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FLIGHT RESPIRATION AND ENERGETICS

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■ **Abstract** We use a comparative approach to examine some of the physiological traits that make flight possible. Comparisons of related fliers and runners suggest that fliers generally have higher aerobic metabolic capacities than runners but that the difference is highly dependent on the taxa studied. The high metabolic rates of fliers relative to runners, especially in insects, are correlated with high locomotory muscle cycle frequencies and low efficiences of conversion of metabolic power to mechanical power. We examine some factors that produce variation in flight respiration and energetics. Air temperature strongly affects the flight metabolic rate of some insects and birds. Flight speed interacts with flier mass, so that small fliers tend to exhibit a J-shaped power curve and larger fliers a U-shaped power curve. As body size increases, mass-specific aerobic flight metabolism decreases in most studies, but mass-specific power output is constant or increases, leading to an increase in efficiency with size. Intraspecific studies have revealed specific genetically based effects on flight metabolism and power output and multiple ecological correlates of flight capabilities.

INTRODUCTION

Flight ability is considered a key trait responsible for the tremendous success and diversity of the insects, birds, and bats. This paper reviews recent advances in our understanding of flight respiration and energetics and the physiological mechanisms that underlie flight ability in these diverse taxa. This is a broad topic, and the interested reader should refer to recent reviews focused on avian flight energetics and biomechanics (1), related reviews in this volume (2, 3), reviews of vertebrate and invertebrate locomotory physiology (4, 5), books on comparative exercise physiology (6), and recent and forthcoming books on animal flight (7, 8). Herein we identify and suggest explanations for comparative patterns in flight energetics and respiration and point attention to serious gaps in our understanding of these topics.

This review is divided broadly into two sections. In the first section, we review physiological correlates of flight, including aerobic and anaerobic metabolism, gas exchange structure and function, and flight muscle biomechanics and bio-

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chemistry. In the second section we examine factors that are associated with variation in flight respiration and energetics of volant animals, including temperature, flight speed, flier body mass, and intraspecific genetic variation.

A recurring theme of flight energetics is a comparison of the mechanical power output of flight to the metabolic power input. The mechanical power output of flying animals has been estimated using various physical and kinematic measurements, combined with biomechanical theory. For example, power output of fliers can be estimated from measures of wing beat frequency, wing stroke amplitude, and body and stroke plane angles, combined with measures of wing and body morphology (9–11). Power outputs can also be estimated from the force outputs of flying or running muscles or bodies in vivo or in vitro (12–14). The metabolic power input is the rate of energy production by metabolic processes that supply ATP to the flight muscles. Metabolic power input has most commonly been estimated using respirometric measures of gas exchange, although other methods such as mass balance (15) and doubly labeled water (16) have been used.

PHYSIOLOGICAL CORRELATES OF FLIGHT

What are the physiological mechanisms that make flight possible? One approach to answering this question is to compare the physiological systems of flying and nonvolant organisms. The evolutionary relationships of the insect orders are poorly known, so we compare the characteristics of insects fliers and runners across many orders and within single orders. Birds are usually compared to mammals by physiologists because they are the two major homeothermic groups, but given their reptilian ancestory, it is perhaps more interesting to compare bird and reptile locomotory physiology. However, since there are so many dramatic differences between birds and extant reptiles, the best comparison for understanding the physiological correlates of avian flight may be to contrast running and flying birds. We compare bat physiological systems to runners of many mammalian orders. These comparisons all imperfectly control for possible historical effects on physiology, which emphasizes the need for future physiological studies of flight that are performed in a phylogenetic context. An approach that may hold particular promise is a study of physiological systems of insect groups such as the stoneflies, which have species ranging from flightless through various degrees of flight capability (17).

Aerobic Flight Metabolism

Fliers are considered paradigms of aerobic performance, and the assertion that they have higher aerobic metabolic rates than do runners or swimmers is common in the literature. Is this paradigm justified? We address this question by considering the mass-specific oxygen consumption rates (V_{O2}) of flying and running insects, birds, mammals, and reptiles. Our analysis focuses on the size range of

1 to 7 g, where these taxa nearly overlap in body size (Table 1). These comparisons can also be made using allometric relationships of aerobic locomotory metabolism for these groups (Figure 1).

Insects Flying insects have mass-specific oxygen consumption rates at least 3-fold greater and often over 30-fold greater than reported for terrestrially locomoting insects at the same body temperature (Table 1, Figure 1). Allometric comparisons of 118 invertebrate flying and running species from diverse orders suggest that the aerobic capacity of a 1-g flier is 28 times that of a 1-g runner, with this factorial difference little affected by body size (Figure 1) (5). Thus the higher V_{O2} of fliers relative to runners seems independent of phylogeny (although a careful study of this question is lacking).

Allometric comparisons (18) and a perusal of Table 1 suggest that flight metabolic rates of insects with asynchronous muscle overlap those of insects with synchronous flight muscle, despite the much higher wing beat frequencies

TABLE 1 Rates of oxygen consumption (ml g^{-1} h^{-1}) of active 1- to 7-g animals

Animal	Mass (g)	Reference	V_{O2}(ml g^{-1} h^{-1})
Flying insects			
“Euglossine bee”	1	(157)	66
“Sphingid moth”	2	(172)	62
Fig beetle	1.3	(173)	61
Cicada	2.8	(49)	39
Tabanid fly	1	(174)	18
Locust	1.7	(175)	13
Running insects			
“Running insect”	2	(5)	2.4
Jumping grasshopper	1.7	(176)	1.3
“Running endothermic beetle”	1.3	(32)	4.5
Hovering hummingbirds			
V_{O2} max, heliox	3.5	(177)	55
“Hummingbird”	2	(25)	45
“Hovering bird”	2	(178)	42
“Running reptile” (30°C)	2	(179)	1.2
Hovering Glossophagine bat	7	(25)	25
Running mammals			
Etruscan shrew	2.4	(180)	24
“Mammal V_{O2} max”	2	(26)	16

Values for animals in quotations are calculated from published allometric regressions between body mass and oxygen consumption or metabolic rate, with 1 ml O_2 (STP) s^{-1} (20.1 W), and a Q_{10} of 2 applied if necessary for temperature correction.

