Hummingbird flight: Sustaining the highest mass-specific metabolic rates among vertebrates

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Abstract. Resting and maximal mass-specific metabolic rates scale inversely with body mass. Small hummingbirds achieve the highest known mass-specific metabolic rates among vertebrate homeotherms. Maximal capacities for O_2 and substrate delivery to muscle mitochondria, as well as mitochondrial oxidative capacities in these animals may be at the upper limits of what are structurally and functionally possible given the constraints inherent in vertebrate design. Such constraints on the evolutionary design of functional capacities may play an important role in determining the lower limits to vertebrate homeotherm size and the upper limits to mass-specific metabolic rate.
Key words. Oxygen consumption; exercise; evolutionary design; muscle; mitochondria; energy metabolism; enzymes.

Introduction

It has long been known by comparative physiologists that mass-specific metabolic rates at rest (VO_2rest/Mb) and during maximal aerobic exercise (VO_2max/Mb) are inversely related to body mass[39,49]. Etruscan shrews, Cuban bee hummingbirds, and Thai bumblebee bats all weigh about 2 g as adults and, as the smallest known vertebrate homeotherms, probably achieve the highest VO_2max/Mb values among this group of animals. The highest mass-specific rates of aerobic metabolism actually measured are those of hummingbirds in hovering[2,12,28,46,47] and forward[3] flight. In this article, I shall attempt to integrate recently available information regarding hummingbird design and performance. On the basis of this information, I shall argue that the upper limits to the design of functional capacities contribute to determining both the upper limits to physiological performance (i.e., VO_2max/Mb) as well as the lower limit to size among vertebrate homeotherms.

Energetic cost of flight

Hummingbirds probably evolved from larger, insect-eating birds. In the course of their invasion of a niche that was occupied exclusively by insects, many of the 342 hummingbird species have become small (ca 5 g) and hover to feed on nectar from flowers[15,33]. VO_2rest/Mb values at the thermoneutral zone are about 4 ml O_2/(g × h)[28]; these increase 10-fold to about 40 ml O_2/(g × h) during hovering[2,12,28,46,47] and forward[3] flight.

Hummingbirds typically hover to feed more than a hundred times a day[26]. Hover-feeding bouts usually last less than a minute and about 20% of daylight hours are spent feeding[8]. The continuous cycle of flying to forage, sitting, and flying again involves dramatic oscillations between rest and exercise. Hummingbird heart rates are about 500 per min at rest and may increase to about 1300 per min during hovering flight[29]. Wing beat frequencies of up to 80 per second have been recorded[13], as well as licking rates of 13 per s[15]. Unlike most other birds, lift is generated in both up- and down-strokes in the wingbeat cycle during hovering flight[51]. To make this possible, both pectoralis and supracoracoideus muscles are highly developed and, together, constitute about 30% of body mass[16,47].

3–4-g rufous hummingbirds *(Selasphorus rufus)* possess about 1 g of flight muscles which consume O_2 at a rate of about 2 ml/min (82 μmoles O_2/min) during flight[47]. This is equivalent to a rate of ATP turnover of close to 500 μmoles/min and is about 10-fold higher than the mass-specific metabolic rates of elite marathon runners at VO_2max[47]. Hovering flight can be quite prolonged; bouts lasting close to an hour in captive hummingbirds have been recorded[28]. The energetic cost of forward flight (up to about 30 km/h) is about the same as that during hovering[3], and is known to be sustainable for even longer periods. The several hundred kilometer nonstop flight of ruby-throated hummingbirds *(Archilochus colubris)* across the Gulf of Mexico may take about 20 h to complete[27]. Among vertebrates, exercise of such high intensity is usually characteristic of 'anaerobic' work sustainable only for relatively short durations[17]. Sustained exercise of the intensity involved in hummingbird flight requires extremely high rates of oxidation of metabolic fuels to CO_2 and H_2O, as well as matching of rates of delivery of metabolic fuels and O_2 to the demand by working muscles.

