Mechanisms and Implications of Animal Flight Maneuverability[1]

Robert Dudley[2]

Section of Integrative Biology, University of Texas, Austin, Texas 78712 and
Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama

Synopsis.   Accelerations and directional changes of flying animals derive from interactions between aerodynamic force production and the inertial resistance of the body to translation and rotation. Anatomical and allometric features of body design thus mediate the rapidity of aerial maneuvers. Both translational and rotational responsiveness of the body to applied force decrease with increased total mass. For flying vertebrates, contributions of the relatively heavy wings to whole-body rotational inertia are substantial, whereas the relatively light wings of many insect taxa suggest that rotational inertia is dominated by the contributions of body segments. In some circumstances, inertial features of wing design may be as significant as are their aerodynamic properties in influencing the rapidity of body rotations. Stability in flight requires force and moment balances that are usually attained via bilateral symmetry in wingbeat kinematics, whereas body roll and yaw derive from bilaterally asymmetric movements of both axial and appendicular structures. In many flying vertebrates, use of the tail facilitates the generation of aerodynamic torques and substantially enhances quickness of body rotation. Geometrical constraints on wingbeat kinematics may limit total force production and thus accelerational capacity in certain behavioral circumstances. Unitary limits to animal flight performance and maneuverability are unlikely, however, given varied and context-specific interactions among anatomical, biomechanical, and energetic features of design.

Introduction

The ability to alter flight speed, trajectory, and body orientation underlies the evolution of flapping flight. Generation, regulation, and transient disruption of aerodynamic forces are required if volant taxa are successfully to orient and maneuver in three dimensions. In hovering or in flight at constant airspeed, total forces acting on the center of body mass as well as rotational moments about each of the three orthogonal body axes are necessarily balanced. Such circumstances are likely to be the exception rather than the rule, however, for animals flying in turbulent air or through obstacle-laden natural environments. Flight must then require continuous corrections to a nominally stable equilibrium. Similarly, various contexts of natural and sexual selection impose demands for linear accelerations, rapid directional change, and evasive responses. Maneuverability via force and moment vectoring is correspondingly a well-recognized feature of pterygote insects and of flying vertebrates (see Norberg, 1990; Dudley, 2000).

Active control of aerial trajectories likely arose early in flight evolution (Maynard Smith, 1952). Flight stability in many taxa is, in part, enabled by restorative aerodynamic torques generated passively on the body and wing structures by the prevailing flow field. However, active generation of rotational torques ensures a rapid response to unintentional course change, and moreover allows for intentional course deviations. Even extant gliding taxa such as some rhacophorid frogs are impressively maneuverable via such mechanisms (see Emerson *et al.*, 1990; Emerson and Koehl,

1990). Among terrestrial vertebrates, gliding behavior has arisen independently multiple times. Most of these lineages are sufficiently flight-capable not only to maintain equilibrium glide trajectories, but also to choose landing sites, make mid-course deviations, and in general enhance kinematic variability in what biologists have otherwise viewed as stereotypical glide paths. Intentional asymmetric deployment of various aerodynamic surfaces about different body axes must underlie such directional changes.

The concept of maneuverability has been variously applied in the animal flight literature, but most generally indicates the ability to change the speed and direction of movement. Application of steady-state aerodynamic theory to flight maneuvers has yielded some insight into the morphological and kinematic underpinnings of turning ability. For example, the minimum radius necessary to make a level banked turn is known to be, for a constant lift coefficient, proportional to the wing loading (Pennycuick, 1971). Such level turns are, however, likely to be rare among flying taxa. Moreover, flapping flight necessarily involves unsteady aerodynamic forces and associated rotational moments, the magnitude of which cannot be predicted using steady-state aerodynamic theory (see Ellington *et al.*, 1996; Dickinson *et al.*, 1999). Most animal flight maneuvers also consist of sequential changes in body orientation and flight velocity that compose a complicated three-dimensional trajectory (*e.g.,* chasing of a conspecific, or full reversal of body orientation). Both the magnitude and direction of aerial locomotor responses are context-specific, volitional in nature, and dependent on unsteady forces generated by flapping wings.