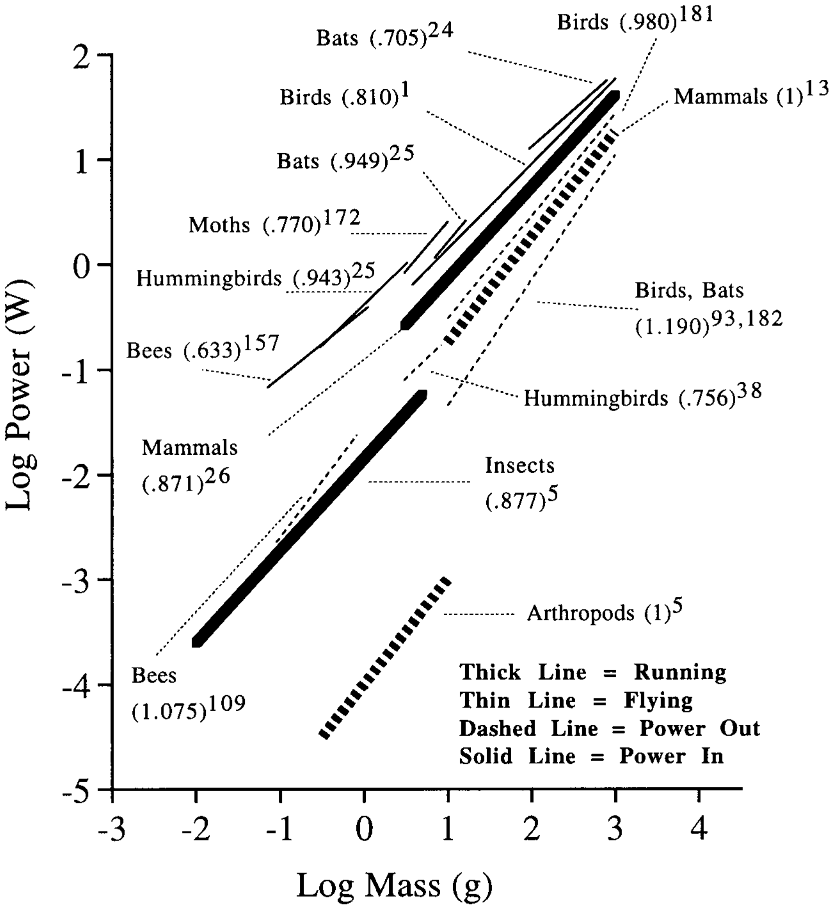

Figure 1 Log power (watts) versus log body mass (grams). The values shown represent either the metabolic power input of locomotion, calculated from respiratory measures of aerobic metabolism, or the mechanical power output of locomotion, calculated from measurements of animal force outputs and/or locomotory kinematics. The value in parentheses is the scaling exponent, and the superscript indicates the reference.

observed in the former group. Comparisons within orders of species that can both fly and run provide similar conclusions. For example, flying locusts and beetles have V_{O2}s at least 10-fold higher than terrestrially locomoting animals at similar body temperatures (Table 1). Thus the data for insects clearly support the notion that flight is correlated with much higher aerobic metabolic rates than running is.

Birds The most dramatic example of evolutionary change in aerobic capacity appears in the comparison of birds and reptiles. Hovering birds have V_{O2}s during flight that exceed those of running reptiles by at least 40-fold and exceed those of resting birds by 5- to 14-fold (19). However, studies of ostriches and emus running on treadmills suggest that running birds can attain V_{O2}s at least 11-fold above rest (20). Running and flying birds exhibit similar scaling of locomotory oxygen consumption rates (21). Thus it appears that the high metabolic rates of exercising birds are not specifically associated with flight.

An alternate explanation is that the high V_{O2} of flying birds relative to ancestral running reptiles is associated with the evolution of endothermic homeothermy (22). However, since the maximal V_{O2} associated with cold exposure is approximately half that associated with flight (23), development of endothermic capacity seems unlikely to completely explain the high exercise V_{O2} of birds. The high V_{O2} of exercising birds may be best correlated with the evolution of the efficient parabronchial lung.

Bats There is good evidence that aerobic locomotory metabolism is higher in bats than in other mammals, but the degree of difference is much smaller than for insects. Some small active insectivores (shrews) have V_{O2}s in the same range as those of bats (Table 1). Thomas (24) estimated that bat flight metabolic rates were about twice that of running mammals. Comparison of allometric data for bats of (25) with those for nonvolant mammals would suggest that 7-g bats have aerobic capacities approximately 50% higher than running mammals (Figure 1, Table 1). The mass-scaling coefficient of V_{O2} in hovering bats is 1 (Figure 1) (25) and only 0.87 for mammals running at maximum aerobic speed (26), so the difference between flight and runner V_{O2} in mammals may increase with size.

Comparison Among Taxa These comparisons of V_{O2} have several important caveats. First, for technical reasons, physiologists attempting to measure gas exchange in fliers generally choose species that hover well in containers and that produce large, easily measurable gas exchange. These sampling biases may cause the available measures of locomotory V_{O2} for fliers to be higher than the distribution of actual values. Within the insects, there is a paucity of gas exchange data for small weak-flying groups such as butterflies and neuropterans. In birds, gas exchange data are particularly difficult to obtain for large species, which depend heavily on gliding. However, for these animals, estimates of metabolic rates from mass balance or doubly labeled water studies suggest that flight metabolic rates are well below predicted metabolic rates from aerodynamic equations (9, 27–29) and well below maximal treadmill V_{O2} for a similarly sized runner.