O_2 fluxes from lungs to muscle fibers

The sustained contractile performance of a set of muscles making up 30% of total body mass and consuming O_2 at a rate of 2 ml/(g × min) requires the support of respiratory and cardiovascular systems with extremely high capacities for O_2 transport. On the basis of morphometric measurements, Dubach[10] estimates that hummingbirds possess lung O_2 diffusion capacities that are 8.5-fold higher than those in mammals of equal body mass. Hummingbird hearts are about twice the size that birds of their mass would be predicted to have[39] and beat at rates of up to 1300/min[29]. These result in cardiac outputs of about 5 times body mass per min and whole body circu-

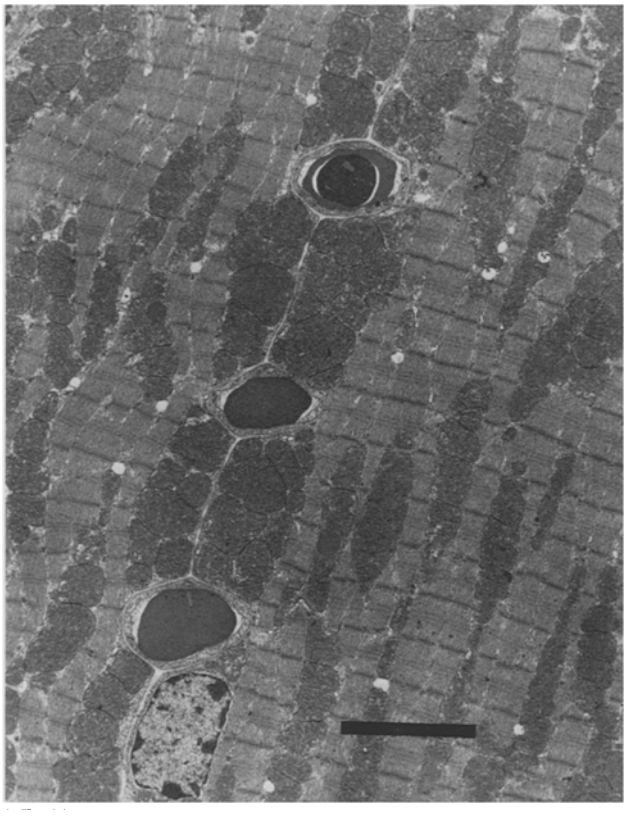

Figure 1. Transmission electron micrograph of longitudinally sectioned hummingbird *(Selasphorus rufus)* pectoralis muscle (kindly prepared by Dr Wayne Vogl, Dept. of Anatomy, University of British Columbia). Shown are portions of two adjacent muscle fibers sectioned longitudinally with capillaries (in cross section) running between them perpendicular to the plane of the section. Subsarcolemmal and interfibrillar mitochondria are apparent. Bar = 5 μm.

lation times estimated at about 1 s[23]. Hummingbirds possess blood with high hematocrits, O_2 capacities, and unloading efficiencies[24]. Capillary volume densities in the flight muscles are 2–6 times higher than those measured in mammalian hindlimb muscles (fig. 1)[46]. Pectoralis and supracoracoideus muscles consist exclusively of unusually thin type II fibers[14, 30, 46]. Together, such high capillary densities and low fiber cross sectional areas result in higher capillary surface to fiber surface ratios than in mammalian skeletal muscles, facilitating high rates of O_2 flux from the capillaries into the muscle fibers[46].

Mitochondrial machines

The mitochondria are the O_2 sinks which ultimately determine the rate at which O_2 fluxes occur from the lungs, through the cardiovascular system, and into the flight muscles. Thus, the maximal capacity for O_2 consumption in muscles is dependent upon mitochondrial content. Mitochondrial volume density (the % fraction of fiber volume occupied by mitochondria) is about 35% in hummingbird flight muscles[46] (fig. 1). Since the O_2 consumption during hovering flight and the fraction of total body mass accounted for by flight muscles are known, it is possible to calculate the rate of mitochondrial O_2 consumption in vivo. The rate of 7–10 ml per cm^3 of mitochondria per min[46] is 2-fold higher than that estimated in the skeletal muscles of mammals (ranging 5 orders of magnitude in body mass) running at VO_2max[22, 48].

Table 1. Comparison of mitochondrial morphometric parameters and respiration rates. Volume densities represent % of fiber volume occupied by mitochondria. Surface densities are cristae surface areas per unit mitochondrial volume.

