (1992) described the lift produced by the tail and how the forces it produces might be used. Similarly, Thomas (1993) has estimated those forces using aerodynamic theory; both have suggested that the lift developed by the tail may be used for pitch control in the same manner as the elevators of an aircraft: With the tail depressed, the increase in lift posterior to the center of the bird's mass may cause the bird to pitch down, and, conversely, with the tail elevated, the bird to pitch up. Hoey (1992) demonstrated, using a gliding model of a raven, that the tail of such a bird may be used to function in this manner. However, observations of birds in the wild rarely confirm this use. Data taken from 60 Hz video of swallows and swifts during foraging indicate that during maneuvering swifts and swallows use the tail as a flap (that is, spread and depressed; Fig. 1) to increase total lifting area (*i.e.*, reduce wingloading), thereby reducing turning radius during hard turning and rapid pitch up maneuvers. Conversely, when pitching strongly down (bunting), the tail is frequently elevated, indicating the bird is using it to spoil lift and descend more rapidly. Strong pitch control in these birds apparently involves the protraction and retraction of the wings to move the center of lift anterior and posterior respectively, which in turn causes the bird to pitch up or down (Tucker, 1992). The most important use of the tail during maneuvering is probably in the compensation for the yawing moment created by asymmetrical lift during rolling. When a bird increases lift on the outside wing, there is a concomitant increase in drag on that wing, causing the bird to yaw away from the intended direc-

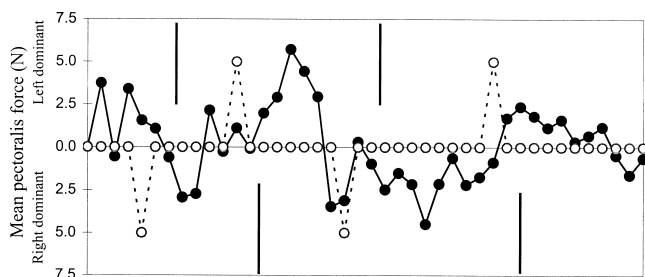


FIG. 2. Open markers (each point a single downstroke) represent the force asymmetry pattern expected if a bird were to fly through the obstacle course by simply creating a bank angle and holding that angle. Points above the symmetry line indicate a greater peak pectoral force production on the left wing; below the symmetry line, a greater right force. Solid markers represent actual force asymmetries of a pigeon flying through an obstacle course, gathered using bilateral strain gauges measuring peak humeral (at the delto-pectoral crest) deformation resulting from pectoralis contraction. Note that the pigeon moved incrementally through the course, using a sequence of force asymmetries.

tion of flight (adverse yaw). By twisting and depressing the tail, birds can produce a laterally directed lifting force that will yaw the bird back toward the turn (Hoey, 1992; Hummel, 1992; Thomas, 1993). Because of the relatively small aerodynamic forces produced by the tail, this mechanism is apparently not useful for birds during maneuvering in slow, flapping flight, even though adverse yaw is created during this type of flight (Warrick and Dial, 1998).

Flapping flight

To create a bank and effect a turn, a gliding bird must only produce a single force asymmetry between the two wings to create the bank, and another to arrest the momentum of the roll and stop the bank at the desired angle. A bird in slow, flapping flight might do the same, with the only difference from a gliding turn being the saltatory nature of lift production and the resulting flight path. However, a study of the force production of the pectoralis muscle of Rock Doves (*Columba livia*; henceforth “pigeons”) in slow flight through an obstacle course revealed that birds may produce a series of force asymmetries with each downstroke throughout the turn (Warrick *et al.*, 1998; Fig. 2). That is, rather than using one aerodynamic asymmetry to establish a bank angle, the birds produced greater force on the wing on the outside of the turn throughout the turn, and moved incrementally through turns during slow flight. Three-dimensional wing kinematics of pigeons later showed that pigeons produce these asymmetries with downstroke velocity asymmetries (Warrick and Dial, 1998), and that high angular accelerations (up to 2,000 radians sec^{-2}) were commonly produced with every downstroke. Moreover, the roll-initiating and arresting force asymmetries were frequently created in the same downstroke, with the birds producing a greater downstroke velocity on the outside wing during the first half of downstroke, and a greater downstroke velocity on the inside wing and during the second half of the downstroke to arrest

