ENERGY METABOLISM IN THE LOCOMOTOR MUSCLES OF THE COMMON MURRE (*URIA AALGE*) AND THE ATLANTIC PUFFIN (*FRATERCULA ARCTICA*)

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ABSTRACT.—To compare the metabolic systems that support the combination of flying and diving with those used to support burst flying and sustained flying, myoglobin concentrations and maximum enzyme activities were determined for selected enzymes of glycolysis, the Krebs cycle, and amino acid metabolism in the pectoral, supracoracoideus, and sartorius muscles of the Common Murre (*Uria aalge*), Atlantic Puffin (*Fratercula arctica*), Rock Dove (*Columba livia*; hereafter "pigeon"), and Ring-necked Pheasant (*Phasianus colchicus*). Glycolytic enzyme levels in the flight muscles were lower in the murre and the puffin than in the pheasant, while both glycolytic and Krebs-cycle enzyme levels resembled those in the pigeon. We believe puffins and murres do not rely extensively on anaerobic glycolysis during diving. In concordance with a role in oxygen storage for diving, the levels of myoglobin in the flight muscles of murres and puffins were higher than those in pigeons or pheasants. They were lower than published values for penguins, however. In contrast to the trends for pigeon and pheasant muscles, the alcid sartorius muscles had a considerably lower aerobic orientation than the flight muscles. *Received 21 November 1986, accepted 9 June 1987.*

IN birds a high anaerobic capacity, as indicated by types and levels of glycolytic enzymes, is correlated positively with locomotory patterns demanding burst flying, extensive diving, or quick maneuvering (Wilson et al. 1963, Kiessling 1977, Mill and Baldwin 1983, Baldwin et al. 1984). During these activities oxygen tension in muscle may be reduced to the point where ATP is produced from substrate-level phosphorylations coupled to lactate production. Anaerobic glycolysis seems the primary source of ATP during flight for burst fliers like the Ring-necked Pheasant (*Phasianus colchicus*; Wilson et al. 1963, Kiessling 1977). Similarly, the take-off, hovering, and quick directional changes of Rock Doves (*Columba livia*; hereafter "pigeon") are thought to be anaerobically supported (Pennycuick 1968, Parker and George 1975). The functional utility of the high glycolytic capacity of diving birds is less clear. Anaerobic glycolysis could fully support diving, in analogy with pheasant flight, or it could permit rapid directional changes during diving, in analogy with pigeon flight. Deeper-diving birds also may have a greater glycolytic capacity relative to shallow-diving birds as a backup system proportional to the depths to which they dive. While most penguin species have anaerobic capacities that are proportional to their diving depths (Baldwin et al. 1984) and show marked bradycardia and lactate production during forced laboratory dives (Scholander 1940), voluntary dives in ponds are aerobic (Butler and Woakes 1984) and free-ranging dives are generally short (reviewed by Baldwin et al. 1984). The studies that established the correlation between diving depth and glycolytic capacity for penguins (Mill and Baldwin 1983, Baldwin et al. 1984), however, did not directly compare enzyme activities in penguins with those in terrestrial birds with varying locomotor strategies. The need for such an integrated approach is underlined by the data from mammals. Although early studies suggested that diving mammals had exceptional glycolytic capacities (Simon et al. 1974), an extensive comparison of pyruvate kinase and lactate dehydrogenase levels in terrestrial and marine mammals showed no differences (Castellini et al. 1981). In addition, because enzyme activities are markedly affected by assay conditions, simultaneous determination of enzyme activities in the different species is a prerequisite for rigorous comparison.

Several alcid species are the ecological counterparts of penguins in the Northern Hemisphere. Two of these, the Atlantic Puffin (*Fratercula arctica*) and the Common Murre (*Uria aalge*), dive to depths of 60 m and 180 m, respectively (Piatt and Nettleship 1985), using their wings and legs for propulsion and steering (Tuck 1961, Spring 1971). Besides being proficient divers, the alcids migrate over long dis-

tances from overwintering areas at sea to land for the breeding season. Just as their morphology represents a compromise between the opposing requirements of diving and flying, their metabolic organization must be compatible with both. For alcids flying and diving are closely associated activities. During the breeding season, foraging dives are sandwiched between flights between the nest and feeding areas (Harris and Hislop 1978).