	Volume density (%)	Suface density (m^2/cm^3)	ml O_2/ (cm^3 × min)	μl O_2/ (m^2 × min)
Cuban iguana[6]	3	25	1	40
Cat[40]	4–6	35	3–5	86–143
Hummingbird[46]	35	58	7–10	121–172
Euglossine bee[5]	43	50	16	320
Blowfly[7, 41]	40	53	23	434

Hummingbird flight muscle mitochondria possess about 58 m^2 of cristae surface area per cm^3 of total volume[46]. This is about 2.3- and 1.6-fold higher than the cristae surface densities found in reptilian[6] and mammalian[22, 40] skeletal muscle mitochondria, respectively, and is close to values estimated in the mitochondria found in insect flight muscles[41, 43] (table 1). Since the cristae contain the respiratory chain enzymes, both high mitochondrial volume densities and cristae surface densities result in the phenomenal capacities for O_2 consumption found in hummingbird flight muscles.

Morphometric measurements reveal that 40% of the mitochondria in hummingbird flight muscles are found under the sarcolemma[46]. The large volume density of subsarcolemmal mitochondria as well as the great abundance of capillaries results in the 'clustering' seen in figure 1. Mainwood and Rakusan[31] proposed that this type of arrangement may allow higher rates of O_2 flux than would be possible if mitochondria were simply distributed at random within muscle fibers. Thus, mitochondrial clustering adjacent to capillaries, as well as high capacities for O_2 flux from the lungs, through the cardiovascular system, and into the muscle fibers may allow respiration and oxidative phosphorylation to occur at higher rates per unit mitochondrial volume (and per unit cristae surface area) in hummingbird flight muscles than in mammalian skeletal muscles at VO_2max (table 1).

Fuels for flight

Phenomenal rates of respiration imply equally phenomenal rates of flux through oxidative pathways. Valuable insights into the structure of metabolic pathways as well as the maximum capacities for flux through them may be gained by measurement of the maximum activities of key metabolic enzymes[34]. Unusually high capacities for both

fatty acid and glucose oxidation are found in hummingbird flight muscles[44,47]. The maximal activities of hexokinase (a rate-determining enzyme responsible for catalyzing glucose phosphorylation and entry into the glycolytic pathway) and carnitine palmitoyltransferase (a rate-determining enzyme involved in long-chain fatty acid oxidation) are the highest recorded for vertebrate skeletal muscle (table 2). Activities of citrate synthase (a Krebs cycle enzyme) are in the range found in hymenopteran flight muscles[1]. Coupled mitochondria isolated from hummingbird flight muscles oxidize pyruvate + malate and palmitoyl coenzyme A + L-car-nitine + malate at similar rates[44], further substantiating the suggestion of high capacities for oxidation of both glucose and long-chain fatty acids (fig. 2).

Table 2. Comparison of required and maximum possible flux rates in hummingbird flight muscles. Values are expressed as μmoles/(g × min). Maximum possible fluxes (rates of glucose and oleate oxidation) are obtained from hexokinase and carnitine palmitoyltransferase (CPT) activities, respectively. CPT activities were not divided by 2 as done previously[47], since recent evidence indicates that CPT_1 (on the outer surface of the inner mitochondrial membrane) is destroyed by Triton X-100 extraction, and only CPT_2 (on the inner surface of the inner mitochondrial membrane) remains active[52]. Oleate is assumed to be the substrate for fatty acid oxidation for the purpose of this comparison.

Substrate	Flux required	Maximum flux possible
Glucose	13.7	18.4
Oleate	3.4	7.1

Since the O_2 consumption and ATP turnover rates in muscle during flight are known, it is possible to calculate the glucose and fatty acid oxidation rates necessary to account for these, assuming that either class of substrate is used exclusively. Comparison of these rates with the maximal pathway fluxes possible (based on measured activities of hexokinase and carnitine palmitoyltransferase (table 2), reveal that oxidation of glucose or long-chain fatty acids can account for the estimated metabolic rate of the tissue during flight[47]. These estimates indicate that flux rates through the hexokinase and carnitine palmitoyltransferase reactions are about 70 and 50% of the maximal capacities at these steps when glucose or long-chain fatty acids are oxidized, respectively.