The concepts of axial and torsional agility are fundamental to all measures of animal flight maneuver-

ability. Agility in general refers to the quickness of movement, and more specifically to the rapidity of change in speed and direction. Axial agility involves the capacity to accelerate in the forward, lateral, and vertical dimensions, whereas torsional agility indicates capacity for rotational acceleration about each of the three mutually orthogonal body axes (*i.e.,* roll, pitch, and yaw; see Fig. 1). Maneuvers involve production of either linked or temporally decoupled rotations about orthogonal body axes, together with modulation of vertical forces, thrust, and sideslip. More derived aspects of maneuverability involve the capture and holding of particular dynamic states, the capacity to sustain maximal forces and torques, and the ability to either link or decouple particular sets of body rotations and translations (see Dudley, 2000). Because so little is known about these latter features of flight performance, discussion of flight agility is here confined to translational and rotational accelerations. Similarly, higher-order derivatives of position with respect to time (*e.g.,* jerk, or the rate of change of acceleration) have received minimal experimental attention and are not considered here.

As earthbound primates, humans generally interpret the concept of acceleration within the boundaries of rectilinear translation. Our ability to walk and run primarily involves two translational degrees of freedom (forward and lateral motion) and one rotational degree of freedom (yaw). By contrast, flight transcends terrestrial locomotor capacity by permitting motion in a third spatial dimension, as well as by dramatically enhancing locomotor possibilities through the addition of two rotational degrees of freedom (pitch and roll). Rotational accelerations may be as important as translational ones in certain aerial contexts, and torsional agility likely assumes a much greater significance for flying animals than is the case for terrestrial taxa. A total of six degrees of kinematic freedom characterizes aerial locomotion, complicating quantitative analysis but greatly enhancing possibilities for displays, pursuit and escape strategies, and other three-dimensional flight behaviors.

AXIAL AND TORSIONAL AGILITIES

Axial agility derives from transient changes in vertical, horizontal, and lateral forces generated by the flapping wings. In the modulation of vertical forces, wing motions are bilaterally symmetric and an increase in stroke amplitude appears to be the predominant means of increasing total aerodynamic force (*e.g., Drosophila*: Lehmann and Dickinson, 1998; hummingbirds: Chai and Dudley, 1995; Chai *et al.*, 1997). Modulation of forward thrust derives primarily from reorientation of an otherwise vertically directed aerodynamic force vector that acts predominantly to offset gravity. Variable partitioning of this output vector between vertical and horizontal components results mostly from changes in body orientation, namely in pitch relative to horizontal. Rapidity of thrust generation is accordingly coupled to torsional agility in pitch. Ad-
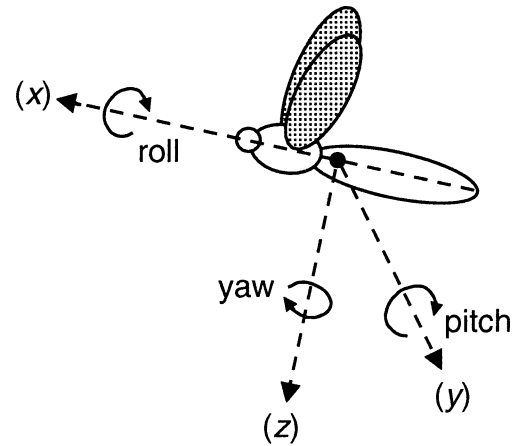

FIG. 1. Free-flying animals are characterized by three rotational and three translational degrees of kinematic freedom. Gravity acts through the center of body mass, which biomechanically is the most appropriate choice for the origin of the three orthogonal body axes. Note that the longitudinal body axis is not necessarily horizontal.

ditional kinematic features such as changes in stroke plane angle and increased wing rotational velocities during pronation and supination may also yield unsteady aerodynamic forces involved in production of thrust (Dickinson, unpublished). As with horizontal forces, lateral accelerations of the body are generally associated with simultaneous body rotation, and most typically with roll. Sideslip without noticeable body rotation is apparently confined to certain Diptera (see Collett and Land, 1975; Nachtigall, 1979).

