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ACTIVITY METABOLISM OF THE LOWER VERTEBRATES

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INTRODUCTION

The physiology of animals during activity has become a topic of widespread investigation. Studies concerning activity have generally been done on mammals, and several aspects of these have been reviewed elsewhere (87, 102, 139, 149). Fewer data are available for avian systems (64). The present review summarizes a growing body of literature concerning activity metabolism in the lower vertebrates: reptiles, amphibians, and fish. It includes a discussion of oxygen consumption during activity, emphasizing maximal oxygen consumption; aerobic scope; the cost of locomotion; and the influence of body temperature on these processes. Anaerobic metabolism, principally the production of lactic acid, is reviewed and its magnitude, thermal dependence, and effect on recovery and oxygen debt are discussed. Finally, the magnitudes of these two factors are compared at different levels of exertion, and phylogenetic differences in activity patterns are emphasized. Aspects of these topics have been reviewed previously for reptiles (21, 63, 65, 151) and, more extensively, for fish (28, 40, 74, 79, 80, 82, 117, 160).

Major differences in ecology, physiology, and morphology exist between and within each of the classes of lower vertebrates; within this diversity, I have tried to emphasize common themes and point out where the groups differ from each other and from the mammals and birds. Such a comparative examination of these different classes is not frequently attempted (49), and the literature concerning these animals has largely developed independently with little intercommunication. I hope this review will stimulate increased interest among people working with these animals and with activity metabolism in mammals and birds, so that a broader comparative outlook on the capacities of and limitations on activity in vertebrates may be achieved.

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AEROBIC METABOLISM

The analysis of aerobic metabolism of vertebrates historically has concentrated on determination of standard or basal metabolism: the minimal maintenance requirement in the absence of external stimulation. Allometric equations predicting resting metabolic rate as a function of body mass and temperature have been generated for several vertebrate classes: mammals (53, 114), birds (1, 116), reptiles (21), amphibians (162), and fish (167). The mass-dependence of resting oxygen consumption is similar in all these groups and is proportional to body mass raised to the 0.75–0.80 power. These relationships have also demonstrated a basic equality among the resting metabolic requirements of the lower vertebrates (reptiles, amphibians, and fish) and a similarity to resting metabolic rates of most invertebrate groups (97). Basal metabolic rates of mammals and birds, however, are six to ten times greater than are those of the poikilothermic groups, even at equal body temperatures (16, 21, 66, 97). The greater aerobic heat production in these former groups is, of course, the basis of their homeothermic condition.

Maximal Oxygen Consumption

More recently, attention has been directed to the determination of the greatest capacity of these organisms for oxygen uptake. Maximal levels of oxygen consumption have been elicited by electrically stimulating animals with low votage shocks or having them swim against a current of water (46, 49, 80). Spontaneous struggling does not appear to produce the highest levels of oxygen uptake (46, 80, 164). Maximal oxygen consumption has now been measured in a number of different species of lower vertebrates: fish (12, 47, 48, 50–52, 68, 76, 78, 86, 89, 94, 107, 115, 133, 136, 145, 146), amphibians (25, 27, 98, 143, 156), and reptiles (2, 7, 8, 17, 20, 22, 23, 69, 83, 90, 125, 134, 138, 164, 166). Maximal levels of oxygen consumption in these animals exceed standard levels by factors of five- to fifteen-fold; consequently, active oxygen consumption by members of these groups approximates basal oxygen consumption of birds and mammals. These homeotherms are capable of similar factorial increments in oxygen consumption (64, 149, 154, 171), achieving much greater absolute levels of uptake. For example, standard and maximal levels of oxygen consumption of a 1 kg reptile at 30°C are 0.07 and 0.40 cm^3O_2 $(g \cdot hr)^{-1}$, respectively; comparable values for a bird are 0.79 and 9.49 cm^3O_2 $(g \cdot hr)^{-1}$ (1, 21, 95). Thus, resting and active oxygen consumption appear to be linked. This factorial increment in aerobic metabolism of approximately ten-fold appears to be a rather standard feature of vertebrate physiology and may represent a basic limitation of the oxygen delivery or utilization systems.