4.5-g hummingbirds ingest nearly 2 g of sucrose per day in the wild[37]. To achieve this, hummingbird intestines possess higher sucrase activities per cm^2 of surface area than other birds[33] and higher densities of intestinal glucose transporters than any other vertebrate species examined thus far[8,25]. Hepatic pyruvate carboxylase and acetylcoenzyme A carboxylase (involved in gluconeogenesis and fatty acid synthesis, respectively) both occur at exceptionally high maximal activities in comparison with other vertebrates[45]. Thus, to help satisfy the short- and

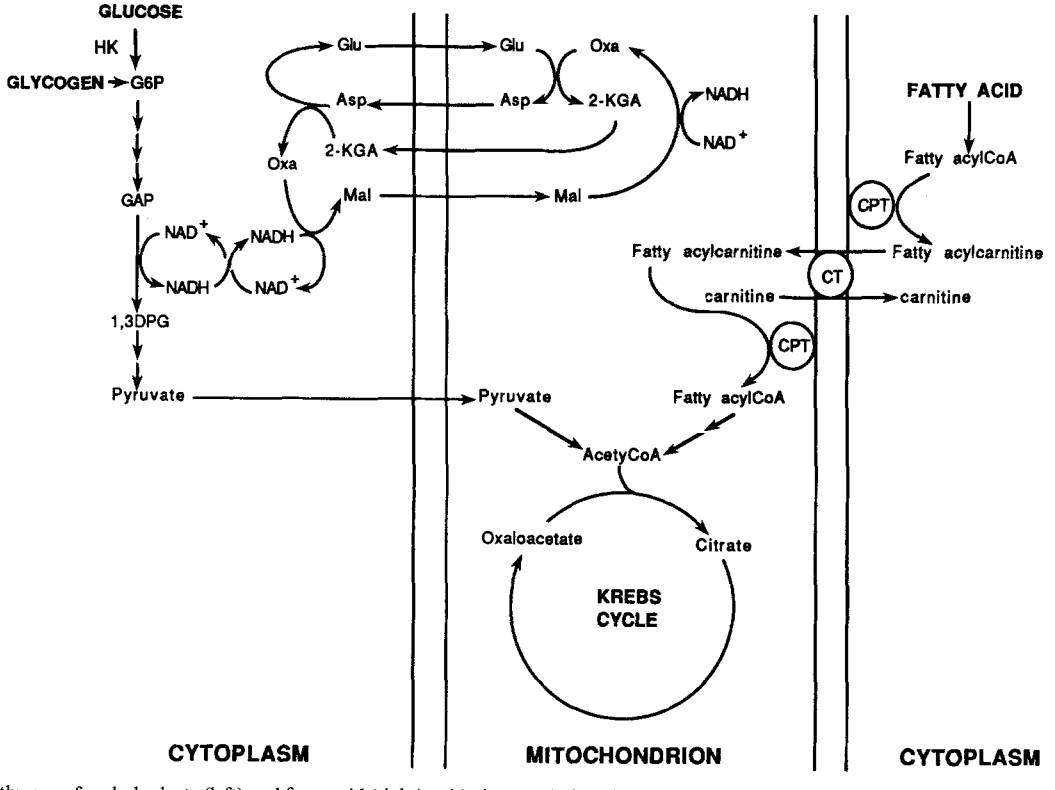

Figure 2. Pathways of carbohydrate (left) and fatty acid (right) oxidation in hummingbird flight muscles. Abbreviations: HK, hexokinase; CPT, carnitine palmitoyltransferase; CT, carnitine acyltranslocase; G6P, glucose-6-phosphate; GAP, glyceraldehyde 3-phosphate; 1,3 DPG, 1,3-diphosphoglycerate; 2-KGA, 2-ketoglutarate; Mal, malate; Oxa, oxaloacetate. Figure is taken from ref. 47 (with permission from the Proc. natl Acad. Sci. USA).

long-term needs of their large and metabolically active flight muscles, hummingbirds may possess the most biosynthetically active livers in nature.

Their high metabolic rates and nectarivorous diets have led many biologists to wonder about the nature of the metabolic fuels used by hummingbirds under various circumstances. The abundance of lipid droplets in electron micrographs[14] and the importance of fats as fuels in birds in general[35] have led to the suggestion that fatty acid oxidation may be the most important ATP-generating catabolic pathway[9, 20]. Certainly, fats play an important role in long-term migratory flights, for which certain hummingbird species prepare by increasing fat content at a rate of about 10% of body mass per day[4]. Ruby-throated hummingbirds start their migration across the Gulf of Mexico with about 40% of total body mass accounted for by fat[35]. There are good reasons for why fats are the preferred fuels for long-distance flights. Fats are stored in non-hydrated form (unlike glycogen) and are more highly reduced than glycogen. These result in energy yields per unit mass from fat oxidation that are close to 10-fold greater than with the oxidation of glycogen[21].