A second concern is that the data for runners represent primarily maximal V_{O2} measured with treadmill studies, whereas the data for most fliers are obtained during hovering when V_{O2} is often not maximal. For fliers, the best (but not perfect) data on maximal V_{O2} come from studies that manipulate air density to increase work load. In hummingbirds, decreasing air density by replacing nitrogen with helium (heliox) leads to increases in V_{O2} 24% higher than during hovering in normal air (30, 31). It is not even clear that these values are representative of the maximal possible V_{O2}, since flight failure in hummingbirds at low air densities appears to be due to mechanical constraints (limits on stroke amplitude) rather than oxygen delivery. Similar studies with carpenter bees flying in heliox indicate that maximal V_{O2}, can be increased to values about 30% higher than those occurring during hovering in normal air (S Roberts, J Harrison & R Dudley, unpublished observations).

An important conclusion drawn from these comparisons is that the difference between flight and running V_{O2} depends on taxa, i.e. large (30-fold) in insects, small (2- to 1.5-fold) in mammals, and perhaps nonexistant in birds (Table 1, Figure 1). These differences are consistent with published measures of power output during locomotion. Insect fliers have mechanical power outputs about 30-fold higher than that of insect runners (Figure 1) (5), whereas maximal aerobic mechanical power output for birds is about double the power output of running mammals (Figure 1). We suggest two mechanisms that might partially explain this observation. First, efficiency (power output divided by power input) increases with size (Figure 1), and insect body masses are lower than those of birds and bats. Although insect, avian, and bat mechanical power outputs and metabolic power inputs show similar scaling relationships (Figure 1), at the small body masses typical of insects, the power output and power input regression lines increasingly diverge. This causes flight metabolic rates to rise relative to flight power requirements and running metabolism in small animals.

A second mechanism that may contribute to the large flight-runner V_{O2} differences among insects, birds, and mammals is a correlation between V_{O2} and the thermal biology of these groups. Both volant and nonvolant birds and mammals are endothermic homeotherms. In contrast, insect fliers are often endothermic homeotherms, whereas insect runners are mostly ectothermic poikilotherms. Insect flier V_{O2}s overlap with those of birds and mammals, whereas insect runners have V_{O2}s well below those of bird and mammalian runners and V_{O2}s similar to those of running reptiles (Table 1; allometric plot of reptilian runners not shown in Figure 1). Many large insect fliers thermoregulate, in part because of the high aerobic metabolic rates associated with flight and perhaps because the flight muscles are centrally located within the insulatable thorax. Most insects do not thermoregulate during terrestrial locomotion probably because of low metabolic rates and peripherally placed locomotory muscles. Therefore, insect leg muscles must function at a range of temperatures often well below the temperature of flight muscle. Among insect runners, the highest V_{O2}s occur for animals that use their flight muscles to warm up during activity (5, 32). Regulation of a high, relatively constant body temperature has been hypothesized to allow the evolution of high-power output systems in insects, birds, and mammals (33).

Anaerobic Flight Metabolism and Non-Sustainable Performance

The use of anaerobic metabolism during flight has received remarkably little attention perhaps because of the dominant view equating flight and aerobic metabolism. This is unfortunate because estimates of power output during loaded take-off suggest that short-term, maximal power outputs are approximately double those during sustainable flight (34–37). In hummingbirds, maximal, short-term (< 1 s) power outputs measured with string-lifting protocols are even higher (up to fourfold) than those sustainable aerobically (38, 39). These short, high-power output flights are likely to be of considerable importance during behaviors such as predation, predator avoidance, mating, and surviving extreme weather.

At present, the mechanisms of ATP production during these short-term, high-power output flights remain unclear. Insect flight muscle generally has very low levels of lactate dehydrogenase (40), and other possible mechanisms of anaerobic metabolism in insects remain unexplored. The flight muscles of some large birds are known to contain high levels of lactate dehydrogenase (41), and anaerobic metabolism is presumed to be critical for flight in all large flying birds (36). However, to our knowledge there are no quantitative data on the kinetics of lactate accumulation during flight in any flying animal.

High-energy phosphate depletion (creatine phosphate in birds and bats; arginine phosphate in insects) is a potential mechanism of rapid ATP production, but arginine phosphate levels have been shown to remain constant at the onset of flight in locusts (42). While it is known that hummingbird flight muscle contains high levels of creatine kinase (43), the kinetics of high-energy phosphagen utilization and how this might vary among flying species is unknown.

Aerobic metabolism in excess of that sustainable is also a possible mechanism of short-term high ATP production. Over the short-term, animals might deplete internal muscle and blood oxygen stores at rates greater than those sustainable by gas exchange systems.

Gas Exchange

Gas exchange in fliers can be modeled as multistep processes, with convective ventilation of the gas exchange organ in series with diffusion of oxygen and carbon dioxide across a membrane (44). In the following section, we focus on the gas phase components of gas exchange in fliers, to facilitate comparisons among insects, birds, and mammals. Unfortunately, except in the case of mammals, there are insufficient data to compare the gas exchange structures of volant and nonvolant groups. Therefore, we compare the mechanisms of gas exchange during flight across the flying taxa and review evidence for variation among fliers within a taxa.

Insects In all the flying insects studied to date, flight is associated with large increases in convective ventilation through the spiracles relative to resting (45–

47). This convection is due to the compression of air sacs or soft elliptical trachea by the body walls or hemolymph (46, 47). Convective gas exchange during flight can occur via (*a*) abdominal pumping, in which rhythmical abdominal contractions synchronized with spiracular openings drive air flow through the spiracles; (*b*) autoventilation of the thorax, in which wing movements cause changes in thoracic volume thus driving convection; or (*c*) draught ventilation, in which air pressure generated by the forward speed of the insect forces air flow in through open thoracic spiracles.