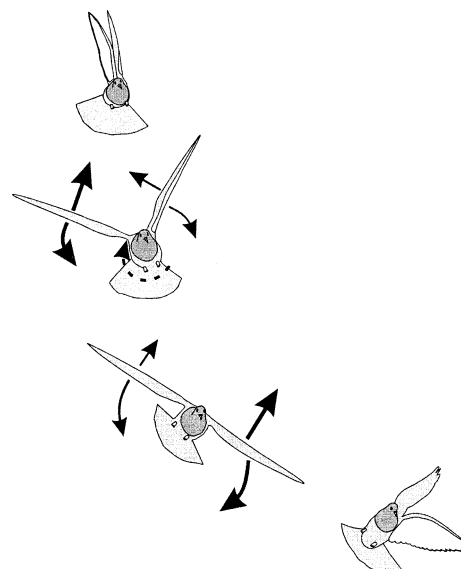


FIG. 3. (A) Pigeons produce force asymmetry (straight arrows) for a bank by creating velocity asymmetries (curved arrows) during the first half of the downstroke, and reversing the asymmetry during the second half of downstroke to arrest the rolling inertia.

the rolling momentum (Fig. 3). The birds also used asymmetries in upstroke velocity to alter bank angle during slow flight (also see Rüppeil, 1971).

The use of variation in downstroke and, to a lesser degree, upstroke velocity to maneuver suggests that the evolution of the pectoral girdle was key to both the high power requirements of slow flight and the ability to maneuver during it. Indeed, given that either ability alone is useless, and that the results of these studies on pigeons could be applied to other birds (*e.g.*, redstarts; Rüppeil, 1971), it seems likely that the extensive skeletal, muscular, and neural specializations of the pectoral girdle of birds are direct results of selective pressures to maneuver in slow flight.

THE UTILITY OF STEADY-STATE MODELS OF MANEUVERABILITY

Studies attempting to correlate flight morphology with ecology and flight behavior routinely assume steady-state models of maneuvering; that is, wing morphology (primarily wing loading and aspect ratio) is taken as the primary index of maneuverability (*e.g.*, Pennycuik, 1975; Norberg, 1986; Moermond, 1990; Bigham and Fenton, 1991; Yong and Moore, 1994; Marchetti *et al.*, 1995; Warrick, 1998). While such correlations make cogent inferences regarding the selective pressures that result in the most extreme flight morphologies (*e.g.*, no one doubts that the extraordinarily low wing loading of frigatebirds is key to their abilities as aerial kleptoparasites), they also tacitly infer that maneuvering performance is less important for species lacking such extreme form. Contrarily, we suggest that with but a few exceptions (again, ecomorphological outliers such as albatross), maneuvering performance—in particular, low-speed maneuvering

performance—is the single most important flight performance parameter for *all* birds, and one that has likely been the selective pressure resulting in the evolution of the majority of musculoskeletal adaptations for flight (Warrick *et al.*, 1998; Warrick and Dial, 1998). To make any suggestion using steady-state models that maneuvering performance is unimportant to birds with higher wingloadings is to reduce the functional morphology of a bird to that of a model airplane.