Recent studies involving the measurement of respiratory quotients (RQ = rate of CO_2 production/rate of O_2 consumption) in hummingbirds engaged in foraging flight indicate that carbohydrate is the metabolic fuel oxidized under these circumstances[47] (fig. 3). Since synthesizing fat from dietary carbohydrate and then oxidizing the fat results in a lower net energy yield (because of the energetic cost of biosynthesis) than oxidizing dietary carbohydrate itself[47], the metabolic strategy adopted by foraging hummingbirds is the one that is most energetically efficient. Indeed, it has been proposed that foraging behavior involving short flights and maintenance of territories result in avoidance of both the direct cost of flying long durations as well as the indirect cost incurred as a result of having to switch to fats as fuels[47].

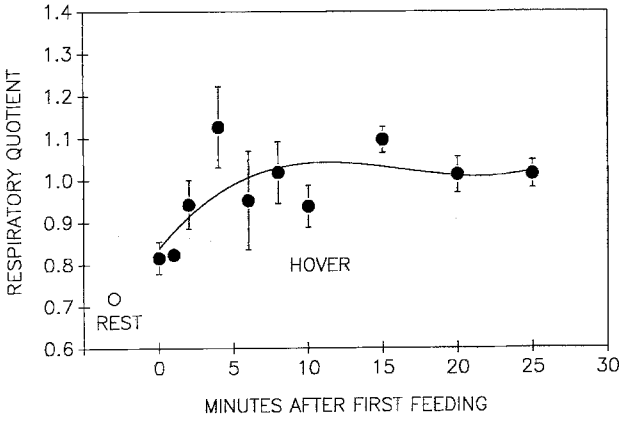

Figure 3. RQ (VCO_2/VO_2) during hovering-feeding as a function of time after the first bout (0 min). Resting values were obtained using restrained birds fasted 1–2 h. Points denote means; error bars denote SEM. Figure is taken from ref. 47 (with permission from the Proc. natl Acad. Sci. USA).

Limits

Nature appears not to have made much use of significant alterations in enzyme catalytic efficiencies in the tuning up of homeothermic vertebrates. For example, turnover numbers (K_{cat}) for the regulatory glycolytic enzyme phosphofructokinase[32, 38] and the Krebs cycle enzyme citrate synthase (Paul Srere, pers. comm.) are highly conserved and are essentially the same in large and small mammals. In mammals, muscle glycolytic enzyme activities increase with body mass, while oxidative enzyme activities scale inversely with body mass, most probably as the result of species-specific differences in enzyme content[11, 19]. Given enzymes of similar or identical properties, the diverse results of Nature's experiments in vertebrate homeotherm design appear to be the outcome of mainly how (and in what proportions) such components have been put together. Larger and faster hearts, high hematocrits and O_2 unloading efficiencies, more capillary surface per muscle fiber surface areas, greater mitochondrial volume densities and cristae surface densities, more enzyme copies in pathways of glucose and fatty acid oxidation and synthesis, and more absorptive intestines, have all formed part of a concerted, integrated pattern of up-regulation of functional capacities.

Comparative physiologists have always been interested in whether vertebrate homeotherms smaller than 2 g are possible. There are obviously many constraints that have precluded the evolution of smaller vertebrate homeotherms. For example, it has been suggested that limitations inherent in the design of vertebrate O_2 delivery (cardiovascular and respiratory) systems result in the smallest birds and mammals being about 2 g in mass[39]. Thus, larger or faster hearts and higher blood hematocrits may be physically impossible or physiologically disadvantageous in such animals. Indeed, higher metabolic rates are achieved only by insects which possess totally different (tracheal) systems for O_2 delivery, as well as mitochondria with higher capacities for O_2 consumption[5, 7, 43] (table 1).

Since the mass-specific resting metabolic rates of birds increase with decreasing body mass according to known scaling relationships[39], and since aerobic metabolism is activated over resting rates (at the thermoneutral zone) about 10-fold during flight, a smaller hummingbird would probably require an even higher muscle mitochondrial volume density than what is already found in existing hummingbirds. Clearly, mitochondrial volume density in locomotory muscles cannot be increased indefinitely without compromising the capacity for mechanical work. Weibel[50], Hochachka[18, 19], as well as Pennycuick and Rezende[36] have suggested that such constraints may play a role in determining the maximum possible aerobic capacity of muscle. Interestingly, no locomotory muscles in vertebrate homeotherms and in insects have been found which possess mitochondrial volume densities in excess of 45% (table 1). Similarly, there are limits to how

much cristae can be contained per unit mitochondrial volume, since greater cristae surface areas necessarily result in less room available for matrix[42]. Cristae surface densities in the range found in hummingbird and insect flight muscles result in distances between the inner surfaces of the cristae equivalent to about 4 average size Krebs cycle enzymes[42], suggesting that any further increase in cristae surface densities (at the expense of matrix volumes) may not be possible.