Maximal levels of oxygen consumption of lower vertebrates appear more closely correlated with the behavioral capacities of these organisms than are standard levels. More active animals tend to be able to sustain much higher levels of oxygen consumption (152), at least among the reptiles and fish. Among the snakes studied this correlation is clear. Racers (*Masticophis, Coluber*), very fast snakes that actively pursue their prey, have high levels of active oxygen consumption: 1.05 cm^3O_2 $(g \cdot hr)^{-1}$; rattlesnakes (*Crotalus*), sit-and-wait predators capable of rapid striking, have lower levels: 0.52 cm^3O_2 $(g \cdot hr)^{-1}$; boas (*Lichanura*), animals incapable of rapid locomotion which rely on constriction to kill prey, have the lowest levels: 0.25 cm^3O_2 $(g \cdot hr)^{-1}$ (138). Similar correlations are apparent among lizards: monitor lizards (*Varanus*), carnivorous predators, achieve substantially higher levels of oxygen transport than do herbivorous iguanid and agamid lizards of equal size (7, 17, 164). Active oxygen uptake is rather low in the sluggish rhynchocephalian *Sphenodon* (166). A similar situation exists in fish: maximum oxygen consumption in active sockeye salmon (*Oncorhynchus*), 0.63 cm^3O_2 $(g \cdot hr)^{-1}$ (47), exceeds that of the more sluggish goldfish (*Carassius*), 0.30 cm^3O_2 $(g \cdot hr)^{-1}$ (82), or largemouth bass (*Micropterus*), 0.37 cm^3O_2 $(g \cdot hr)^{-1}$ (12). Maximal oxygen consumption is even lower in reclusive cave-adapted fishes: 0.06–0.16 cm^3O_2 $(g \cdot hr)^{-1}$ (33). Unfortunately only fragmentary data are available for oxygen consumption in the tunas (55), highly active, predatory, and homeothermic animals that might be expected to achieve the highest aerobic levels among the fishes.

These correlations between activity and oxygen consumption do not apply to amphibians. In this group, animals capable of the greatest amount of short-term activity have the lowest levels of maximal oxygen consumption (25). For example, leopard frogs (*Rana*), with considerable powers for rapid locomotion, have a lower maximal oxygen consumption, 0.49 cm^3O_2 $(g \cdot hr)^{-1}$, than those of the more sluggish toad (*Bufo*), 1.53 cm^3O_2 $(g \cdot hr)^{-1}$ (143).

The correlation between maximal oxygen consumption and behavior complicates an examination of the mass dependence of this factor. Maximal oxygen consumption in 14 species of reptiles was found to be proportional to body mass to the 0.80–0.82 power (21, 165), an exponent similar to that describing standard oxygen consumption. Consequently, smaller reptiles can achieve higher rates of mass-specific oxygen consumption than can larger animals. A similar mass-dependence of maximal oxygen consumption has been reported for both birds (95) and mammals (130). Not enough data have been collected under comparable conditions to permit interspecific comparisions among fish or amphibians. However, within four different species of fish, maximal oxygen consumption has been found to be directly proportional to body mass rather than to a fractional power of it

(12, 48, 51, 88, 136, 137). The ratio of active to standard oxygen consumption increases with increasing body size in these groups. However, in speckled trout (*Salvelinus*), the mass dependence of active oxygen consumption is temperature-dependent. Values of the mass-dependent exponent b (in the equation $Y = a X^b$, where Y is organismal oxygen consumption and X is body mass and a and b are constants) decrease from 0.91 at 5°C to 0.73 at 20°C (105). More extensive examinations will be required before the mass-dependence of active metabolism in fish or amphibians can be stated with confidence.

Maximal oxygen consumption is strongly affected by body temperature in the lower vertebrates, as are most other physiological processes. In many species, active oxygen consumption increases exponentially with increasing temperature, generally with Q_{10}'s of 1.5–2.0, up to lethal or debilitating thermal levels (2, 7, 8, 17, 69, 78, 79, 83, 90, 143, 164). However, in a large number of species investigated, maximal oxygen consumption is attained at some intermediate, nonlethal temperature and remains constant at higher temperatures ($Q_{10} = 1.0$) (12, 17, 20, 22, 23, 47, 68, 81, 86, 89, 125, 164, 166). This latter type of response is particularly apparent and is highly consistent among iguanid and agamid lizards. The lowest temperature at which maximal oxygen consumption is attained is often the same as preferred body temperature or body temperature of the animal in its natural environment (21, 164). A limitation of oxygen transport at higher temperatures is clearly suggested, either because of internal physiological factors (18) or limitation of environmentally available oxygen (47).

Aerobic Metabolic Scope

Normal behavioral activities require levels of oxygen consumption intermediate between standard and maximal levels. The capacity to which activity can be aerobically supported is indicated by the difference between these maximal and minimal levels of oxygen consumption in any particular physiological state. This difference, the *scope for activity,* was utilized by Fry (78), in his seminal paper on activity metabolism in fish, as an index of work capacity. Determination of this metabolic scope has been an important theme in the study of energetics of lower vertebrates. Since anaerobic metabolism may play a major role in activity energetics of these animals (125), this measurement of oxygen consumption is currently referred to as *aerobic metabolic scope* (17).