Because so few data are available on the accelerational capacities of volant forms, biomechanical limits to axial agility are unclear. Vertical force production in hovering flight is limited by the maximum stroke amplitude for at least some flying taxa (see Dudley, 2000). In forward flight, however, wing flapping velocities are augmented by the translational airspeed, an effect which partially mitigates aerodynamic demands on wingbeat kinematics. Hummingbirds, for example, fail to sustain hovering flight at stroke amplitudes near 180°, but in fast forward flight exhibit stroke amplitudes well below this value (see Greenewalt, 1960; Chai and Dudley, 1995). Because of aforementioned coupling between thrust and body orientation, the rapidity of horizontal displacements is likely constrained by the rapidity of changes in body pitch. Such angular accelerations, in turn, depend both on the magnitude of applied torque and on the inertial responsiveness of the body (see below). As an extreme example of agility in forward flight, the steeply inclined stroke plane angles seen in some hoverflies enable rapid forward acceleration by facilitating reorientation of the net aerodynamic force vector with little or no change in body angle (Ellington, 1984*b*; Ennos, 1989). Some of the highest horizontal accelerations described for insects have in fact been derived for hoverflies (see Dudley, 2000), although axial agilities generally have never been systematically compared among taxa.

Torsional agility refers to the rapidity of change in

body roll, pitch, and yaw. Such rotations may act either together with or independently of translational accelerations, and the extent to which body rotations may simultaneously impede axial agility (or *vice versa*) is unknown. Alteration of body pitch can derive from bilaterally symmetric changes in stroke amplitude, stroke plane angle, mean positional angle of the wings, or angle of attack at any stage of the flapping cycle. More derived kinematic features, such as wing rotational velocities or contralateral wing proximity at either end of the half-stroke, may also contribute to variable pitching moments and alterations of body angle during flight. In contrast, bilaterally asymmetric motions of the wings, legs, or body segments yield the rotational moments underlying body roll and yaw. Pigeons, for example, use bilateral asymmetry in the downstroke velocity to generate banked turns (Warrick and Dial, 1998). For tethered and free-flying animals, a wide variety of wing kinematic asymmetries underlying rotational moments has similarly been identified (see Norberg, 1990; Dudley, 2000). Leg and abdominal deflections are known in insects to contribute to yawing, pitching, and even rolling moments (*e.g.,* Götz *et al.*, 1979; Zanker, 1990; Lorez, 1995). Anatomical or motor asymmetries do not necessarily preclude stable flight. For example, damage to or even loss of one wing (in insects with two wing pairs) can result in compensatory asymmetric kinematics to achieve symmetric force production and rectilinear flight trajectories (see Dudley, 2000).

The angular acceleration of an object about any axis equals the ratio of the applied torque to the moment of inertia about the rotational axis in question. Lower moments of inertia will therefore increase torsional agility. In both pitch and yaw, body responsiveness to aerodynamic torque is enhanced if the distance between the wing base and the center of body mass is reduced. For example, the evolutionary tendency within Diptera towards reduction in the number of abdominal segments likely increases body responsiveness in pitching (see Komárek, 1929; Ellington, 1984a). Neotropical butterfly species better capable of evading avian predators exhibit body centers of mass that are relatively closer to the wing base axis, consistent with reduced rotational inertia of the body and greater rapidity of changes in body angle (Srygley and Dudley, 1993). However, experimental manipulations of the center of body mass for one butterfly species yielded no change in evasive capacity relative to net-wielding humans (Srygley and Kingsolver, 2000). Agility-related features of body design have not been determined in flying vertebrates, in part because the relevant rotational axis and centers of aerodynamic force production are harder to identify. It would, however, be of great interest to compare relative body elongation and mass distribution among highly maneuverable bats and birds.