It may not be possible for vertebrate homeotherms to be significantly smaller than the smallest known hummingbirds, shrews and bats. Among the many reasons for this are those that relate to constraints and limitations in the design of locomotory muscles and the systems that support their function. Small hummingbirds, in particular, appear to have pushed the possibilities of vertebrate design for aerobic performance close to the absolute limit.

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1 Alp, P. R., Newsholme, E. A., and Zammit, V. A., Activities of citrate synthase and NAD^+-linked isocitrate dehydrogenase in muscle from vertebrates and invertebrates. Biochem. J. *154* (1976) 689–700.
2 Bartholomew, G. A., and Lighton, J. R. B., Oxygen consumption during hover-feeding in free-ranging Anna hummingbirds. J. exp. Biol. *123* (1986) 191–199.
3 Berger, M., Sauerstoffverbrauch von Kolibris *(Colibri coruscans* und *C. thalassinus)* beim Horizontalflug, in: BIONA Report 3, pp. 307–314. Ed. W. Nachtigall. Akad. Wiss. Mainz G. Fischer, Stuttgart and New York 1985.
4 Carpenter, F. L., Paton, D. C., and Hixon, M. A., Weight gain and adjustment of feeding territory size in migrant hummingbirds. Proc. natl Acad. Sci. USA *80* (1983) 7259–7263.
5 Casey, T. M., and Ellington, C. P., Energetics of insect flight, in: Energy Transformations in Cells and Organisms, pp. 200–210. Eds W. Wieser and E. Gnaiger. Georg Thieme Verlag, Stuttgart and New York 1990.
6 Conley, K. E., Christian, K. A., Hoppeler, H., and Weibel, E. R., Capillary and mitochondrial unit in muscles of a large lizard. Am. J. Physiol. *256* (1989) R982–R989.
7 Davis, R. A., and Fraenkel, G., The oxygen consumption of flies during flight. J. exp. Biol. *17* (1940) 402–407.
8 Diamond, J. M., Karasov, W. H., Phan, D., and Carpenter, F. L., Digestive physiology is a determinant of foraging bout frequency in hummingbirds. Nature *320* (1986) 62–63.
9 Drummond, G. I., Microenvironment and enzyme function: control of energy metabolism during muscle work. Am. Zool. *11* (1971) 83–97.
10 Dubach, M., Quantitative analysis of the respiratory system of the house sparrow, budgerigar and violet-eared hummingbird. Respir. Physiol. *46* (1981) 43–60.
11 Emmett, B., and Hochachka, P. W., Scaling of oxidative and glycolytic enzymes in mammals. Respir. Physiol. *45* (1981) 261–272.
12 Epting, R. J., Functional dependence of the power for hovering on wing disc loading in hummingbirds. Physiol. Zool. *53* (1980) 347–352.
13 Greenewalt, C. H., Hummingbirds. Doubleday, New York 1960.
14 Grunyer, I., and George, J. C., Some observations on the ultrastructure of the hummingbird pectoral muscles. Can. J. Zool. *47* (1969) 771–774.
15 Hainsworth, F. R., Energy regulation in hummingbirds. Am. Sci. *69* (1981) 420–429.
16 Hartman, F. A., Locomotor mechanisms of birds. Smithson. Inst. misc. Collect. *143* (1961) 1–91.
17 Hochachka, P. W., Fuels and pathways as designed systems for muscle work. J. exp. Biol. *115* (1985) 149–164.
18 Hochachka, P. W., Limits: How fast and how slow muscle metabolism can go, in: Advances in Myochemistry, vol. 1, pp. 3–12. Ed. G. Benzi. John Libbey, Eurotext 1987.
19 Hochachka, P. W., Emmett, B., and Suarez, R. K., Limits and constraints in the scaling of oxidative and glycolytic enzymes in homeotherms. Can. J. Zool. *66* (1988) 1128–1138.
20 Hochachka, P. W., Neely, J. R., and Driedzic, W. R., Integration of lipid utilization with Krebs cycle activity in muscle. Fedn Proc. *36* (1977) 2009–2014.