Abdominal pumping appears to be the predominant mechanism of convective ventilation in the hymenopterans (46, 48). Thoracic autoventilation is the primary mechanism of convective ventilation in locust (46), dragonfly (46), and cicada (49). Draught ventilation and thoracic ventilation predominate in Cerambicid, Elaterid, and Anthribid beetles, and a combination of thoracic autoventilation and abdominal pumping produces convection in Scarabid and Buprestid beetles (47). Comparative explanations for these differences are lacking. Unfortunately, there are no quantitative data on convective ventilation in insect runners for comparison, nor are there data for comparison of different insect fliers with varying flight ability and V_{O2}.

Final delivery of oxygen from the trachea to to the mitochondria occurs via the tracheoles, small (< 1 μm diameter) air passageways formed by a single layer of cells. Theoretical calculations suggest that diffusion could suffice for oxygen transport through the tracheolar step (45), although this hypothesis has not been tested. The fractional volume of tracheoles relative to the fractional volume of mitochondria should provide a quantitative measure of the capacity of the tracheoles to perform this final step in oxygen delivery. Unfortunately, no data exist on the morphology of the tracheal system that allow us to address quantitative differences in tracheal structure associated with flight. Electron microscopic studies demonstrate that flight muscle has a high density of tracheoles (45), but to our knowledge there have been no systematic studies of the tracheole supply to nonflight locomotory muscles in insects.

Wigglesworth & Lee (50) have compared the tracheoles of the flight muscles of nine insect species of six orders. In all these insects, tracheoles enter into the flight muscle within invaginated plasma membrane and T-tubular systems (50). In all these species, very small tracheole branches (40–200 nm diameter) penetrate the sarcomeres and contact or even encircle virtually every mitochondrion. Observations of the tracheoles to the flight muscles of a fly and a butterfly suggest that these tubes are fluid-filled at rest and air-filled during activity (50). Together these data suggest that gas exchange to the mitochondria of the active flight muscle should occur primarily in the gas phase.

Muscle P_{O2} varies little between resting and flight (8–10 kPa) (51), which suggests that increases in oxygen conductance closely match the need for oxygen delivery during flight. This finding is consistent with the high safety margin for oxygen delivery observed for honey bees. Flight metabolic rate and performance do not decrease until atmospheric P_{O2} drops below 10 kPa (52). In contrast, flight metabolic rate increases with hyperoxia and decreases with moderate hypoxia in a dragonfly (53), which suggests a small safety margin for oxygen delivery in these animals. It is possible that insects using abdominal pumping to drive convection are less sensitive to atmospheric hypoxia and altitudinal variation because they are able to decouple ventilation from flight muscle activity. This might not be possible in animals in which flight muscle movements simultaneously drive wing movements and ventilation (53). In honey bees, there is also evidence for increases in ventilation during flight at higher temperatures (in honey bees), which may increase respiratory water loss and aid thermoregulation (54).

Birds In birds, the onset of flight is accompanied by strong (17-fold) increases in ventilation (19, 55). As in insects, ventilation occurs via compression of air sacs (56). Increases in ventilation occur primarily due to increases in breathing frequency (55). Ventilation (liters per minute) during flight scales similarly to V_{O2} in birds, suggesting that ventilatory response to flight is size independent (55). In contrast to current data for insects, avian flight studies have found that rises in ventilatory air flow exceed elevations in V_{O2} (57–59) and that blood P_{CO2} falls while blood P_{O2} rises (57). This hyperventilation has been attributed to hyperthermia (and the need for increased evaporative cooling) and/or lactate acidosis (55). The increased ventilation during flight is driven by a combination of mechano-receptive feedback and feed-forward locomotor inputs (60, 61).

The ratio of wing beat frequency to ventilation frequency is highly variable in birds, and the importance of such locomotory-ventilatory coupling has been controversial. However, recent studies support the hypothesis that coordinating wing beat and respiratory rhythm produces energetic savings in birds (62–64).

The high aerobic metabolism achieved by birds is associated with the evolution of the parabronchial lung (56). Its cross-current gas exchange structure leads to greater efficiency of oxygen transfer than the mammalian lung (56). The diffusing barrier of the bird lung has a mean harmonic thickness approximately 40% of mammals (19), and a gas exchange surface area two to four times greater than in mammals (65). This may partially explain the hypoxia tolerance of birds, although other factors such as the insensitivity of cerebral blood flow to hypocapnia may be more important (19).

Bats Like insects and birds, bats demonstrate strong increases in both tidal volume and ventilation frequency during flight (66, 67). As for insects and birds, contractions of the flight muscles are integrated with ventilation. Wing beat frequencies and breathing rates are identical during flight, with this coupling apparently aiding inspiration (66, 68, 69). Unlike insects, but similarly to birds, bats hyperventilate during flight, with increases in pulmonary ventilation exceeding increases in V_{O2} by 20 to 40% (66, 67). This hyperventilation has been hypothesized to be due to thermoregulation, a means to increase oxygen delivery, or an acid-base regulatory response (24).

Mammals provide the best data for the comparison of gas exchange structure and function between volant and nonvolant species. Bats in the small ($<$10 g) size range have lung volumes and surface areas about two to three times that of nonvolant mammals, about a 10% shorter blood-gas diffusion barrier, and an approximately threefold greater lung diffusing capacity (70). Bat lung variables increase less with size than they do in running mammals and have lower scaling exponents than V_{O2} during hovering (25), which may partly explain the poor endurance and lack of hovering ability in larger bats (70).