This is not to say that steady-state models of maneuvering performance are of no use, but rather that the inferences they make must be qualified, and a simple distinction made between the efficiency and efficacy of maneuvering flight. Low wing loading is not required for high maneuverability; any bird capable of producing mass specific power sufficient for slow, flapping flight can effect a turn of very small radius (“facultative maneuverability”; Warrick *et al.*, 1998). Particularly during landing, the vast majority of birds exhibit extreme feats of this type of maneuverability hundreds of times a day—if for only brief periods. It is this temporal component of maneuvering performance that is required to qualify the inference of steady-state models: Birds with low wing loadings are more efficient at maneuvering; when they need to make turns of small radii, they can do so without slowing and flapping—which is energetically much more expensive (Baudinette and Schmidt-Nielsen, 1974; Hails, 1979). Thus, for birds that spend a great deal of *time* maneuvering (*e.g.*, frigatebirds, swallows), low wing loading has clearly been a selective advantage—perhaps even ecologically defining (Norberg, 1986, 1990; Warrick, 1998). Conversely, if maneuvering is restricted to a few, short—but critical—moments (*e.g.*, takeoff and landing), efficiency of maneuvering becomes unimportant. In short, wing loading can be used as an index of steady-state performance and time spent maneuvering, but not as a measure of absolute maneuverability.

STABILITY: STAYING UPRIGHT

Why would selection favor the use of variation in downstroke velocity, and the often violent movements that result, as the means for maneuvering? Ironically, the answer may lie with wing loading. All birds—even the largest volant species, have relatively low wing loadings relative to, for example, airplanes. Combined with their extremely low inertia: surface area ratios, even the slightest change in incident air velocity over a bird’s wings and body can result in dramatic changes in flight path. Without authoritative mechanisms to compensate (pronation/supination and flexion/extension) during gliding flight, and downstroke velocity asymmetries during flapping flight), birds would be at the mercy of their frequently violently uneven locomotor substrate. To make matters worse, turbulence is unpredictable; unlike animals moving across a terrestrial substrate, volant animals have few—if any—visual cues that allow them to anticipate the vagaries in air. As a result, one might expect selection to have

resulted in extraordinary mechanisms allowing birds to react to such perturbations. The use of strong velocity asymmetries during flapping maneuvering is probably just such a mechanism. At high speed, changes in angle of attack produce large changes in aerodynamic force; that is, the short, quick muscle contractions of pronation/supination get big results, and are probably the most effective mechanisms to produce stabilizing asymmetries at high speed. However, during low speed flapping flight, angle of attack is probably close to maximum (Warrick and Dial, 1998), and its use as a producer of asymmetry is thus restricted. Moreover, since aerodynamic force produced varies as a function of the square of downstroke velocity, small asymmetries in bilateral pectoralis muscle contraction again produce strong reactions. As a matter of routine, birds seem to consistently use the most effective control mechanisms available to them given their mode of flight.

Gliding flight

Again, our understanding of stabilizing mechanisms employed by birds in gliding flight has traditionally been taken directly from aeronautical research. Curiously, the simplest and presumably cheapest way to enhance stability—dihedral (holding the wings slightly elevated relative to the body when gliding)—is rare, and only seen in large raptors with low wing loadings (harriers, vultures) that fly slowly in turbulent air. That many birds glide with some destabilizing anhedral (wings drooping slightly) suggests that the other stabilizing mechanisms available to them are more than adequate. Further, given that dihedral diminishes gliding performance, its infrequent use suggests that a premium is placed on maximizing lift to drag ratio (that is, maximizing efficiency) during gliding.

Whatever the case, pronation and supination as strong mechanisms, and the tail as a weaker mechanism in less turbulent air, are clearly used in stabilizing. It is currently unknown if muscle spindles (Maier and Eldred, 1971) or Golgi tendon organs (Haiden and Awad, 1981) are used to initiate spinal reflexes in reacting to turbulence. However, yawing moments of a pigeon’s body have been shown to elicit activity, through a neck reflex, in wing extensors, contralateral supinators and tail muscles that would correct the yaw (Bilo and Bilo, 1983), and similar responses to roll have been reported in pigeons (Brown, 1963). It is not difficult to imagine both ipsilateral and contralateral reflex arcs involving more proximal pronators (pectoralis, scapulohumeralis caudalis) and supinators (possibly the supracoracoideus; Poore *et al.*, 1997), as well as tail muscles such as the levator caudae and depressor caudae (Gatesy and Dial, 1996) participating in maintaining stability. Particularly interesting is the possible function of the *M. coracotriceps*, a small, slow tonic muscle found in many birds (Rosser and George, 1985). Extending between the origin of the expansor secundariorum and the insertion of the humerotriceps, this muscle is densely (nearly 15,000/g