21 Hochachka, P. W., and Somero, G. N., Strategies of Biochemical Adaptation. Saunders, Philadelphia 1973.
22 Hoppeler, H., and Lindstedt, S. L., Malleability of skeletal muscle in overcoming limitations: structural elements. J. exp. Biol. *115* (1985) 355–364.
23 Johansen, K., The world as a laboratory: physiological insights from Nature's experiments, in: Advances in Physiological Research, pp. 377–396. Eds H. McLennan, J. R. Ledsome, C. H. S. McIntosh and D. R. Jones. Plenum Press, New York 1987.
24 Johansen, K., Berger, M., Bicudo, J. E. P. W., Ruschi, A., and De Almeida, P. J., Respiratory properties of blood and myoglobin in hummingbirds. Physiol. Zool. *60* (1987) 269–278.
25 Karasov, W. H., Phan, D., Diamond, J. M., and Carpenter, F. L., Food passage and intestinal nutrient absorption in hummingbirds. Auk *103* (1986) 453–464.
26 Krebs, J. R., and Harvey, P. H., Busy doing nothing – efficiently. Nature *320* (1986) 18–19.
27 Lasiewski, R. C., The energetics of migrating hummingbirds. Condor *64* (1962) 324.
28 Lasiewski, R. C., Oxygen consumption of torpid, resting, active, and flying hummingbirds. Physiol. Zool. *36* (1963) 122–140.
29 Lasiewski, R. C., Body temperatures, heart and breathing rate, and evaporative water loss in hummingbirds. Physiol. Zool. *37* (1964) 212–223.
30 Lasiewski, R. C., Galey, F. R., and Vasquez, C., Morphology and physiology of the pectoral muscles of hummingbirds. Nature *206* (1965) 404–405.
31 Mainwood, G. W., and Rakusan, K., A model for intracellular energy transport. Can. J. Physiol. Pharmac. *60* (1982) 98–102.
32 Mansour, T. E., Wakid, N., and Sprouse, H. M. Studies on heart phosphofructokinase. Purification, crystallization, and properties of sheep heart phosphofructokinase. J. biol. Chem. *241* (1966) 1512–1521.
33 Martinez del Rio, C., Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. Physiol. Zool. *63* (1990) 987–1011.
34 Newsholme, E. A., and Crabtree, B., Maximum catalytic activity of some key enzymes in provision of physiologically useful information about metabolic fluxes. J. exp. Zool. *239* (1986) 159–167.
35 Odum, E. P., Connell, C. E., and Stoddard, H. L., Flight energy and estimated flight ranges of some migratory birds. Auk *78* (1961) 515–527.
36 Pennycuick, C. J., and Rezende, M. A., The specific power output of aerobic muscle, related to the power density of mitochondria. J. exp. Biol. *108* (1984) 377–392.
37 Powers, D. R., and Nagy, K. A., Field metabolic rate and food consumption by free-living Anna's hummingbirds *(Calypte anna)*. Physiol. Zool. *61* (1988) 500–506.
38 Ramadoss, C. S., Luby, L. J., and Uyeda, K., Affinity chromatography of phosphofructokinase. Archs Biochem. Biophys. *175* (1976) 487–494.
39 Schmidt-Nielsen, K., Scaling. Why is Animal Size So Important? Cambridge Univ. Press, Cambridge 1984.
40 Schwerzmann, K., Hoppeler, H., Kayar, S. R., and Weibel, E. R., Oxidative capacity of muscle and mitochondria: correlation of physiological biochemical and morphometric characteristics. Proc. natl Acad. Sci. USA *86* (1989) 1583–1587.
41 Smith, D. S., The structure of flight muscle sarcosomes in the blowfly *Calliphora erythrocephala* (Diptera). J. Cell Biol. *19* (1963) 114–138.
42 Srere, P. A., Organisation of proteins within the mitochondrion, in: Organized Multienzyme Systems. Catalytic Properties, pp. 1–61. Ed. G. Rickey Welch. Academic Press, New York and London 1985.
43 Suarez, R. K., Oxygen and VO_2max: are muscle mitochondria created equal? Proc. 7th Int. Hypoxia Symp. (1992) in press.