We examined the metabolic organization of the locomotor muscles in puffins and murres to elucidate the metabolic strategies that support the combination of diving and flying. To compare the metabolic capacities of these alcids with those of birds whose metabolic strategies are reasonably well defined, we studied the Ring-necked Pheasant, a burst flyer (Wilson et al. 1963, Kiessling 1977), and the pigeon, a bird capable of sustained flight (Pennycuick 1968, Parker and George 1975). Our specific aims were to compare the metabolic systems that support extensive flying and diving with those used to support burst or sustained flying, to examine whether glycolytic capacity was proportional to diving depth in these alcids, and to compare the metabolic organization of the major flight muscles (pectoral and supracoracoideus) and an important leg muscle (sartorius) because both wings and legs are used in underwater propulsion.

Puffins and murres are logistically difficult to obtain, making determination of *in situ* metabolic flux impossible. Instead, we measured the maximal activities of glycolytic and Krebs-cycle enzymes to assess anaerobic and aerobic potential; this has been done in previous studies, including those on penguins (Crabtree and Newsholme 1972, Kiessling 1977, Castellini and Somero 1981, Mill and Baldwin 1983, Baldwin et al. 1984). We measured myoglobin concentrations as an indication of the oxygen stores available to the muscles (Weber et al. 1974, Pages and Planas 1983) and the levels of enzymes that contribute intermediates to the Krebs cycle. Because we worked with frozen tissues, we measured only enzymes that are stable to freezing (Farrar and Farrar 1983).

MATERIALS AND METHODS

Experimental animals.—Five Common Murres and 5 Atlantic Puffins were collected in early July 1984 at Witless Bay, Newfoundland (47°15'N, 52°40'W) by shooting as they surfaced (Environment Canada/Canadian Wildlife Permit A SK 18-84 and with the permission of the Newfoundland Wildlife Division). The carcasses were placed in −2°C seawater during transport back to the wharf (maximum 2 h). There tissues were dissected, wrapped in aluminum foil, and frozen in 2-methylbutane (Eastman Kodak, Rochester, New York) previously chilled in a liquid nitrogen bath. Samples were stored at −25°C until assayed. Five pheasants and 5 pigeons were obtained live from commercial suppliers, decapitated, and dissected immediately. Tissues were stored as above.

Enzyme assays.—Muscle samples were freed of connective tissue and fat, weighed, minced with a scalpel, and homogenized with a Polytron (Brinkman Instruments) for 30 s in 10 ml/g ice-cold extraction buffer. For all enzymes except $NADP^+$-linked isocitrate dehydrogenase, the extraction buffer was 50 mM imidazole-HCl, 50 mM KCl, 1 mM EDTA, 2 mM 2-mercaptoethanol (omitted for citrate synthase assay), pH 7.4. For $NADP^+$-linked isocitrate dehydrogenase, the extraction buffer was 50 mM Pipes [piperazine-NN'-bis(2-ethanesuphonic acid)], 10 mM $MgCl_2$, 5 mM 2-mercaptoethanol, 1 mM EDTA, 5 mM $MnCl_2$, 2 mM ADP, 5 M glycerol, 0.1 mM phenylmethylsulphonyl fluoride, pH 7.4. The homogenate was centrifuged at 25,000 × *g* for 40 min at 4°C (600 × *g* for 3 min for $NADP^+$ isocitrate dehydrogenase) in a Sorvall SS-34 rotor. The supernatant was used immediately for the assays. All biochemicals were obtained from Sigma Chemical Co. (St. Louis, Missouri). Enzymes were assayed with a UV/Vis recording spectrophotometer (Varian Cary 210). The cuvette temperature was maintained at 38 ± 0.5°C throughout the assays using a circulating water bath. Determinations of activity were done in triplicate. Enzyme activities are expressed as μmol of substrate transformed$\cdot min^{-1} \cdot g^{-1}$ wet mass of tissue. Enzymes were assayed by following changes in absorbance at 340 nm, except citrate synthase, which was assayed at 412 nm. Preliminary experiments were run to determine the substrate concentrations required to give maximal activities. All pH values were adjusted at 38°C. The composition of the reaction mixtures is given below.