muscle—fifteen times the density of any known muscle; Rosser and George, 1985) equipped with muscled spindles (Rosser and George, 1985). A reduced (once thought vestigial) portion of the triceps, this muscle would be particularly well-suited to detecting stretch in the triceps, which have been implicated in the supination of the wing (Dial and Gatesy, 1994).

We should also here note that birds are more stable in the roll axis than some models suggest (*e.g.*, Norberg and Rayner, 1987). Unless the inside wing creates no dorsally directed lift, the magnitude of the resulting angular acceleration from increased lift on one wing (*e.g.*, by turbulence) is not simply proportional to the ratio of this force to inertia of the rotating body. Any lifting force produced by the inside wing will move the center of rotation for the roll laterally, meaning that some or all of the mass of the bird (*i.e.*, the body) must be lifted against gravity by the force asymmetry (“translational roll”; Warrick and Dial, 1998). Thus, in terms of preventing unwanted roll, the most effective response to a turbulence-induced lift asymmetry would be an ipsilateral pronation reflex and contralateral supination.

Flapping flight

Flapping flight would seem less susceptible to extrinsic perturbation, although empirical evidence to support this intuition is lacking. Most researchers have noted that when flapping at higher speeds, birds rarely have tails spread (Thomas, 1993; Tobalske and Dial, 1994, 1996), and at lower speeds, simply hold them spread and depressed as a flap (Warrick and Dial, 1998), suggesting that they are not dependent upon the extra control afforded by the tail during these times. Flapping flight is probably more stable for several reasons: 1) during upstroke, the wings are at least partially folded (*e.g.*, Tobalske and Dial, 1994, 1996), reducing their exposure to turbulent air; 2) the rapid oscillation of the mass of the wings through the lateral plane creates a gyroscopic effect—that is, a laterally projected centrifugal force—that stabilizes the bird. The stabilizing effect of this force would be in the yaw and roll axes; pitch would be unaffected. Moreover, a portion of the aerodynamic force of the wings flapping through the downstroke arc is directed laterally, and would produce a similarly stabilizing effect.

The need of animals of low inertia and wingloading to maintain positive control using strong aerodynamic and kinematic mechanisms that produce high angular accelerations, coupled with the saltatory nature of lift production, makes low-speed flapping flight particularly rigorous. But while the skeletal adaptations for extreme rigidity (the synsacrum, notarium, uncinat processes of the ribs etc.) are often cited as an evolutionary response to the violence of flapping flight, other adaptations to the rapid oscillations of the body have largely been overlooked. Of particular relevance to the discussion of maneuvering/stability is the functioning of the optic and vestibular systems during this extremely energetic form of locomotion.

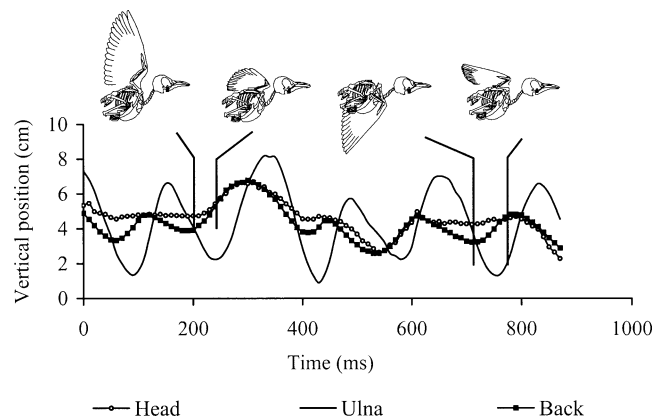


FIG. 4. Head (circles) and body (squares) vertical oscillations, and humeral excursion during the wingbeat cycle of a Black-billed Magpie taken from x-ray film (200 fps).