The use of aerobic scope as a predictor of activity capacity is recognized to have certain limitations. It assumes that the efficiency of aerobic energy transduction is constant under different physiological conditions, e.g. at different temperatures (6). It also assumes that maintenance processes are sustained at pre-activity levels (125); and if these are temporarily aban-

doned, activity capacity is underestimated. On the other hand, in order to supply oxygen to the contracting skeletal musculature, the ventilatory and circulatory systems must also increase work output and consume a fraction of the increased oxygen uptake. An estimated 20% of the aerobic scope is required for these systems in active fish (112). Increased gill ventilation also increases osmoregulatory costs for fish (136, 137). It is estimated that as much as 40% of the aerobic scope associated with swimming at maximal sustained speed in fish is devoted to these systems (160).

Another potential difficulty with the association between aerobic scope and work capacity is the assumption that maximal levels of oxygen consumption are achieved simultaneously with maximal work output. This may not be the case for some lizards at lower than preferred thermal levels (22, 23), or for amphibians (25). Measurement of aerobic scope may thus overestimate work capacity. If these provisions are kept in mind, aerobic scope presents a convenient method of assaying the potential aerobic work component of an organism's metabolism.

More active animals among fish and reptiles tend to have higher aerobic scopes, a reflection of their greater levels of maximal oxygen consumption. The aerobic scopes of very active sockeye salmon (*Oncorhynchus*) and more sluggish goldfish (*Carassius*) are 0.58 and 0.28 cm^3O_2 $(g \cdot hr)^{-1}$, respectively (47, 78). The more active aquatic turtle *Pseudemys* has an aerobic scope 75% greater than that of the more terrestrial *Terrapene* (83). Homeotherms have aerobic scopes far exceeding those of the lower vertebrates: 8.70 and 0.33 cm^3O_2 $(g \cdot hr)^{-1}$ for a 1 kg bird and reptile, respectively (1, 21, 95). Aerobic scope is temperature-dependent and is often maximal at normal field temperatures or preferred body temperature in organisms in which maximal oxygen consumption has a thermal plateau (78, 164). This maximization is a consequence of increased maintenance levels at higher temperatures. In species lacking this thermal plateau, aerobic scope increases with temperature up to lethal levels.

Cost of Transport

As physical performance (e.g. speed of locomotion) increases, oxygen consumption increases until maximal values are attained. The exact form of that increase varies considerably and depends upon the type of locomotion employed, the species in question, and its body mass and temperature. To determine this dependence, oxygen consumption is measured while an animal walks on a treadmill, flies in a wind tunnel, or swims against a current.

As swimming speed increases in fish, oxygen consumption increases exponentially according to the relationship $Y = ae^{bX}$, where Y is oxygen consumption, X is swimming speed, and a and b are constants (47). Although a linear relationship between activity and oxygen consumption was

reported earlier (13, 147), more recent studies have all found a logarithmic dependence of aerobic metabolism on swimming speed (12, 47, 51, 52, 76, 78, 86, 115, 127, 136, 137, 145, 146, 157, 159). The difference between the observed oxygen consumption and standard metabolism generally increases as the square of the cruising speed (79). This exponential increase has also been found for oxygen consumption during swimming by a sea turtle (*Chelonia*) (134); however, a linear approximation may describe these data equally well.

In contrast to fish swimming, oxygen consumption increases as a linear function of speed in terrestrial mammals (139, 150) and in walking birds (77). Studies on terrestrial reptiles (3, 57, 70, 126, 149) have also found a linear increment in oxygen consumption with increasing speed. Oxygen consumption of birds during flight has a low dependence on speed or has a minimal value at intermediate air speeds (28, 153, 155). The physical bases of the differences in the power requirements of different locomotory patterns in water and air and on land are not fully understood.

Aerobic locomotory energetics are most commonly compared by calculation of the *cost of transport,* the amount of energy required to move a unit of mass over a unit distance (139, 154, 161). The cost of transport is obtained by dividing the mass-specific oxygen consumption by the speed; the *net cost of transport* first subtracts the resting oxygen consumption from the total (139). The net cost of transport is velocity-dependent in animals that have nonlinear aerobic energetics as a function of speed, such as fish and flying birds. It is independent of speed in terrestrial reptiles and mammals. The cost of transport is very dependent on body mass. A large animal expends less energy to move a unit of its mass than does a smaller animal. The net cost of locomotion decreases as the –0.40 and –0.33 power of body mass in terrestrial mammals and reptiles, respectively (139, 149). The minimal cost of locomotion in fish decreases as the –0.24 power of mass (47, 139). Consequently, the velocity-dependence of aerobic metabolism is considerably less in larger animals. Higher speeds can be attained before aerobic scope is reached. For instance, larger fish are capable of sustaining much higher speeds than are smaller individuals (12, 48, 51).