Aldolase (ALD) (E.C. 4.1.2.13): 0.2 mM NADH, 1.5 mM fructose-1,6-bisphosphate, 50 mM triethanolamine/HCl, excess glycerol-3-phosphate dehydrogenase, triose phosphate isomerase, pH 7.4. Fructose-1,6-bisphosphate was omitted for the control. *Pyruvate kinase* (PK) (E.C. 2.7.1.40): 100 mM KCl, 10 mM $MgCl_2$, 0.2 mM NADH, 5 mM ADP, 5 mM phosphoenolpyruvate, 50 mM triethanolamine/HCl, excess lactate dehydrogenase, pH 7.4. Phosphoenolpyruvate was omitted for the control. *Lactate dehydrogenase* (LDH) (E.C. 1.1.1.27): 0.2 mM NADH, 1.5 mM pyruvate for pheasant and pigeon muscle and 2 mM pyruvate for murre and puffin muscle, 50 mM triethanolamine/HCl, pH 7.4. Pyruvate was omitted for the control. *Citrate synthase* (CS) (E.C. 4.1.3.7): 50 mM triethanol-

TABLE 1. Glycolytic enzyme activities in locomotor muscles. Values represent the mean activity (μmol·min^{-1}·g^{-1} wet mass) ± SD for each muscle type measured in 5 birds. Data were analyzed as explained in Materials and Methods, and the results are shown by letters following the values. Values with different letters differ significantly ($P < 0.05$). Lowercase letters indicate differences among the values for one enzyme in a column (interspecific comparisons); capital letters indicate significant differences among the values in a row (intraspecific comparisons).

	Pectoral	Supracoracoideus	Sartorius
Aldolase			
Pheasant	319 ± 69 a, A	291 ± 16 a, A	126 ± 20 a, B
Pigeon	117 ± 43 b, A	145 ± 21 ab, A	60 ± 6 b, B
Puffin	62 ± 20 c, A	86 ± 29 b, A	70 ± 24 b, A
Murre	116 ± 10 b, A	103 ± 29 b, A	57 ± 10 b, B
Pyruvate kinase			
Pheasant	1,761 ± 221 a, A	1,505 ± 182 a, A	970 ± 68 a, A
Pigeon	568 ± 58 b, AB	771 ± 159 b, A	443 ± 56 b, B
Puffin	369 ± 25 c, A	412 ± 143 c, A	464 ± 134 b, A
Murre	672 ± 117 b, A	757 ± 165 b, A	443 ± 69 b, B
Lactate dehydrogenase			
Pheasant	2,523 ± 270 a, A	2,409 ± 207 a, A	1,039 ± 100 a, B
Pigeon	1,015 ± 88 b, B	1,872 ± 137 ab, A	664 ± 54 c, B
Puffin	666 ± 24 c, C	1,189 ± 67 c, A	936 ± 207 ab, B
Murre	1,184 ± 203 b, A	1,583 ± 297 bc, A	758 ± 108 bc, B

amine/HCl, 0.2 mM acetyl coenzyme A, 0.2 mM 5′,5′-dithiobis-(2-nitrobenzoic acid), 0.125 mM oxaloacetate, pH 7.4. Oxaloacetate was omitted for the control. *$NADP^+$-linked isocitrate dehydrogenase* (ICDH) (E.C. 1.1.1.42): 70 mM Tris/HCl, 0.5 mM $NADP^+$, 1 mM $MnCl_2$, 8 mM $MgCl_2$, 1.5 mM isocitrate, 10 mM citrate, pH 7.4. Isocitrate and citrate were omitted for the control. *Malate dehydrogenase* (MDH) (E.C. 1.1.1.37): 50 mM K^+-phosphate buffer, 0.2 mM NADH, 0.5 mM oxaloacetate, pH 7.4. Oxaloacetate was omitted for the control. *Glutamate dehydrogenase* (GDH) (E.C. 1.4.1.3): 50 mM triethanolamine/HCl, 0.2 mM NADH, 1 mM ADP, 2.5 mM EDTA, 100 mM ammonium acetate, 10 mM α ketoglutarate, pH 7.4. α ketoglutarate was omitted for the control. *Glutamate pyruvate transaminase* (GPT) (E.C. 2.6.12): 0.2 mM NADH, 80 mM K^+-phosphate buffer, 0.8 mM alanine, 18 mM α ketoglutarate, excess LDH, pH 7.4. α ketoglutarate was omitted for the control. *Glutamate oxaloacetate transaminase* (GOT) (E.C. 3.5.1.1): 80 mM K^+-phosphate buffer, 40 mM aspartate, 0.2 mM NADH, excess MDH, 12 mM α ketoglutarate, pH 7.4. α ketoglutarate was omitted for the control.

Myoglobin was measured following the method of Reynafarje (1963) and is expressed as mg/g wet mass.