THE NEURAL CONTROL OF MANEUVERING AND STABILITY: ISOLATING THE VESTIBULAR AND VISUAL SYSTEM FROM EXTRANEOUS INPUTS

The vertical accelerations of unsteady flapping flight: the avian neck as a shock absorber

During flapping flight where lift production ceases during upstroke (“vortex-ring gait”; Rayner, 1988), a bird will experience downward accelerations due to gravity and upward accelerations due to lift. Among vertebrates, many forms of locomotion produce similar stresses, but only volant species would experience these oscillations ten times a second (a typical avian wingbeat frequency). There are at least two sensory functions that could be severely impacted by such rapidly alternating accelerations: vision, and static equilibrium. Vision might be affected by simply introducing extraneous visual flow. Similarly, the maculae of the inner ear, which in all vertebrates use the acceleration due to gravity to provide information regarding the position of the head (Kardong, 1995), would be subjected to accelerations that might compromise this function. Given that birds probably do not need to continuously confirm the vertical oscillations of the body during flapping flight, it follows that there may have been selective pressure to isolate the head from these vertical accelerations, leaving their eyes and maculae free to gather only useful information about their paths through and positions in space. Digitized (Videopoint 2.1) x-ray cine film (200 frames sec^{-1}) of a single Black-billed Magpie (*Pica pica*) flying in a wind tunnel at 8 m sec^{-1} show that they have the ability to isolate the head from the movement of the body during flapping flight. In level flight, the bird’s body fell an average (\pm standard deviation) of 1.44 ± 0.30 centimeters with every upstroke, while it restricted head vertical movement to as little as 0.14 cm during a wingbeat cycle (average for all wingbeats = 0.43 ± 0.21 centimeters; Fig. 4). The degree to which the bird decoupled vertical movement of the head and body appeared to depend on whether or not the bird was changing position in the tunnel test chamber. For ex-

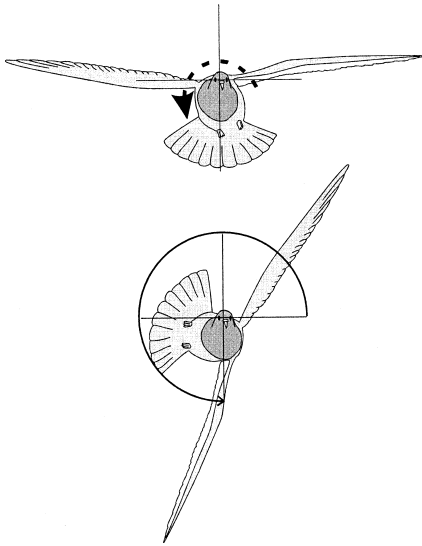


FIG. 5. Head nystagmus in a pigeon. Through approximately 270° of body roll, the bird will maintain a head level posture, and will not allow its head to rotate with the body until the roll has exceeded 300° .

ample, the head exactly followed the body during a brief climb, but was immediately isolated from the sinusoidal body excursion (as it was at the beginning of the series; Fig. 4) as soon as level flight was re-established. This suggests that the isolation of the head from the vertical accelerations may be important in allowing an uncluttered vestibular 'picture' of the bird's substantive changes in vertical position. While the anatomical details of this dampening mechanism are undescribed, a spinal reflex involving the flexors and extensors of the dorsal and ventral cervical musculature (*e.g.*, the semispinalis capitis, biventer cervicis; longus colli) seems likely.