Because animal bodies are generally longer than they are wide, moments of inertia in roll about the longitudinal body axis have been generally assumed to be less than in pitch and yaw. However, the dependence of moment of inertia on the square of the distance of mass from a rotational axis indicates that the contributions of wing mass to total rotational inertia can be considerable. Wings of flying vertebrates represent about 10–15% of total body mass, and are often longer than the body (see Thollesson and Norberg, 1991; van den Berg and Rayner, 1995). In eight bat species, moment of inertia in roll is dominated by that of the wings, which contribute on average 93% of the total roll inertia (Thollesson and Norberg, 1991). For twenty-one Panamanian butterfly species ranging in body mass from 65 to 1,054 mg, wing inertia averaged 87% of total roll inertia (unpublished data, R. Dudley). However, roll inertia of the wing-body system in these butterflies was only about 1% of the inertia in pitch and yaw about the center of body mass, suggesting a much faster inertial response about the roll axis. No kinematic data are presently available to test this hypothesis for butterflies. Note also that inertial contributions of wing virtual mass during body rotation are not included in these estimates because of the unknown magnitude of angular accelerations during actual maneuvers. In contrast to the long and heavy wings of many Lepidoptera, relative wing size is much lower in dipterans and hymenopterans, and presumably in other insect taxa characterized by high wingbeat frequencies (see Ellington, 1984a; Dudley, 2000). Reduced wing contributions to rotational inertia may in part underpin the apparently greater agility of such taxa, although the parallel effects of smaller total body size may also be important (see below).

Flying vertebrates differ from insects in that an often elongate tail may contribute aerodynamically to torsional agility. The uropatagial membrane in most bats is attached to the hindlegs and to the tail vertebrae; modification of airflow over the body is likely in steady forward flight, whereas rotational moments can be generated on the uropatagium via asymmetric hindlimb motions. In birds, muscles at the base of the tail are phasically active and dynamically versatile during wing flapping (*e.g.,* Gatesy and Dial, 1993; Bilo, 1994). Active contributions of the tail to roll, pitch, and yaw are all likely possibilities. Aerodynamic models of the avian tail (*e.g.,* Thomas, 1993) typically exclude flow interactions with the body (Rayner, unpublished), whereas further complexities involved in modelling tail function include dynamically variable fan angles, unsteady forces on the tail during maneuvers, and aeroelastic twisting of individual tail feathers that may enhance force and moment production (see Norberg, 1994). Artificial manipulation of feathers provides an experimental means of testing many of these possibilities, although it is essential to measure aerodynamic responses directly, rather than to infer performance characteristics indirectly from such measures as foraging efficiency (*e.g.,* Cuervo *et al.*, 1996). In barn swallows, reduction of tail streamer length impairs a number of measures of flight maneuverability

(Buchanan and Evans, 2000), a finding consistent with a direct aerodynamic role of the tail in torsional agility.

Alone among flying animals, birds regularly replace their aerodynamic surfaces via an annual molt. The energetic costs of feather replacement are well-known to be high, but perhaps of equal significance is an increase in the metabolic cost of flight and a reduction in maneuverability for molting birds (see Chai, 1997; Swaddle and Witter, 1998; Rayner and Swaddle, 2000). Intriguingly, morphological asymmetries between wings have comparable effects on flight performance of starlings (Swaddle *et al.*, 1996), and such costs may not be confined to avian fliers. For example, houseflies captured by barn swallows exhibit a greater wing asymmetry relative to their uncaptured counterparts (Møller, 1996). Consequences of such asymmetries for axial and torsional agility have not been measured directly in insects, but represent fertile ground for experimental manipulation.

THE ALLOMETRY OF MANEUVERABILITY

The mass of flying animals ranges over many orders of magnitude. Allometric influences on flight performance are particularly striking when we consider the largely non-overlapping body size distributions of insects and of bats and birds. The positive allometry of flight speeds ensures that translational speeds of volant vertebrate predators substantially exceed those of their insectan prey (see Norberg, 1990; Dudley, 2000). However, successful predation and evasion obviously derive from features of flight performance supplemental to absolute airspeed. Under isometric size change, translational accelerations should scale as $mass^{-1/3}$, whereas the magnitude of rotational acceleration of an object about any axis varies theoretically in proportion to $mass^{-2/3}$ (see Andersson and Norberg, 1981; Vogel, 1988). Smaller taxa may thus be more successful in behavioral contexts requiring a high degree of aerial agility. For example, success in mate capture is inversely proportional to body size in a number of insect taxa (see Convey, 1989; Banks and Thompson, 1985; McLachlan and Allen, 1987). Do such outcomes derive biomechanically from an enhanced maneuverability in smaller individuals?