Statistical comparisons.—Bartlett's test indicated that the variances of the raw data scores were not homogeneous for 7 of the 10 sets of data. The data were ranked, and an ANOVA was performed on the ranks followed by a Ryan-Einot-Gabrial-Welsch comparison of means (SAS Inst. 1982). The data are presented as means ± SD (n).

RESULTS

Interspecific comparisons.—Pheasant flight muscles consistently had the highest glycolytic enzyme activities, the lowest myoglobin concentrations, and the lowest Krebs-cycle enzyme activities (Tables 1 and 2). Pigeon and murre flight muscles had similar levels of glycolytic and Krebs-cycle enzymes. While puffin flight muscles had lower levels of glycolytic enzymes, levels of Krebs-cycle enzymes were similar to those of pigeon and murre flight muscles. Generally, the two diving species had significantly higher myoglobin concentrations in the pectoral and supracoracoideus muscles than did the pigeon and pheasant (Table 2).

Enzyme levels showed different interspecific trends in the sartorius muscle than in the flight muscles. Although pheasant muscle again showed the highest activities of glycolytic enzymes (Table 1), its levels of Krebs-cycle enzymes were similar to those of pigeon sartorius (Table 2). The levels of glycolytic enzymes in the sartorius of the pigeon, murre, and puffin were similar (Table 1). CS levels imply that the sartorius muscles of diving birds have a lower aerobic capacity than those of pigeons or pheasants (Table 2). Myoglobin concentrations, however, were similar in the sartorius from the four species (Table 2).

TABLE 2. Levels of Krebs-cycle enzymes and myoglobin in locomotor muscles. Values are presented and compared as explained in Table 1. Lowercase letters indicate interspecific differences for the enzyme levels in a given locomotor muscle; capital letters indicate intraspecific differences.

	Pectoral	Supracoracoideus	Sartorius
Citrate synthase			
Pheasant	10.5 ± 2.9 b, A	9.7 ± 0.9 b, A	5.9 ± 2.8 a, A
Pigeon	51.3 ± 10.9 a, A	29.1 ± 6.7 a, B	7.4 ± 1.2 a, C
Puffin	46.3 ± 5.4 a, A	31.6 ± 2.3 a, B	2.2 ± 0.9 b, C
Murre	51.1 ± 3.7 a, A	27.0 ± 4.2 a, B	1.5 ± 0.4 b, C
NADP+-linked isocitrate dehydrogenase			
Pheasant	3.1 ± 1.5 b, A	2.9 ± 0.1 b, A	11.5 ± 5.3 a, A
Pigeon	72.5 ± 16.4 a, A	37.6 ± 4.9 a, B	19.4 ± 0.8 a, B
Puffin	82.6 ± 13.7 a, A	44.6 ± 4.8 a, A	10.2 ± 3.0 a, B
Murre	60.0 ± 9.1 a, A	35.9 ± 8.2 a, B	3.8 ± 0.7 a, B
Malate dehydrogenase			
Pheasant	388 ± 58 b, AB	377 ± 22 c, B	477 ± 76 b, A
Pigeon	1,149 ± 120 a, A	787 ± 125 b, B	524 ± 35 ab, C
Puffin	1,364 ± 318 a, A	1,169 ± 95 a, A	682 ± 98 a, B
Murre	1,213 ± 81 a, A	852 ± 74 b, B	257 ± 25 c, C
Myoglobin (mg/g wet mass)			
Pheasant	0.51 ± 0.36 c, B	0.71 ± 0.24 b, B	5.19 ± 1.97 a, A
Pigeon	7.20 ± 2.07 b, AB	1.48 ± 0.61 b, B	7.30 ± 1.80 a, A
Puffin	12.54 ± 2.58 ab, A	9.38 ± 4.09 a, A	8.06 ± 5.54 a, A
Murre	14.10 ± 1.22 a, A	11.93 ± 1.78 a, A	6.31 ± 3.25 a, B

Because the enzymes of amino acid metabolism can contribute intermediates to the Krebs cycle, the levels of enzymes of amino acid metabolism and of the Krebs cycle may be correlated. We found little evidence of such correlation, however. Only the interspecific differences of GPT in the flight muscles resembled those of Krebs-cycle enzymes (Table 3) as GPT levels were consistently lowest in pheasant flight muscle. In contrast to the equivalence of Krebs-cycle enzyme levels in pigeon, murre, and puffin flight muscles, GPT levels were significantly higher in flight muscles of pigeons and murres than of puffins. Comparison of GPT levels in the sartorius indicated that the pigeon is highest, followed by the murre, the puffin, and finally the pheasant. GOT levels were generally lower in the muscles of the divers than in those of the nondivers (Table 3). Although GDH levels were higher in flight muscle of divers than nondivers, GDH levels in pheasant and murre sartorius were similar and higher than those of puffin or pigeon (Table 3).