The angular accelerations of rolling maneuvers: the importance of a fixed horizon

As in the case of vertical accelerations, no other vertebrates (except bats) would be subjected to angular accelerations of the magnitude (up to 2,000 radians sec^{-2} ; Warrick and Dial, 1998) and frequency observed in maneuvering birds. Birds have long been observed to have the ability and tendency to rotate their heads in the direction opposite of the roll (head nystagmus), and thus hold their heads level as their bodies rotate around the roll and yaw axes (Money and Correia, 1972; Bilo and Bilo, 1983; Bilo, 1994; Fig. 5). Moreover, video of aerially foraging swallows shows that not only is the head held level, but that rolling maneuvers are *always reversed* to re-establish level flight—even if the roll was over 270° (Warrick, personal observation). This complete aversion to rolling the head is remarkable (particularly in birds as acrobatic as swallows); indeed, only a few species are known to routinely roll 360° (*e.g.*, Common Ravens *Corvus corax*; Van Vuren, 1984). Because of the highly moveable saddle joints between the most cephalad

cervical vertebrae (Baumel, 1979), and because of the large number of these joints (birds possess from 13 to 25 cervical vertebrae), the range of nystagmic movement can be extreme (up to 270° on the longitudinal axis). Unlike eye nystagmus, which maintains only a fixed visual field of reference, the head nystagmic reflex also isolates the semi-circular canals from the rotational acceleration of the roll. The advantage of isolating the semicircular canals is unclear, but it is tempting to speculate. Because the semicircular canals only respond to acceleration, they cease to provide roll information after the initial banking force asymmetry has ceased. By holding the head still, neither the eyes nor the semicircular canals will sense the roll; conversely, if the head were rolled with the body, the eyes would detect roll, but after the initial force asymmetry of bank initiation ended the semicircular canals would not—even if the bird were still rolling. Furthermore, at the end of the roll, the deceleration would be detected by the semicircular canals—an input indistinguishable from a rotation the direction opposite from the just-completed roll. In most vertebrates, this deceleration input is accompanied by eye nystagmus (again, in a direction opposite to the original nystagmus accompanying the roll). However, because of their relatively fixed eyes, birds cannot exhibit this reflex without moving the entire head—which would then subject the semicircular canals to another angular acceleration. In short, lacking eye mobility, birds may not be able to “end” vestibular nystagmus without creating irreconcilable visual and vestibular inputs—and such inputs may produce a loss of equilibrium that birds can ill-afford. By isolating both systems, birds may ensure that the stable visual cues are always corroborated by stable vestibular cues. However, previous studies suggested that not all birds consistently exhibit this behavior (Money and Correia, 1972). Furthermore, while vestibular inputs have been implicated in reflexive control of flight muscles (*i.e.*, the flexors, extensors, and supinators of the wing; Bilo and Bilo, 1978, 1983) in a pigeon held in a harness, this mechanism has not been examined in a flying bird.

In a preliminary effort to clarify if and when birds tend to isolate their vestibular and visual systems from the angular accelerations of roll, and the importance of this isolation to flight performance, we subjected two pigeons to angular accelerations just before we released them to fly to a perch. The birds flew several flights with and without a collar that could be adjusted to restrict their head rotation to as little as 30° , thereby forcing their heads to follow their bodies when rolled by the handler. The collar was a plastic tubular sleeve (20 mm inside diameter, 8 cm long, 3.7 g), with a longitudinal slit, fitted around the neck such that it did not restrict breathing but prohibited the animal from moving its head independently of the body. The animal was able to hold its head upright, but was unable to rotate or retract its head. As a result, both angular and vertical accelerations experienced by the body were translated directly to the head. The rotational acceler-

ation experienced by the body and the head were then measured by digitizing (Video Point) high speed video (Red Lake Inc.; 250 fps) of the flights. Their performance in recovering from handler induced rolls was compared with that when they were allowed complete range of cervical movement. Vertical accelerations resulting from the handler's release were also documented, although we could not distinguish between head and body acceleration. A mattress was placed beneath the flight path, in the event that birds were unable to continue normal flight. The birds were also released with no rotation or bank angle, and at various static (that is, no rotational acceleration) bank angles (up to 180°).