Comparisons Across the Flying Taxa Flight is accompanied by strong increases in ventilation in all taxa. In birds and bats, data suggest that ventilation changes exceed increases in V_{O2}, while the limited data for insects suggest close matches between V_{O2} and ventilation during flight. In all taxa, there is a tendency for wing beats to be coupled with and aid in the driving of ventilation. Throughout the fliers there is some evidence that ventilation and respiratory water loss can vary with air temperature, providing thermoregulatory benefits.

The high capacity of the insect tracheal system to deliver oxygen may be the reason why some flying insects achieve higher mass-specific oxygen consumption rates than do any birds or mammals (71). The tracheal systems of insects do have very small liquid diffusion distances (< 1 μm) (50) relative to normal 10- to 20-μm capillary-to-mitochondria diffusion distances in birds. This may allow greater oxygen flux in the critical terminal step of oxygen delivery, which may be why some insects have evolved oxygen and ATP utilization capacities beyond any found in other animals. Another possible, but apparently slight, advantage for tracheated relative to capillary-supplied muscles is that the volume of the insect muscle occupied by the trachea (1–7%) (45) may be smaller than the volume of the vertebrate muscle occupied by capillaries (9% in hummingbirds) (72). However, the general hypothesis of the superiority of the insect tracheal oxygen delivery system has not been well tested and seems to be contradicted by the hypoxia insensitivity of avian flight metabolism (31, 58, 59).

Muscle

The available information for flight muscle physiology differs greatly among taxa. There is a growing body of information on the in vitro contractile performance of insect flight muscle, but a dearth of similar information in birds and bats. However, there are more in vivo flight muscle power output and fiber type data for birds. Therefore, in the following section we consider all the flying taxa together and attempt to relate what is known about flight muscle properties to flight energetics.

Muscle Fiber Types The high aerobic metabolism of flight is generally supported by highly aerobic flight muscle. Insect and hummingbird flight muscle have particularly high Krebs cycle enzyme and mitochondrial content and low activities of lactate dehydrogenase (40, 41, 71, 72). The high oxidative capacity in insect and bird flight muscles appears to be due in part to high oxidative enzyme content and to utilization of a high fraction of the enzyme capacity (73, 74). Comparisons of the flight and leg muscles of insects and birds are rare but generally support the contention that leg muscles are more heterogeneous in fiber type, have lower capillary densities, and generally contain lower levels of oxidative enzymes and higher levels of lactate dehydrogenase compared to flight muscles (75–79). An exception is the leg muscle of the highly cursial emus, which is similar to avian flight muscle in fiber type composition and enzyme activities, correlating with their similar scope for aerobic activity (80).

Evidence in both birds and insects also supports the hypothesis that different fiber types within the flight muscle maintain sustainable and nonsustainable flight. Avian flight muscle contains primarily fast oxidative glycolytic (FOG) fibers with a smaller percentage of fast glycolytic (FG) fibers (21). The FOG fibers of birds have very high mitochondrial and Krebs cycle enzyme content and high capillarity densities relative to most vertebrate skeletal muscle (43, 81, 82). The FG fibers are relatively large, metabolize glycogen anaerobically, and are believed to be used during burst performance such as take-off and acceleratory flight (83, 84).

Most insect flight muscle is composed of relatively homogeneous, highly oxidative fibers (85). However, at least some species contain distinctly smaller and more oxidative pink fibers and larger, less-oxidative white fibers (dragonflies, hemipterans, cockroaches) (86, 87). It is not known whether burst performance in insects requires recruitment of the less-oxidative-fiber types, as is believed to occur in birds.

Variation in muscle fiber types appears to be associated with flight capabilities in birds. The flight muscle of large birds, which are primarily short-burst flyers, consists of primarily FG fibers, whereas the flight muscle of birds capable of continuous flapping flight have primarily FOG fibers (88). There is also evidence that birds that primarily use flapping flight have smaller oxidative fibers and greater capillary density than birds that glide, whereas gliders have more or larger slow oxidative fibers (78). Similarly, passerine birds, which migrate longer distances, have smaller fibers and higher capillary densities (82).

Muscle Cycle Frequencies A general pattern among animals is that muscle metabolism and power output increase with the frequency of contraction (89, 90). To what extent is the relatively high cost of insect flight associated with high muscle cycle frequencies? Available data suggest that this frequency is a central factor. Most insect fliers have substantially higher muscle cycle frequencies than do insect runners (5). Insects with asynchronous muscle have the highest frequencies (bees have cycle frequencies 11 times greater than similarly sized 1-g runners). Fliers with synchronous flight muscle have similar to fivefold higher values than do insect runners, with frequency explaining most but not all of the differences in energetic cost (5). Among insect clades (Saturniid moths, Sphinx moths, bumblebees, euglossine bees), variation in flight metabolic rate with size is largely explained by variation in wing beat frequency, with mass-specific metabolic rate per wing stroke being independent of size in most of these groups (5, 18).

High locomotory cycle frequencies occur in flying birds and bats relative to runners. Ten-gram birds and bats have wing beat frequencies 1.5- to 1.8-fold greater than the predicted cycle frequency of a 10-g mammalian runner at maximum galloping speed (91–93). These frequency differences are similar to the difference in flight metabolic rates for these groups (Table 1, Figure 1).

The high cycle frequency of fliers, and the higher wing beat frequencies of smaller fliers, may partly explain the higher V_{O2} of these groups. Muscle efficiency tends to decrease in smaller animals with higher cycle frequencies. Calculated efficiencies for endothermic runners decrease with size, from 70% in humans to 7% in 44-g quail (94). Estimated efficiencies for moderately sized avian flight muscle are 10 to 13% (95). Values for muscle efficiency of insect fliers range from 5 to 16%, and decrease as size decreases and wing beat frequency increases within a clade (11, 96–98).