Expression of metabolic data as the cost of transport permits comparision of the various locomotory modes. Animals adapted for swimming have a much lower net cost of transport than do those specialized for flying or running; fliers have lower net locomotory costs than do runners (139, 154). The minimal cost of locomotion is least for fish, being only one eighth that of a terrestrial runner if both animals weigh 1.0 kg (139). The cost of transport is similar in equal-sized fish of several different families of very different anatomy, stamina, and swimming mode: salmonids, cyprinids, anguillids, and sparids (47, 136, 139, 145, 170). These differences appear to

have little influence on locomotory costs at low speeds. The net cost of transport in swimming sea turtles (*Chelonia*) is twice that predicted for a fish of equal size (134). In spite of the fact that the turtle is well-adapted for aquatic existence, it must surface to breathe; this behavior undoubtedly decreases its swimming efficiency.

The net cost of transport of lizards running at low speeds is equal to or slightly less than that of mammals of equal size (3, 70, 126, 149). Consequently, the sprawling gait and "push-up" position of the limbs of these animals do not result in a less efficient means of locomotion (3, 149). The net cost of locomotion in a snake (*Thamnophis*), however, is only half that predicted for a quadruped runner of equal weight (57). Relatively few experiments have been carried out on reptiles moving on treadmills; reptiles are generally difficult to train and tend to engage in rapid bursts of speed. No measurements have been reported on aerobic cost of transport in amphibians.

Comparisions based on the net cost of transport obscure the real differences in energetic expense of locomotion in homeotherms and poikilotherms. The much lower maintenance costs of the latter animals are reflected by the fact that the metabolic rate of a poikilotherm moving at a certain speed is considerably below that of a homeotherm moving at the same speed. Thus, a 630 g lizard has a metabolic rate of 0.58 cm^3O_2 $(g \cdot hr)^{-1}$ when walking at 0.5 km hr^{-1}. This is below the resting metabolic rate of a mammal of equal size [0.70 cm^3O_2 $(g \cdot hr)^{-1}$], which would consume 1.5 cm^3O_2 $(g \cdot hr)^{-1}$ walking at this speed (149). Given, however, the equality of transport costs in the two groups, the poikilotherm reaches the limit of its aerobic scope at a much lower speed than does the homeotherm. The highest walking speed that can be sustained by the lizard *Iguana* for one hour without exhaustion is 0.4 km hr^{-1} (126). A large oxygen debt is accumulated by the agamid lizard *Uromastix* while walking at 0.5 km hr^{-1}, indicating anaerobic metabolism at this speed (70). These speeds are considerably below those sustained by mammals: a ground squirrel of a size comparable to these lizards can sustain running at nearly 3 km hr^{-1} (150). A similar relationship holds for aquatic homeotherms and poikilotherms. However, the lower cost of transport during swimming is reflected in the greater speeds that can be sustained by aquatic poikilotherms: sockeye salmon (*Oncorhynchus*) weighing 1–2 kg can swim at 4.6 km hr^{-1} without becoming exhausted (51). Higher levels of speed in all these animals entail the use of anaerobic metabolism.

Temperature sometimes influences the cost of transport. In fish, oxygen consumed while swimming at any particular speed is positively temperature-dependent; swimming is more expensive at higher temperatures (12, 47, 136). If, however, the standard oxygen consumption is subtracted from

the observed, the temperature-dependence is reduced. In sockeye salmon (*Oncorhynchus*) as speed increases, the temperature-dependence decreases until at burst speed the aerobic increment is temperature-independent (147). This is not the case for rainbow trout (*Salmo*) or largemouth bass (*Micropterus*), in which the temperature-dependence of the aerobic increment increases with increasing temperature (12, 136). In lizards, the cost of walking at any speed is independent of body temperature (70, 126). Consequently, the added aerobic increment above resting levels decreases with increasing temperature. For all these organisms, maximal sustainable speeds will be attained at the temperature at which aerobic scope is maximal. For example, maximal cruising speed is attained at 20°C in goldfish (*Carassius*), which coincides with maximal aerobic scope (81, 82).