Empirical consequences of body size for maneuverability, and specifically for axial and torsional agilities, have been largely limited to investigation of the maximum capacity of flying animals to lift vertical loads. By progressively attaching weights of increasing mass to various insects, bats, and birds, Marden (1987) determined the amount of weight that test animals were unable to lift during takeoff. These data suggest that maximum lifting capacity scales overall with muscle mass (and presumably body mass) to the power 1.0, although vertical accelerations were not measured directly in this study (see Dudley, 2000). By contrast, use of a modified load-lifting method (Chai *et al.*, 1997) revealed a negative intraspecific allometry for vertical lifting capacity in a Neotropical orchid bee species (unpublished data, M. Dillon and R. Dudley).

Studies with hummingbirds using this modified method moreover suggest an inverse relationship between peak performance and lifting duration (Chai and Millard, 1997). The ability to sustain force production may be just as important as the absolute level of performance in some behavioral contexts. In particular, metabolic underpinnings to features of axial agility cannot be excluded. Because of these and other factors (including the confounding effects of phylogenetic relatedness among species), the empirical allometries of vertical force and associated power production are best regarded as unresolved for flying animals (see Dudley, 2000).

At present, no experimental data address the maximum rotational capacities of either insect or vertebrate taxa. Reconstruction of roll, pitch, and yaw angles during maneuvers is technically challenging (see Wagner, 1986*a*; Schilstra and van Hateren, 1999), and neither typical nor maximum angular accelerations have been compared among different flying animals. In addition to features of body design, relative wing size may also influence the allometry of torsional agility. In both bats and birds, wing mass increases in proportion to total mass to the power 1.1 (see Thollesson and Norberg, 1991; van den Berg and Rayner, 1995). Larger vertebrate taxa thus tend to have relatively heavier wings, potentially increasing the relative inertial resistance of the wing-body system to rotation. By contrast, wing area of insects scales in proportion to body mass to the two-thirds (Dudley, 2000), and wing mass presumably also scales isometrically. Wing moments of inertia are influenced by the spanwise distribution of wing mass as well as by the total wing mass, however, and wing location relative to the body at the initiation of turns will also contribute to the instantaneous inertial responsiveness of the system. Instantaneous wing position during maneuvers may thus have important inertial as well as obvious aerodynamic consequences.

SEX AND DEATH:
THE THREE-DIMENSIONAL PERSPECTIVE

Flight by animals involves continuous course corrections and directional changes over various time scales, but actual use of the intrinsic capacity for maneuverability remains largely undescribed for most naturally occurring behaviors. General features of wing and body kinematics that contribute to flight agility have been broadly delineated, but biomechanical understanding of three-dimensional flight trajectories and maneuvers is much less complete. For example, chasing by territorial flies of intruders involves continuous readjustment of forward, lateral, and torsional velocities (*e.g.,* Collett and Land, 1975; Wagner, 1986*b*; Zeil, 1993). In such behavioral contexts, torsional and axial agilities may not be as important as the ability to carry out a linked series of directional changes. Models of optimal tracking and evasion strategies during two-dimensional predator-prey interactions have assumed constant translational velocities for the participants (*e.g.,* Howland, 1974; Weihs and Webb,

1984), whereas three-dimensional chases likely involve both rotational and translational accelerations. Conversion of potential to kinetic energy is a further possibility during aerial interactions.