What flight muscle characteristics are responsible for the generation of high wing beat frequencies? Synchronous flight muscle is similar to other fast muscles, possessing a well-developed sarcoplasmic reticulum and fast contraction kinetics (99, 100). Some insect fliers have asynchronous flight muscle, in which the muscle can oscillate at a frequency much higher than motoneuron activity (101). Asynchronous flight muscle has slow, weak isometric contractions but maximal velocities among the fastest measured for muscle (102). The high frequencies of asynchronous muscle are attributable to specialized characteristics, including stretch-activation, reduction of the sarcoplasmic reticulum, high stiffness, and low strain (101–103).

Muscle Power Output Flight muscles can produce high power output. Power output of synchronous insect flight muscle ranged from 60 to 90 W kg^{-1}, as determined with workloop techniques at normal operating temperatures (35–40°C) (96). These values are within the range of the aerodynamically calculated required power outputs, assuming substantial elastic energy storage (96). Power outputs of in vitro muscle preparations have yielded maximal power outputs up to approximately 100 W kg^{-1} using workloop techniques, but this value is thought to underestimate maximal power output in vivo for technical reasons (104, 105).

The mechanical power output of bird muscle has been estimated using in vivo bone-strain measurements of pectoralis muscle force and filming of wing kinematics. These measurements indicate that muscle-mass-specific power output ranges from 40 to 104 W kg^{-1}, consistent with respirometric measures of power input and efficiencies of about 12% (12, 95, 106). Similar estimations of muscle power output have been made for hummingbirds from aerodynamic models (107).

Modulating the Flight Muscle Very little is known about how muscle power output is modulated within individuals. During load carriage or flight at high speeds, power output in bumblebees is increased by increasing wing beat frequency and lift coefficient (108). Variation in power output in euglossine bees or hummingbirds exposed to low air density increases primarily from increases in stroke amplitude (30, 109). Both wing beat frequency and stroke amplitude modulation contribute to variation in power output for *Drosophila melanogaster* steering in a virtual flight arena (110).

The mechanisms responsible for such flexibility are poorly known but have been best studied in insects. Octopamine increases twitch tension and rate of flight muscle contraction and is released during flight in locusts (111–115). Frequency of neuronal activation may be important for synchronous flight muscle, as increasing the frequency of electrical stimulation of muscle activation can increase power output (116) . Interestingly, in some cases, large variations in speed occur without any changes in wing beat frequency or stroke amplitude. In these cases, variation in flight performance is due to variation in stroke plane angle or lift coefficient (117, 118).

FACTORS ASSOCIATED WITH VARIATION IN FLIGHT RESPIRATION AND ENERGETICS

Temperature

The contractile properties of muscle, particularly rate parameters (i.e. shortening velocity and relaxation time), are strongly temperature dependent (116, 119). Accordingly, power production of isolated flight muscle generally increases with muscle temperature to a point [insects (96, 103, 104, 119–121), bats (122)], then decreases as muscle temperature continues to rise (123).

The muscle temperature for optimal power production varies among species and apparently has been influenced by natural selection. For example, the optimal temperature for muscle power production and flight ability in the heterothermic bat *Murina leucogaster* spans 30 to 40°C (122), which is a much broader and generally lower optimal temperature range than that of muscles from homeothermic mammals and birds. Moreover, the optimal muscle temperature in the ectothermic, winter-flying geometrid moth *Operophtera bruceata* (15–20°C) (124) is much lower than in the sphingid moth *Manduca sexta* (40–44°C) (124) and bumblebees (38–41°C) (104), which fly at elevated, well-regulated muscle temperatures. Interestingly, the temperature sensitivities of the metabolic enzymes citrate synthase and pyruvate kinase do not differ between *O. bruceata* and *M. sexta* (125), suggesting that at least some of the thermal characteristics of these enzymes are conserved.

The body temperatures of extremely small flying insects (i.e. *Drosophila*, midges, stingless bees) conform to air temperatures despite any heat gain from metabolism or solar radiation. Their thermal conformance is due to extremely high rates of convective cooling caused by their high surface area-to-volume ratios and wing movements. In turn, metabolism, wing beat frequency, and aerodynamic power production of small insects flying at moderate air temperatures are positively correlated with air temperature (126–130). However, it has not yet been demonstrated in small, ectothermic insects that flight metabolism and kinematic performance decrease when air temperature exceeds optimal muscle temperature.

There is some evidence that insects may exhibit morphological variation that compensates for thermal effects on muscle power output. *Drosophila* developing in cool climates or laboratory conditions have relatively larger wings (lower wing loading) than conspecifics developing in a warmer environment, and it has been proposed that this morphological variation is an adaptive response to enhance power production and flight ability at low air temperatures, when wing beat frequency is low (131). However, whether this is a general developmental response in small ectothermic flyers and whether this morphological variation affects power production during free flight at different air temperatures remain unknown.

Birds, bats, and many large insects regulate muscle temperature close to the optimal muscle temperature during flight, which allows them to fly and remain active over a wide range of ambient thermal conditions. The functional importance of such thermoregulation is illustrated by honey bee (132) and dragonfly (123, 133) vertical force production during tethered flight, which decreases at muscle temperatures above or below optimal temperatures. Although insect flight thermoregulation has received considerable attention, the mechanisms by which birds and bats thermoregulate during flight are still unknown, since heat exchange (metabolic heat gain, radiation, convection and evaporation) has not been measured as a function of temperature during flight for these groups. Some insect groups, particularly sphingid moths and certain bumblebee species, maintain flight metabolic rates independent of air temperature (18, 134–137) and thus thermoregulate by varying convective and radiative heat loss (134, 135). However, other endothermic insects strongly decrease wing beat frequency (138–142) and metabolic heat production (54, 138, 139, 143) during flight in hot conditions, which helps maintain muscle temperature near optimal values. Hummingbirds also decrease wing beat frequency and metabolic rates as air temperature rises, although to a lesser degree than the insects cited above (144–146).