A detailed analysis of the efficiencies involved in aerobically supported locomotion will not be undertaken here. Such an examination has generally only been attempted for fish [but see (134)], and Webb (160) has recently prepared an excellent summary of that literature.

ANAEROBIC METABOLISM

Both intense activity and exposure to hypoxic environments result in anaerobic metabolism in skeletal muscle. Under both these circumstances, demand for high-energy phosphate groups exceeds the supply that can be sustained through aerobic metabolism. The fact that both of these circumstances in vertebrates result in the formation of large quantities of the same compound, lactic acid, has tended to emphasize their similarities. However, the selective demands of each situation are quite different. During hypoxia or anoxia, it is important to sustain anaerobic metabolism for as long as possible since the time of return to aerobic conditions is not always predictable. During activity, the purpose of anaerobic metabolism is to generate in the shortest period of time as many high-energy phosphate compounds as can be utilized. These distinct demands cannot always be satisfied by the same metabolic pathways, and the invertebrate groups with the highest tolerance of anoxia generally do not accumulate lactic acid under anoxic conditions (100). One cannot easily extrapolate from anoxic tolerance to anaerobic activity capacity. For instance, among the reptiles, turtles have an immense anoxic tolerance in comparison with other groups and can form much greater quantities of lactic acid under anoxic conditions (14, 21, 106). However, their capacity for anaerobic activity metabolism does not appear to be any greater than that of other reptiles (83, 84). Likewise, although cyprinid fish appear to have impressive tolerance of anoxia (43, 146), their capacities for anaerobic activity metabolism are smaller than those of the salmonids (71), which also have a greater aerobic capacity. Consequently,

the applicability of data on hypoxic tolerance to activity metabolism appear somewhat limited and the literature on the former is not reviewed here.

Because of the limited aerobic metabolic scope of the lower vertebrates and their low aerobically sustainable speeds, anaerobic metabolism is particularly important in activity energetics, particularly for terrestrial poikilotherms. Methods of measuring anaerobic metabolism have generally consisted of assaying changes during activity of metabolites within the blood or skeletal muscle. Because of diffusion of compounds into the blood and inhomogeneities of metabolite formation in different areas of skeletal muscle (36, 37), it is difficult to quantify the contribution of anaerobic to total activity metabolism by these techniques. Analysis of whole body homogenates has been used for these comparisons (20, 24).

Lactic Acid Metabolism

The principal form of anaerobic metabolism during activity in the vertebrates is the catabolism of carbohydrates to lactic acid. In the lower vertebrates, blood lactate concentration increases greatly after a bout of intense activity, generally five- to ten-fold (5, 18, 22, 24, 31–34, 36–39, 59, 62, 67, 73, 84, 93, 96, 104, 122, 125, 142, 143, 148, 158, 164). In a summary of blood lactate data for reptiles (21), the following values were associated with different activity levels: resting, 0.5–2.0 mM; moderate and sustainable activity, 3.0–9.0 mM; vigorous and exhausting activity, 9.0–20 mM. Similar values have been reported for fish (40, 117) and amphibians (104, 143) with comparable activity levels; however, lower values for sustained activity may be obtained if blood is removed through a cannula rather than by heart puncture (73). These ranges may be contrasted with those of the blood of anoxic reptiles, which may reach 33 mM in diving lizards (126) and 108 mM in turtles (106). Concentrations of lactate in skeletal muscle are substantially higher than blood levels and reach values as high as 42 mmoles kg^{-1} muscle in lizards (24), 27 mmoles kg^{-1} in frogs (104), and 59 mmoles kg^{-1} in fish (36) after exhausting activity. These high concentrations of lactate can cause major disruptions in blood and muscle pH and disrupt enzymatic function and oxygen transport. The very limited data available on lactic acid formation during voluntary activity suggest that animals avoid the formation of very high concentrations of lactic acid when possible (24, 58, 143).

Muscle glycogen appears to be the principal source of the lactic acid formed, although quantitative comparisons between the two components are few. In rainbow trout (*Salmo*), all of the lactate formed in the muscle can be accounted for by glycogen breakdown and vice versa (148). Essentially all the lactic acid formed during activity in the lizard *Iguana* is the result of glycogen catabolism (124). Glycogen is very rapidly depleted

during intense activity (37, 67, 122), being 50% catabolized in 2 min, and 80% depleted if activity is continued (11, 40, 148). Liver glycogen generally does not change during short-term activity (39, 40, 67, 99, 108, 124, 169) but it does decrease in some species (67, 109, 110). It may be utilized to replenish other carbohydrate stores if the animal is not fed (40, 99). Levels of blood glucose either remain constant (32, 93, 113, 125, 144) or increase (33, 67, 104, 141) during activity. Skeletal muscle in fish and amphibians possesses very low levels of hexokinase and consequently may be unable to utilize glucose as a rapidly expendable fuel for activity (60, 118). It has consequently been concluded that blood glucose contributes little to activity metabolism (39); however, until turnover studies using labeled glucose are completed, this conclusion is premature.