Evolutionary selection for enhanced flight performance will be greatest in the contexts of predation and sexual selection. Variation in body mass alone is known to influence the outcome of such events. In birds, for example, increases in total body mass via lipid deposition reduce takeoff accelerations and the ability to escape from predators (Hedenström, 1992; Witter and Cuthill, 1993). This effect has been sufficiently pronounced as to have influenced historical patterns of fat deposition by great tits in the face of variable predation intensity by sparrowhawks (Gosler et al., 1995). The rapid maneuvers and accelerations associated with aerial mate capture further illustrate the critical importance of axial and torsional agilities. For example, dragonflies with attached weights exhibit reduced mating success relative to unmanipulated counterparts (Marden, 1989). Implications of weight-loading for flight performance are nonetheless likely to be taxon- and context-specific. For example, butterflies to which weights have been attached exhibit no systematic reduction in field survivorship relative to controls, although the impact of predator-induced mortality is not known in these cases (see Srygley and Kingsolver, 2000; Kingsolver and Srygley, 2000).

Relevant components of axial and rotational agility may also vary according to behavioral context. For example, success at territorial defense in one dragonfly species increases with increasing body length, whereas mating success is highest at intermediate body lengths (Moore, 1990). Different size-related features of maneuverability undoubtedly influence the outcome of such distinct types of aerial interaction. By way of extremes in the insect order Odonata, helicopter damselflies (Pseudostigmatidae) are an exclusively New World taxon noted for large body size (wing lengths up to 88 mm) together with very low wingbeat frequencies (see Fincke, 1992). These predators capture orb-weaving spiders by hovering in front of the web, adeptly flying forwards, grabbing the prey, and then rapidly reversing direction to avoid entanglement. Nonetheless, such insects are remarkably easy to catch, and may in fact be unpalatable to vertebrate predators (O. M. Fincke, personal communication.). Any comparative study of flight maneuverability among different taxa requires modern phylogenetic approaches if such potentially confounding influences on adaptation are to be identified.

For many flying animals, natural and sexual selection likely work in concert to promote enhanced maneuverability. For example, flying insects are regularly the subject of attack by insectivorous birds and bats. Males of many insect species also attempt to capture females during chases, selecting for maneuverability in the context of mate choice (Thornhill and Alcock, 1983). Dragonflies well illustrate the multiple selective forces acting on flight performance. Male dragonflies defend territories and chase out male conspecifics (intrasexual selection), pursue mates (intersexual selection), capture prey items in the air (natural selection for aerial pursuit), and evade both aerial and terrestrial predators via flight (natural selection for escape). Traits that are under sexual selection can evolve rapidly (Andersson, 1994), and synergistic interaction between such varied selective forces has likely promoted rapid evolution in diverse features of maneuverability. Reciprocal escalation between biotic selective agents and the target of selection is another likely outcome of such interactions (see Vermeij, 1987), promoting ever-increasing levels of performance. According to biological context, different morphological, biomechanical, and energetic traits interact with one another and contribute to overall aerial agility. Unitary definitions of maneuverability seem particularly unrealistic when considering the multiple and varying aerial demands required of animals over geological timescales.

REFERENCES

Andersson, M. 1994. *Sexual selection.* Princeton Univ. Press, Princeton.

Andersson, M. and R. Å. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biol. J. Linn. Soc. 15:105–130.

Banks, M. J. and D. J. Thompson. 1985. Lifetime mating success in the damselfly *Coenagrion puella*. Anim. Behav. 33:1,175–1,183.

Bilo, D. 1994. Course control during flight. *In* M. N. O. Davies and P. R. Green (eds.), *Perception and motor control in birds*, pp. 227–247. Springer Verlag, Berlin.

Buchanan, K. L. and M. R. Evans. 2000. The effect of tail streamer length on aerodynamic performance in the barn swallow. Behav. Ecol. 11:228–238.

Chai, P. 1997. Hummingbird hovering energetics during moult of primary flight feathers. J. Exp. Biol. 200:1,527–1,536.

Chai, P., J. S. C. Chen, and R. Dudley. 1997. Transient hovering performance of hummingbirds under conditions of maximal loading. J. Exp. Biol. 200:921–929.

Chai, P. and R. Dudley. 1995. Limits to vertebrate locomotor energetics suggested by hummingbirds hovering in heliox. Nature 377:722–725.

Chai, P. and D. Millard. 1997. Flight and size constraints: Hovering performance of large hummingbirds under maximal loading. J. Exp. Biol. 200:2,757–2,763.