What behavioral, physiological, or biomechanical explanations can be offered for the decrease in metabolic rate and wing beat frequency with air temperature? The decrease in flight metabolism and wing beat frequency at high air temperatures is probably not due to varying aerodynamic requirements, since the decrease in air density and the increase in kinematic viscosity with rising air temperature (147) predict a very slight increase in aerodynamic power requirements (148). The decrease in flight metabolism as air temperature rises could result from increasing mechanochemical efficiency (perhaps due to an increase in elastic energy storage at high muscle temperatures) and/or decreasing mechanical power output at higher air temperatures, as suggested by the similar thermal sensitivity of wing beat frequency. Indeed, the hummingbird *Archilochus colubris*, which lowers flight metabolism at high air temperatures, increases the mechanochemical efficiency of hovering flight as air temperature rises by decreasing wing beat frequency and increasing stroke amplitude. As a result, mechanical power output is independent of air temperatures (145). Thermal variation in muscle efficiency and power input could also be due to temperature-specific variation of an unsteady aerodynamic mechanism (149), such as varying the wing's angle of attack. Thus it is not clear whether the decrease in flight metabolism and wing beat frequency at higher temperatures in some flying insects is due to active thermoregulation or some passive consequence of temperature on the flight system.

Speed

All volant taxa are capable of varying flight speed, and the aerodynamic mechanisms and energetic consequences of this variation have been the subjects of numerous theoretical and empirical investigations. Animal flight theory predicts that total mechanical power requirements for steady-state flapping flight should vary with flight speed, with the greatest power required at the slowest and fastest speeds, and the minimum at some intermediate speed (9). The resultant U-shaped curve for total mechanical power is a composite of four distinct power components: the induced, the profile and parasite powers (collectively termed the aerodynamic power requirements), and the inertial power. Induced power is the power required to impart sufficient momentum on the air to generate lift and thrust. Induced power is inversely proportional to flight speed and is a major power requirement during hovering and at low-speed flight. Profile power is the power required to overcome drag on the wings and is directly proportional to flight speed. Parasite power, which is proportional to the cube of flight speed, is the power required to overcome drag forces on all body parts exclusive of the wings. Inertial power is the power required to accelerate the wings during each stroke. Importantly, if the kinetic energy of the oscillating wings can be stored as elastic strain energy in the flight muscles or other structures of the flight motor (as is thought to be true for most flyers), then inertial power requirements can be significantly reduced.

The power requirements during forward flight have been predicted for a variety of animals based on their morphology and flight kinematics. However, only one study has measured in vivo mechanical force production and mechanical power output by flight muscles at a range of airspeeds. In a major technological advance, Dial et al (95) recently measured wing kinematics and in vivo pectoralis muscle force to determine the mechanical power output for a magpie (*Pica pica*) flying at airspeeds of 0 to 14 m s^{-1}. At low speeds, their results closely agreed with the predictions of aerodynamic theory, with mechanical power output highest during hovering ($\sim$21 W kg^{-1}) and decreasing to 9 W kg^{-1} at an airspeed of 4 m s^{-1}. However, mechanical power output remained relatively constant at speeds between 4 and 12 m s^{-1} and increased only marginally at the maximum speed of 14 m s^{-1}. The coefficient of variation for power output and wing kinematics was lowest at the slowest (0–2 m s^{-1}) and fastest (12–14 m s^{-1}) flight speeds, suggesting that performance was at or near maximal. In contrast, at intermediate speeds, increased variability of wing beat patterns and power output suggests an ability to alter wing and tail configurations to maintain constant power requirements (150).

Metabolic power input has been measured during hovering and forward flight only in bumblebees and hummingbirds (151, 152). The speed-dependence of oxygen consumption in these groups is very different from the power output versus speed relationship for the much larger magpie. In bumblebees and hummingbirds, which generate lift and thrust during both the upstroke and downstroke of the wing cycle, metabolic rates do not vary between hovering and flight speeds up to 4 and 7 m s^{-1}, respectively. Although no kinematic data are available for hummingbirds at various airspeeds, the independence of bumblebee metabolism and flight speed between 0 and 4 m s^{-1} is consistent with the constant wing beat frequency and amplitude of bumblebees flying across a similar range of flight speeds (152). In these animals, flight speed across this range is increased by decreasing the body angle and increasing the stroke plane angle relative to the horizon such that forward thrust is produced (152).

During flight at very high airspeeds, parasite power requirements apparently become very high. For hummingbirds, metabolism increases by roughly 35% as flight speeds increase from 7 to 11 m s^{-1}. Although bumblebee metabolism has not been measured at flight speeds exceeding 4 m s^{-1}, wing beat frequency in this group significantly increases by approximately 7% as airspeed increases from 4 to 7 m s^{-1} (108). Thus the power curve for these species is not U-shaped, but rather J-shaped, with power requirements changing little from hovering to intermediate flight speeds and increasing only at high speeds. A J-shaped power curve may be applicable to most small flyers, particularly those with low advance ratios (the ratio of flight velocity to wing velocity) (25). However, more data on the interactive effect of body size and speed on flight energetics are necessary to test these models.

Body Mass

The effect of body mass on burst flight performance has received much attention (34–39), so here we focus instead on the effects of body mass on sustainable aerobic flight metabolism and mechanical power requirements. Within several broad taxonomic groups (bees, moths, birds, and bats), interspecific mass-scaling coefficients of metabolic rate (or available power) during forward and hovering flight are generally lower than 1, ranging from 0.63 to 0.94 (Figure 1). In contrast, the scaling coefficients of mechanical power requirements, when calculated from contemporary aerodynamic theory during sustained flapping flight, are usually near or slightly greater than 1 (Figure 1). Thus as flyers get bigger, mechanical power requirements increase at a greater rate than metabolic power production. This results in a higher calculated mechanochemical efficiency in larger fliers. Moreover, flight at high and low speeds becomes increasingly limited with increasing mass because mechanical power requirements appear to increase at these speeds in larger fliers.