Intraspecific comparisons.—For pigeon, puffin, and murre muscle, enzyme activities were generally higher in the flight muscles than in the sartorius. Furthermore, the pectoral muscles had higher levels of Krebs-cycle enzymes than the supracoracoideus muscles (Tables 1 and 2). These three species also showed some indication of higher glycolytic enzyme activities in the supracoracoideus than in the pectoral muscle (Table 1). By contrast, the pheasant muscles generally had similar enzyme levels. For pigeon and puffin, myoglobin concentrations were similar in the three muscles (Table 2). In pheasants the sartorius had the highest levels of myoglobin, while in the murre this order was reversed.

DISCUSSION

The glycolytic and Krebs-cycle enzyme activities of the flight muscles of the puffin and the murre more closely resemble those in the pigeon than those in the pheasant. If the alcids relied extensively on anaerobic metabolism to support diving, the glycolytic enzyme levels should have resembled those in the pheasant. Instead, the alcids seem more like pigeons, which are thought to use the anaerobic capacity in the flight muscles to power short-duration, energy-intensive activities like hovering and taking off (Pennycuick 1968, Parker and George 1975, Aulie 1983). Anaerobic glycolysis in the puffin and murre flight muscles should by analogy serve

TABLE 3. Enzymes of amino acid metabolism in locomotor muscles. Values are presented and compared as explained in Table 1. Lowercase letters indicate interspecific differences for enzyme levels in a given locomotor muscle; capital letters indicate intraspecific differences.

	Pectoral	Supracoracoideus	Sartorius
Glutamate-pyruvate transaminase			
Pheasant	0.25 ± 0.13 c, AB	0.12 ± 0.06 c, B	0.26 ± 0.15 c, A
Pigeon	5.38 ± 0.97 a, A	2.89 ± 0.35 a, B	1.23 ± 0.23 a, C
Puffin	1.69 ± 0.28 b, A	0.93 ± 0.09 b, B	0.29 ± 0.06 c, C
Murre	3.90 ± 0.78 a, A	2.24 ± 0.24 a, B	0.90 ± 0.04 b, C
Glutamate-oxaloacetate transaminase			
Pheasant	65.1 ± 5.4 b, A	65.6 ± 9.9 a, A	84.2 ± 17.2 a, A
Pigeon	166.2 ± 29.0 a, A	61.9 ± 17.3 ab, C	78.7 ± 5.6 a, B
Puffin	80.3 ± 20.7 b, A	33.7 ± 14.7 b, B	6.3 ± 1.4 b, C
Murre	47.8 ± 6.1 c, A	26.5 ± 3.8 b, A	15.7 ± 1.7 b, B
Glutamate dehydrogenase			
Pheasant	1.29 ± 0.31 c, A	0.93 ± 0.60 b, A	1.48 ± 0.65 ab, A
Pigeon	3.57 ± 0.21 b, A	0.42 ± 0.13 b, B	0.36 ± 0.11 b, B
Puffin	19.00 ± 2.05 a, A	5.63 ± 2.96 a, B	0.73 ± 0.27 b, C
Murre	14.91 ± 1.62 a, A	5.68 ± 1.51 a, A	1.91 ± 0.75 a, B

primarily for bursts of rapid activity during either flight or diving. Thus, in birds as in mammals (Castellini et al. 1981), diving does not require exceptionally high levels of glycolytic enzymes. Nonetheless, in accordance with their considerable diving capacities, the alcids have higher levels of myoglobin in their flight muscles than do the terrestrial birds.

From enzyme activities, histology, myoglobin concentrations, and buffering capacities in the swimming muscles and from diving times, Mill and Baldwin (1983) and Baldwin et al. (1984) concluded that penguins dive aerobically to intermediate depths. They suggested that the anaerobic capacity is used during bursts of rapid swimming and that only larger penguins rely extensively on anaerobic glycolysis during long dives (Mill and Baldwin 1983). The glycolytic capacity of alcid flight muscles is also related to diving depth. Because puffin flight muscles have lower levels of the three glycolytic enzymes than do pigeon flight muscles, however, the correlation may be spurious and cannot indicate a greater use of glycolysis in the deeper-diving murre. Puffins and murres fly before and after foraging dives, and lactate accumulation would curtail their capacity for continued flight and feeding. Resolution of the metabolic strategies used to support diving in alcids (as well as in penguins) will require metabolic studies in voluntarily diving birds, similar to those carried out on the Weddell seal (Kooyman et al. 1983, Guppy et al. 1986).