Collett, T. S. and M. F. Land. 1975. Visual control of flight behaviour in the hoverfly, *Syritta pipiens* L. J. Comp. Physiol. A 99:1–66.

Convey, P. 1989. Influences on the choice between territorial and satellite behaviour in male *Libellula quadrimaculata* Linn. (Odonata: Libellulidae). Anim. Behav. 109:125–141.

Cuervo, J. J., F. de Lope, A. P. Møller, and J. Moreno. 1996. Energetic cost of tail streamers in the barn swallow (*Hirundo rustica*). Oecologia 108:252–258.

Dickinson, M. H., F. O. Lehmann, and S. P. Sane. 1999. Wing ro-

tation and the aerodynamic basis of insect flight. Science 84: 1954–1960.

Dudley, R. 2000. *The biomechanics of insect flight*: *Form, function, evolution*. Princeton Univ. Press, Princeton.

Ellington, C. P. 1984*a*. The aerodynamics of hovering insect flight. II. Morphological parameters. Phil. Trans. R. Soc. London B 305:17–40.

Ellington, C. P. 1984*b*. The aerodynamics of hovering insect flight. VI. Lift and power requirements. Phil. Trans. R. Soc. London B 305:145–181.

Ellington, C. P., C. van den Berg, A. P. Willmott, and A. L. R. Thomas. 1996. Leading-edge vortices in insect flight. Nature 384:626–630.

Emerson, S. B. and M. A. R. Koehl. 1990. The interaction of behavioral and morphological change in the evolution of a novel locomotor type: ''Flying'' frogs. Evolution 44:1,931–1,946.

Emerson, S. B., J. Travis, and M. A. R. Koehl. 1990. Functional complexes and additivity in performance: A test case with ''flying'' frogs. Evolution 44:2153–2157.

Ennos, A. R. 1989. The kinematics and aerodynamics of the free flight of some Diptera. J. Exp. Biol. 142:49–85.

Fincke, O. M. 1992. Behavioural ecology of the Giant Damselflies of Barro Colorado Island, Panama (Odonata: Zygoptera: Pseudostigmatidae). *In* D. Quintero and A. Aiello (eds.), *Insects of Panama and Mesoamerica*: *Selected studies*, pp. 102–113. Oxford Univ. Press, Oxford.

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

Gosler, A. G., J. J. D. Greenwood, and C. Perrins. 1995. Predation risk and the cost of being fat. Nature 377:621–623.

Götz, K. G., B. Hengstenberg, and R. Biesinger. 1979. Optomotor control of wing beat and body posture in *Drosophila*. Biol. Cybern. 35:101–112.

Greenewalt, C. H. 1960. *Hummingbirds*. Doubleday & Co., Garden City.

Hedenström, A. 1992. Flight performance in relation to fuel load in birds. J. Theor. Biol. 158:535–537.

Howland, H. C. 1974. Optimal strategies for predator avoidance: The relative importance of speed and maneuverability. J. Theor. Biol. 47:333–350.

Kingsolver, J. G. and R. B. Srygley. 2000. Experimental analyses of body size, flight and survival in pierid butterflies. Evol. Ecol. Res. 2:593–612.

Komárek, J. 1929. Die Reduktion des Dipterenkörpers aus flugtechnischen Ursachen und die morphologisch-systematischen Folgen. Proc. Tenth Int. Congr. Zool., Budapest, 1927, pp. 1,060–1,067.

Lehmann, F.-O. and M. H. Dickinson. 1998. The control of wing kinematics and flight forces in fruit flies (*Drosophila*) species. J. Exp. Biol. 201:385–401.

Lorez, M. 1995. Neural control of hindleg steering in flight of the locust. J. Exp. Biol. 198:869–875.

Marden, J. H. 1987. Maximum lift production during takeoff in flying animals. J. Exp. Biol. 130:235–258.

Marden, J. H. 1989. Bodybuilding dragonflies: Costs and benefits of maximizing flight muscle. Physiol. Zool. 62:505–521.