The maximal rate of lactic acid formation during activity has been investigated in reptiles and amphibians and is termed the *anaerobic scope* (24). This is assayed as the increment in lactic acid content of the whole body over short (e.g. 30 sec) periods of maximal activity. In small lizards, there is little interspecific variability in anaerobic scope; values range between 11 and 19 mmoles (kg body weight·min)$^{-1}$ at 30°–37°C (24). In amphibians, however, pronounced interspecific differences exist, and anaerobic scope varies over a ten-fold range [1.6–14 mmoles (kg·min)$^{-1}$] at 20°C (25, 26). Slower moving and aquatic amphibians have low anaerobic scopes; more active, saltatory forms produce lactic acid rapidly. The temperature-dependence of anaerobic scope in lizards is quite low, with Q_{10}'s ranging from 1.1 to 1.3 above 20°C; anaerobic scope in amphibians is more sensitive to temperature (Q_{10}'s = 1.5–3.9).

The *anaerobic capacity* is the amount of lactic acid formed during activity to exhaustion (24). As with aerobic scope, values for small lizards show little interspecific variation (10–17 mmoles kg^{-1} body mass) in contrast to amphibians (~1.2–16 mmoles kg^{-1}) (4, 24, 26, 27, 61, 104). Active racer snakes (*Masticophis, Coluber*) have higher anaerobic capacities than do rattlesnakes (*Crotalus*) or boas (*Lichanura*) (138). More sluggish box turtles (*Terrapene*) have a greater lactate formation during activity than aquatic *Pseudemys* (83). Neotenic salamanders (*Ambystoma*) form less lactate while swimming vigorously than do metamorphosed individuals of the same species (61). The thermal dependence of anaerobic capacity is low, with Q_{10}'s generally below 1.5 for both lizards and amphibians (24, 26). There is some indication that anaerobic capacity is maximized at preferred body temperature in iguanid lizards (20, 23). Few comparable data exist for fish, but the temperature-dependence of maximal blood lactate concentration after activity is very low (32, 67). In fact, such concentrations can in certain instances be greater at lower temperatures than higher.

Although the maximal capacities for lactate formation found among fish, amphibians, and reptiles are similar, fish appear more sensitive to its effects than do members of the other groups. Exercised reptiles and amphibians rarely die after intense activity, unlike some species of fish, which do so frequently enough to be a considerable problem in the fisheries industry (35, 158). Mortality is common in fish of several species with average blood lactate concentrations of 17–26 mM after exercise (10, 34, 128, 129). Mortality is positively correlated with concentration of lactic acid in the blood (10, 128). Physical damage to the scales and mucus is not a contributory cause (41); nor is the lactate ion per se involved. Acidosis associated with lactic acid diffusion into the blood is probably the important factor (35, 111). The decreased pH is associated with a depression of blood oxygen-capacity, decrease of blood bicarbonate, and disruption of circulation (35). Similar acidosis after activity in reptiles is also observed, but is never lethal (18, 84, 163).

Other anaerobically generated products appear to play a distinctly minor role in the overall energetics of activity in the lower vertebrates. The concentration of pyruvic acid in fish blood and skeletal muscle doubles during strenuous activity; however, its concentrations are only 1% of those of lactic acid and its accumulation does not account for much high-energy phosphate production (37, 40, 62, 169). Changes in concentrations of other glycolytic or Krebs-cycle intermediates do not occur or are small in comparison with increments in lactic acid concentration during activity in carp (*Cyprinus*) muscle (72). Whole-body concentrations of pyruvate, succinate, and alanine remain constant or increase very little during burst activity in small lizards (*Sceloporus, Xantusia*) and amphibians (*Xenopus, Batrachoseps*) (A. F. Bennett, unpublished observations). Anaerobically formed compounds, succinate and alanine, accumulate in the blood of sea turtles (*Chelonia*) during diving, but their concentration is again only 1% of that of the lactic acid accumulated (101). A study on hypoxic metabolism in fish suggested the anaerobic production of short-chain volatile acids (43). However, further studies on hypoxic fish have not found an accumulation of these compounds (56, 71). No change in the concentration of any of 17 amino acids was found during hypoxia (71). Respiratory quotients (RQ) in excess of 1.0 have been reported in goldfish (*Carassius*) (RQ = 1.32) and trout (*Salmo*) (RQ = 1.16) during enforced swimming (115), indicating some form of anaerobic metabolism. These values declined to 1.03 and 0.91, respectively, during steady-state swimming. In spontaneously active fish, RQs in excess of 1.0 developed only in goldfish and only under hypoxic conditions. The source of the excess carbon dioxide is unknown but may come from blood bicarbonate as a result of lactic acid entry into the blood.