The levels of GDH, GOT, and GPT can be interpreted in several, though not mutually exclusive, ways. As participants in anapleurotic reactions, they indicate a tissue's capacity for stepping up Krebs-cycle activity. Furthermore, they can reflect a tissue's capacity to metabolize amino acids. The high GDH and GPT activities in the diving birds relative to the pigeon and pheasant suggest that the muscles of the diving birds have a good capacity for increasing Krebs-cycle flux and for amino acid metabolism. The levels of GOT do not follow the trends shown by GDH and GPT, however. Because GOT plays a central role in the malate-aspartate shuttle in the absence of a glycerolphosphate shunt, GOT levels should reflect the importance of aerobic glycolysis as well as the two previous criteria. Seen in this context, the lower GOT activities in the flight muscles of puffins and murres suggest that they rely less on aerobic glycolysis than the pigeon and pheasant and that lipids and amino acids are important fuels for the diving birds.

Alcids use their legs and wings to dive (Tuck 1961, Spring 1971), and we hypothesized that the leg muscles would show metabolic adaptations similar to those of the flight muscles. We found that, relative to the flight muscles, the leg muscles generally had lower enzyme activities. Comparisons of glycolytic and aerobic enzyme activities showed that the alcid sartorius has a more pronounced glycolytic orientation than the flight muscles in the alcids or the sar-

torius muscles in pheasants or pigeons. Because alcids walk little (Tuck 1961), the leg muscles are presumably specialized for bursts of glycolytic activity during diving, perhaps for the directional changes described by Spring (1971). By contrast, the aerobic capacity of the sartorius in pheasants and pigeons correlates well with their considerable walking.

Comparison of the metabolic organization of penguins and alcids suggests that the requirements of flying and diving have led the alcids to maintain a higher aerobic capacity. The Little Penguin (*Eudyptula minor*) is approximately 25% heavier than the murre and 120% heavier than the puffin. The deepest recorded dive of the Little Penguin is 60 m (Mill and Baldwin 1983). Both murres and puffins have lower glycolytic enzyme activities than does the Little Penguin (Mill and Baldwin 1983), although the Little Penguin dives only as deep as the puffin. By contrast, CS activities in the pectoral muscle of the murre and puffin are approximately 100% higher than those in the Little Penguin (Mill and Baldwin 1983), a difference greater than that predicted by scaling considerations.

Myoglobin levels suggest that Little Penguins are better divers than murres, despite the opposite impression from diving depths. Myoglobin concentration in Little Penguin pectoral muscle is approximately twice that in murre and puffin pectoral muscles. Little Penguin supracoracoideus myoglobin concentration is approximately two times higher than that in murre and three times higher than that in puffin (Baldwin et al. 1984). These differences may reflect a compromise in alcids between diving and flying. The increased levels of mitochondrial enzymes needed to support flight may limit the quantity of myoglobin that can be maintained in the flight muscle. During flight myoglobin functions more in the delivery of oxygen to mitochondria than in the storage of oxygen. Less myoglobin is required for oxygen delivery than for oxygen storage. In alcid flight muscles, myoglobin levels are equivalent to or higher than those in pigeon muscles and must suffice for the delivery of oxygen to mitochondria during flight.

The demands of flight are also reflected in the intermuscular differentiation of metabolic organization. CS levels are similar in Little Penguin pectoral and supracoracoideus muscles, while in the alcids pectoral levels of CS are twice those in the supracoracoideus. The similar enzyme levels in the Little Penguin pectoral and supracoracoideus reflect the capacity to generate forward propulsion during the entire wing cycle (Clark and Bemis 1979), while the differences between the alcid pectoral and supracoracoideus reflect the need for the pectoral to generate lift as well as forward propulsion during flight.

Our data indicate that a pattern of metabolic organization similar to that of pigeons supports the impressive foraging dives of puffins and murres. Higher myoglobin levels of alcid flight muscles represent the major difference between alcids and pigeons. The adaptations that are generally thought to facilitate diving, including an increased oxygen storage capacity (Scholander 1940), a fusiform body shape, and reduced wing area, seem modified in the murres and puffins to meet the requirements of flight.

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