44 Suarez, R. K., Brown, G. S., and Hochachka, P. W., Metabolic sources of energy for hummingbird flight. Am. J. Physiol. *251* (1986) R537–R542.
45 Suarez, R. K., Brownsey, R. W., Vogl, W., Brown, G. S., and Hochachka, P. W., Biosynthetic capacity of hummingbird liver. Am. J. Physiol. *255* (1988) R699–R702.
46 Suarez, R. K., Lighton, J. R. B., Brown, G. S., and Mathieu-Costello, O., Mitochondrial respiration in hummingbird flight muscles. Proc. natl Acad. Sci. USA *88* (1991) 4870–4873.
47 Suarez, R. K., Lighton, J. R. B., Moyes, C. D., Brown, G. S, Gass, C. L., and Hochachka, P. W., Fuel selection in hummingbirds: ecological implications of metabolic biochemistry. Proc. natl Acad. Sci. USA *87* (1990) 9207–9210.
48 Taylor, C. R., Structural and functional limits to oxidative metabolism: insights from scaling. A. Rev. Physiol. *49* (1987) 135–146.
49 Taylor, C. R., Maloiy, G. M. O., Weibel, E. R., Langman, V. A., Kamai, J. M. Z., Seeherman, H. J., and Heglund, N. C., Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic animals. Respir. Physiol. *44* (1980) 25–37.
50 Weibel, E. R., Design and performance of muscular systems: an overview. J. exp. Biol. *115* (1985) 405–412.
51 Weis-Fogh, T., Energetics of hovering flight in hummingbirds and in *Drosophila*. J. exp. Biol. *56* (1972) 79–104.
52 Woeltje, K. F., Kuwajima, M., Foster, D. W., and McGarry, J. D., Characterization of the mitochondrial carnitine palmitoyltransferase enzyme system. II. Use of detergents and antibodies. J. biol. Chem. *262* (1987) 9822–9827.

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Metabolic biochemistry and the making of a mesopelagic mammal

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Abstract. Large seals such as northern and southern elephant seals and Weddell seals are able to dive for startling duration and enormous depth. The current dive duration record is 120 minutes (recorded for the southern elephant seal); the current depth record is 1.5 km (recorded for the northern elephant seal). Equally striking is the widespread observation that these seals when at sea spend close to 90% of the time submerged and often at great depth. For practical purposes, these species can be viewed as true mesopelagic animals when they are at sea. A review of current knowledge indicates that low power output but high efficiency metabolic functions of skeletal muscles coupled with inherently low (and potentially further suppressible) metabolic rates constitute strategic biochemical components in the 'making' of a mesopelagic mammal.
Key words. Seal metabolism; metabolic efficiency; metabolic suppression; seal muscle enzymes.

The problem

The literature and international symposia on diving metabolism and physiology were unusually lively during the 1980's because of an apparent paradox: a seeming discordance between laboratory and field data on the significance of the Scholander diving response. Studies of simulated laboratory diving consistently observed powerful bradycardia coupled with peripheral vasoconstriction, serving to redistribute cardiac output with preferential perfusion of the heart and brain. In contrast, heart rate measurements of voluntary diving frequently showed little or no evidence of such patterns, which together are termed the diving response. With the development of microcomputer devices for monitoring voluntary diving in the sea[9, 10, 24, 25], this paradox has been largely resolved, and the dialogue is now far more reserved, implying relatively broad agreement between the diverse workers in this area. However, as we enter the 1990's, the diving discipline is again confronted with another equally perplexing paradox: namely, the apparent ability of large (Weddell, southern elephant, and northern elephant) seals to dive for longer times than would be required for resting metabolic rates to consume all onboard O_2 supplies. What is more, the currently available field data indicate that these large seals when diving at sea are submerged close to 90% of the time for periods of weeks to several months[6, 12, 13, 24, 25]. Hence, living in the 'slow lane' appears to be the normal metabolic state of affairs for these species. The main goals of this essay are first, to review the fundamental metabolic and physiological processes underlying these apparent low metabolic rates during diving, and secondly, to consider their ecological implications.

Background and current developments

Antecedents to the above metabolic paradox are evident in the literature as far back as the late 1930's in the work of Scholander and Irving, and based on laboratory experimentation (see Scholander[28]). We first confronted the problem in our 1982/1983 Antarctic research program studying voluntary diving in the Weddell seal. These studies[9, 11, 12, 27] showed that for some free dives, the total amount of O_2 available could only sustain low metabolic rates, lower than RMR, the resting metabolic rate of the species. The amounts of lactate formed dur-