Two birds flew forty-four trials (twenty-two each), seven (six by pigeon 1, one by pigeon 2) of which were without the restrictive collar. Without the collar, the birds were able to, through head nystagmus, reduce or completely eliminate the rolling angular accelerations experienced by the body (maximum body acceleration = 10,819° sec⁻², mean = 4,514 ± 2,969° sec⁻²; maximum head acceleration = 1,594° sec⁻², mean = 418 ± 555° sec⁻²), and displayed no difficulty recovering from any induced roll. In contrast, when the birds wore the restrictive collar, and were thus unable to isolate the head from vertical and roll accelerations (mean body angular acceleration = 3,588 ± 1,950° sec⁻²; mean head angular accelerations = 2,721 ± 3,206° sec⁻²), in thirteen of thirty-six flights (33.33%) the birds were unable to complete the flight to the perch, flying out-of-control to the mattress (*i.e.*, they crashed). In the one remaining flight with a collar the bird was released with no vertical or angular acceleration, and flew normally. Considering only those flights where some angular acceleration was induced, the birds crashed eleven of twenty-two (50%) flights; for flights where only vertical acceleration was induced, the birds crashed twice in fourteen flights (14%). In a logistic regression model including head angular acceleration, and body angular and vertical acceleration, only the head angular acceleration coefficient was significant ($P = 0.04$). However, the model was a poor predictor of the probability of crashing, correctly predicting only 30% of the crashes.

The sequence of events during these crashes was consistent: the birds initially righted themselves, reversing the direction of the induced roll with one wingbeat, but then quickly (<200 m sec; maximum of two wingbeats) lost equilibrium. They continued to flap powerfully, frequently pitching up dramatically and tumbling end over end until they tumbled to the ground [mattress]. In all cases, after the birds landed, they regained their equilibrium, and took off normally from the mattress and flew straight to the perch.

To further investigate how the collar and limited head mobility affected flight performance, the pigeons were flown through a slalom obstacle course of acetate barriers (for a complete description of the course, see Warrick *et al.*, 1998). Without the collar, the birds flew quickly through the course, banking normally (Warrick

et al., 1998); with the collars restricting head movement, the birds flew very slowly through the course without banking—a kind of moving hover, where turns were effected by a series of yawing moments. This behavior, taken with their ability to take off from the ground normally strongly suggests that the collar had the desired effect: it only prevented the birds from isolating their heads from the angular accelerations of roll.

The variation in induced roll recovery performance with the collar may be a result of error in measuring head excursion (from two-dimensional views) and thus the angular acceleration and visual flow experienced by the vestibular and visual systems of the bird. It may also be that the accelerations we imposed were beneath the threshold for disrupting the bird's equilibrium. Our peak induced body angular acceleration of 10,819° sec⁻² is lower than the average acceleration in roll observed in pigeons in slow maneuvering flight (34,377° sec⁻²; Warrick and Dial, 1998). Whatever the case, further study is required to fully illuminate the role and limitations of the vestibular and visual system in birds. Of particular interest would be the performance of a strain of pigeons known as "tumbler," which are known (and prized) for their tendency to tumble about their longitudinal axis while in flight. The precise nature of this behavior is unclear (*i.e.*, purposeful display or neurological defect), but these birds offer a possible phylogenetically controlled contrast to the more typical pigeon behavior described here.

The graceful—even sedate—impression we have of bird flight (largely a product of our own poor sampling rate) belies a violent physical reality. The ability to eliminate the sensory clutter created by their own locomotion may have been an extremely important step for birds to fully realize the ecological and evolutionary potential of flight—a step that may have been taken on the ground. Vestibular and visual isolation may well be selected for in highly active bipeds; if so, the cervical structure of theropods may have been pre-adapted for the rigors of flapping flight. However, the transition from cursorial to aerial locomotion and maneuvering was not as simple as growing large wings. Wing planform of early fliers (*e.g.*, *Archaeopteryx*, *Eoalulavis*) can be used as an index of gliding maneuvering performance and the efficiency of maneuvering flight, but it provides little insight into maneuverability during low-speed, flapping flight—and within this regime resides the story of the evolution and diversification of birds.

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