Maynard Smith, J. 1952. The importance of the nervous system in the evolution of animal flight. Evolution 6:127–129.

McLachlan, A. J. and D. F. Allen. 1987. Male mating success in Diptera: Advantages of small body size. Oikos 8:11–14.

Møller, A. P. 1996. Sexual selection, viability selection, and developmental stability in the domestic fly *Musca domestica*. Evolution 50:746–752.

Moore, A. J. 1990. The evolution of sexual dimorphism by sexual selection: The separate effects of intrasexual selection and intersexual selection. Evolution 44:315–331.

Nachtigall, W. 1979. Schiebeflug bei der Schmeißfliege *Calliphora erythrocephala* (Diptera: Calliphoridae). Entom. Gen. 5:255–265.

Norberg, R. Å. 1994. Swallow tail streamer is a mechanical device for self-deflection of tail leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. Proc. R. Soc. London B 257:227–233.

Norberg, U. M. 1990. *Vertebrate flight*. Springer-Verlag, Berlin.

Pennycuick, C. J. 1971. Gliding flight of the white-backed vulture *Gyps africanus*. J. Exp. Biol. 55:13–38.

Rayner, J. M. V. and J. P. Swaddle. 2000. Aerodynamics and behaviour of moult and take-off in birds. *In* P. Domenici and R. W. Blake (eds.), *Biomechanics in animal behaviour*, pp. 125–157. BIOS Scientific Publishers Ltd., Oxford.

Schilstra, C. and J. H. van Hateren. 1999. Blowfly flight and optic flow. I. Thorax kinematics and flight dynamics. J. Exp. Biol. 202:1,481–1,490.

Srygley, R. B. and R. Dudley. 1993. Correlations of the position of center of body mass with butterfly escape tactics. J. Exp. Biol. 174:155–166.

Srygley, R. B. and J. G. Kingsolver. 2000. Effects of weight loading on flight performance and survival of palatable Neotropical *Anartia fatima* butterflies. Biol. J. Linn. Soc. 70:707–725.

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

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

Thollesson, M. and U. M. Norberg. 1991. Moments of inertia of bat wings and body. J. Exp. Biol. 158:19–35.

Thomas, A. L. R. 1993. On the aerodynamics of birds' tails. Phil. Trans. R. Soc. London B 340:361–380.

Thornhill, R. and J. Alcock. 1983. *The evolution of insect mating systems*. Harvard Univ. Press, Cambridge.

van den Berg, C. and J. M. V. Rayner. 1995. The moment of inertia of bird wings and the inertial power requirement for flapping flight. J. Exp. Biol. 198:1,655–1,664.

Vermeij, G. J. 1987. *Evolution and escalation*. Princeton Univ. Press, Princeton.

Vogel, S. 1988. *Life's devices*: *The physical world of animals and plants*. Princeton Univ. Press, Princeton.

Wagner, H. 1986*a*. Flight performance and visual control of flight of the free-flying housefly (*Musca domestica* L.) I. Organization of the flight motor. Phil. Trans. R. Soc. London B 312:527–551.

Wagner, H. 1986*b*. Flight performance and visual control of flight of the free-flying housefly (*Musca domestica* L.) II. Pursuit of targets. Phil. Trans. R. Soc. London B 312:553–579.

Warrick, D. R. and K. P. Dial. 1998. Kinematic, aerodynamic and anatomical mechanisms in the slow, maneuvering flight of pigeons. J. Exp. Biol. 201:655–672.

Weihs, D. and P. W. Webb. 1984. Optimal avoidance and evasion tactics in predator-prey interactions. J. Theor. Biol. 106:189–206.

Witter, M. S. and I. C. Cuthill. 1993. The ecological costs of avian fat storage. Phil. Trans. R. Soc. London B 340:73–92.

Zanker, J. M. 1990. The wing beat of *Drosophila melanogaster*. III. Control. Phil. Trans. R. Soc. London B 327:45–64.

Zeil, J. 1993. Sexual dimorphism in the visual system of flies: The free flight behaviour of male Bibionidae (Diptera). J. Comp. Physiol. A 150:395–412.