Currently, no evidence exists for the operation of other anaerobic pathways during activity in normoxic situations.

Recovery and Oxygen Debt

The effects of physical activity persist a long time in the lower vertebrates. Fish in particular require a long recovery period until the pre-active state is reestablished. Blood lactate levels continue to increase for 2–3 hr after activity to exhaustion (36–40, 62, 142); resting levels are not restored for 8–24 hr (10, 11, 32–34, 36–39, 93, 96, 132). Tunas may eliminate a lactate burden more rapidly (5). A very long post-active period is also required for elimination of white-muscle lactate (37, 62, 93, 110) and resynthesis of white-muscle glycogen (11, 37, 99, 122); recovery of pre-active levels is more rapid in red muscle (110). Exercise-trained or fed fish recover more rapidly than untrained or starved individuals (39, 93, 99, 122).

Several ideas have been advanced to explain this slow recovery. The temperatures at which these experiments have been done have been generally low (10°–15°C), and diffusion of lactic acid from the muscle might have been impaired; however, lactate appears very rapidly in the blood during activity even at low temperatures (37). Some evidence suggests impairment of blood circulation after activity, but this has not been quantified (37, 40). The oxygen-carrying capacity of the blood may become depressed by low blood pH and thus retard aerobic catabolism of the lactate (37, 140, 158). Probably a combination of all these factors is involved in slowing recovery in fish. Blood lactate also requires several hours to return to pre-active levels in amphibians and reptiles (25, 104, 125). Rate of elimination of blood lactate in the lizard *Iguana* is maximal at 35°C (the preferred body temperature and the temperature of maximal aerobic scope) (125).

The time required for elimination of the oxygen debt per se—the oxygen consumption in excess of pre-active levels—is quite variable. In fish, oxygen consumption has been reported to return to pre-active levels in 3 (47), 4–6 (99), and more than 10 hr (96). In amphibians, similar variability is reported, with values ranging from 1–1.5 hr (25, 143) to 4–6 hr (61, 156). Oxygen debts in large lizards are mostly eliminated in 30 min (17). It is unclear whether these differences reflect methodology or physiological differences between the species investigated. The size of the debt is generally temperature-dependent and is greatest at the highest temperature examined (17, 143, 156). In sockeye salmon (*Oncorhynchus*), however, maximal debt occurs at 15°C (the temperature of maximal oxygen consumption and aerobic scope) and decreases at higher temperatures (47). The oxygen debt is most rapidly repaid at the temperature of maximal aerobic scope (17, 47, 143, 156).

The time course of the oxygen debt repayment is generally shorter than that of lactate elimination. Oxygen debt in one species of amphibian is completely eliminated before any net amount of lactate is catabolized (25). In other members of this group, oxygen consumption returns to resting levels long before lactate is eliminated (25, 104, 156). Oxygen consumption and blood lactate concentration return to pre-active values in 3 hr and 8 hr, respectively, in sockeye salmon (*Oncorhynchus*) (34, 47). In view of these results, these processes do not seem tightly coupled in the lower vertebrates and the oxygen debt is thus primarily alactacid. It is consequently inadvisable to attempt to estimate lactic acid production or total energetic output during activity from measurements of oxygen consumption alone or to estimate the excess oxygen consumption required to eliminate a lactate burden.