In response to such limitations, aerobic hovering is found only in insects, hummingbirds, and the smallest bats, whereas many large birds must rely on unsustainable anaerobic power reserves to provide the energy needed for short bursts of hovering or very fast flight. In some instances, very large birds, such as condors and albatrosses, must taxi against headwinds or drop from elevated perches to achieve sufficient lift and momentum to reach minimal power speeds. Ultimately, a mass is reached at which power requirements for all speeds exceed available metabolic power and flight is not possible. However, there is some debate as to whether the maximal size of extant birds is purely a result of this limitation because larger fliers are found in the fossil record.

Despite the reasonable congruence between aerodynamic theory, measured metabolic data, and observed flight performance, there are notable exceptions regarding the allometry of flight energetics and kinematics. For example, Chai & Millard (38) examined hovering in hummingbirds ranging in body mass from 3 to 8.4 g (11 individuals representing 4 species), and a scaling coefficient of 0.76 for mechanical power output can be calculated from their results. However, a scaling coefficient of 0.95 has been calculated for metabolic power input for 10 hovering hummingbird species spanning a similar size range (25). This comparison suffers from small sample sizes (particularly for mechanical power output), phylogenetic bias, and different methodologies for measuring gas exchange. However, it begs a comprehensive scaling study of hummingbird flight metabolism and mechanical power output to determine whether the allometry of hummingbird flight energetics truly deviates from aerodynamic theory and the patterns generally observed in other fliers.

The intraspecific mass scaling of flight performance of some insects, particularly dipterans, also often disagrees with predictions from aerodynamic theory. In hovering tachinid flies (*Nowickia* sp.), the scaling coefficient of flight metabolic rate is 1 (153). A possible explanation for these results is that the larger body masses of some flies were due to food ingestion, which increases flight metabolic requirements in bees (154). In robber flies (Diptera: Asilidae), the interspecific mass-scaling coefficient of flight metabolism is 1.06 (155). In this case, however, the disproportionately high rates of metabolism in larger species were due to the fact that their body temperatures exceed ambient temperature by 3 to 6°C, whereas smaller species are strict thermoconformers.

Perhaps the most unusual recent finding is the significant positive relationship between wing beat frequency and wing length during hovering in the mosquitos *Anopheles gambiae* and *A. arabiensis* (156). For geometrically similar fliers, wing beat frequency should theoretically scale with length to the power of -0.5 (9), and interspecific mass-scaling coefficients in this range are reported for other small insects such as bees (157, 158) and homopterans (159). In these mosquitoes, however, wing length might be largely fixed relative to the variation in body mass, with a mass-scaling of wing length much lower than that predicted for isometry (0.33). As a result, higher wing beat frequencies (and perhaps metabolic rates) may be required in larger individuals to compensate for the relatively smaller wing areas. These examples suggest that extreme caution is needed when predicting the intraspecific mass dependence of flight parameters from interspecific allometric relationships.

Intraspecific Variation in Flight Respiration and Energetics

Although broad-scale comparisons of taxa and mode of locomotion provide insight into general patterns of organismal design, understanding the evolution of variation in flight-related physiological parameters seems most tractable for intraspecific studies. With such studies it is possible to link individual behavior to variation in physiological or morphological traits. Several interesting patterns of intraspecific variation have been observed. Male *Plathemis lydia* dragonflies with greater ratios of flight muscle to body mass have greater mating success but reduced fat reserves (160). African races of the honey bee *Apis mellifera* have greater flight metabolic rates (161), higher thorax/body mass ratios, and lower wing-loading than do European honey bees (162), suggesting a greater flight capacity in African bees that may correlate with their greater attack vigor and high colonial growth rates. High-altitude honey bees have larger thoraxes and larger wings (163), which should enhance their flight performance at low air densities.

Allozymic variation of metabolic enzymes can also affect organismal flight performance. *Colias* butterfly populations from different altitudes vary in the frequency of several allozymes, and the different forms of these allelic isozymes affect flight ability and the temperature of optimal flight performance (164). In honey bees, the proportion of the electrophoretically fast and medium alleles of cytoplasmic malate dehydrogenase (MDH) exhibit clines on three continents (165). Bees with the fast and medium alleles differ in their flight metabolic rates in hives with naturally mated queens (166) and in hives with singly inseminated queens in which all genes not tightly linked to to the MDH locus were randomly distributed between workers with different MDH phenotypes (167). Similarly, in *D. melanogaster,* there are latitudinal clines in the frequency of allozymes of glycerophosphate dehydrogenase (GPDH) on three continents, with the electrophoretically fast form of GPDH found in higher proportions at low latitudes (168). These allozymes may differ in their kinetics and temperature dependence (169). Flies with different GPDH allozymes differ in their power output during tethered flight and in the temperature dependence of flight, with phenotypes with the fast GPDH allozymes having higher power outputs at higher rearing and flight temperatures (128). Together, these studies support the hypothesis that metabolic allozymes produce small but measurable genetic effects and that variation in these allozymes might be important in understanding why genotypes perform differently in different environments.

Intraspecific studies allow us to directly link variation in flight physiology to its genetic and/or environmental bases. Direct evidence for genetic effects on intraspecific variation in tethered flight performance has been presented for isogenetic lines of *D. melanogaster.* These lines show heritabilities of wing beat frequencies and aerodynamic power outputs ranging from 0.24 to 0.42 (170). Selection for upwind flight ability of *D. melanogaster* increases the flight effort of fruitfly populations, although it does not change the population-level maximal performance (171). Future studies that incorporate traditional and modern molecular genetic experimental designs may eventually allow us to understand some of the genetic bases to the tremendous diversity observed in flight respiration and energetics of animals.

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