The general topic of lactate catabolism and elimination, mainly in mammalian systems, has been reviewed and details of the general process may be found in (123). The fate of the large amounts of lactate formed during strenuous activity in the lower vertebrates is largely unknown and may well be different from that of mammalian systems. The original experiments on the fate of lactate were performed on isolated amphibian skeletal muscle, and about 80% of the lactate utilized was estimated to be reconverted to carbohydrate stores, the remainder being oxidized (120, 121). A similar ratio was estimated for in vivo lactate metabolism in trout (*Salmo*) (99). A smaller amount of glycogen is resynthesized in mammalian than in amphibian white muscle under identical in vitro conditions (15). In mammalian systems in vivo during recovery from activity, most of the lactate is rapidly oxidized to carbon dioxide (54, 75). Since similar in vivo experiments have not been performed in lower vertebrates, it is not known whether most of the lactate is resynthesized to glycogen or glucose, is oxidized to carbon dioxide, or is synthesized into other compounds, e.g. fatty acids. Excretion of lactate has not been observed, even in an aquatic medium (61, 119, 160). Muscle glycogen levels are eventually reestablished, but the site of lactate catabolism or carbohydrate mobilization is in doubt. Trout (*Salmo*) liver has been shown to have a high capacity for lactate catabolism (30). However, in another study, 27 of 36 species of fish examined had very low levels of lactic dehydrogenase in their livers, and it was concluded that this organ has a negligible role in metabolizing blood lactate in fish (62). Skeletal muscle, both white and red, has some capacity for lactate oxidation (15, 30). Considerable interspecific variation may exist in the fate of the lactate; only further experimentation, particularly in vivo experimentation, will resolve the rather uncertain situation that now exists.

COMPARISON OF AEROBIC AND ANAEROBIC METABOLISM

The relative contributions made by aerobic and anaerobic pathways to activity metabolism is dependent upon work output. At low-level sustainable locomotion, aerobic catabolism of carbohydrates and fats probably accounts for all of the work output. It is expected that a certain amount of anaerobic metabolism, causing a rise in blood lactate, may occur at the initiation of exercise until oxygen supply systems catch up with oxygen requirements. If activity is prolonged, this initial anaerobiosis will make little contribution to overall energetics. This viewpoint is largely supported by the relatively low levels of blood lactate maintained during moderate activity in lizards and fish (11, 39, 73, 122, 126). In experiments using cannulated fish, blood lactate remained at resting levels up to 93% of critical swimming speed (73). However, muscle lactate levels may increase even during sustained swimming in fish (109), so that it is not possible without whole body studies to rule out a net anaerobic contribution to low speed locomotion. It is necessary to distinguish here between lactic acid formation and a net accumulation of lactic acid. As long as no lactate accumulates or is excreted, oxygen consumption totally accounts for the energetic output of an animal. Lactate may be formed in white muscle or other tissue, enter the blood, and be catabolized aerobically elsewhere, especially in red muscle or gill tissue (30, 168, 169). In the former case, white muscle could provide a readily metabolizable compound to support contractile activity in the red muscle.

There is a large literature on different muscle fiber types and differential reliance upon them during locomotion in fish. This topic has been well reviewed (29) and is only summarized here. Skeletal muscle tissue is generally divided into red and white fiber types, although there are several intermediate categories in fish (131). The red fibers show higher concentrations of aerobic enzymes, greater oxygen consumption, and higher concentrations of glycogen and lipid than do white fibers. The former are thought to be primarily aerobic, whereas the latter are primarily anaerobic. It is important to keep in mind, however, that these are only distinctions in a continuum of function. Red fibers have some anaerobic ability and white fibers also function aerobically. More active fish have a greater proportion of red fibers in their total body musculature, generally localized in discrete superficial bands, than do more sedentary, sluggish animals (44, 92). These red muscle bands are primarily responsible for low-speed locomotion, and white muscle only becomes active at intermediate or maximal swimming speeds (45, 91, 103, 108–110, 135, 146, 159). The exact contributions made

by each system are in some dispute and are probably highly species-specific. In general, however, aerobically supported metabolism functions at low speeds, supplemented by anaerobic metabolism during burst speeds. For sustainable (1 hr) swimming by trout (*Salmo*) at critical speed, the anaerobic contribution to total energetic output is less than 5% (159).

However, when pursued, lower vertebrates cannot sustain such activity and often are exhausted within 1–2 min (9, 23, 24, 26, 31, 40, 67, 85, 96). Fatigued and unresponsive, the animals lose their orientation and equilibrium. Schooling species of fish break their schools and move to concealment (40). Efforts have been made to quantify the energetics of this burst behavior, both to determine the total amount of energy an organism can mobilize and to partition that metabolism into its aerobic and anaerobic components. This is done by simultaneously measuring oxygen consumption and lactic acid production during the active period (20), a method that does not take into account the anaerobic contribution made by dephosphorylation of adenosine triphosphate (ATP) and creatine phosphate. The contribution from these sources may be relatively minor (72) or large (110). Full analysis and determination of the time course await further experimentation.

In many reptiles and amphibians, burst behavior is fueled mainly, in some cases almost exclusively, by anaerobic metabolism. During 2–5 min of activity, lactic acid formation accounts for 58–96% of the total ATP production (20–25, 83, 125, 138). During the first half-minute of activity, the anaerobic contribution is even greater (24, 25). Between 95 and 99.7% of the glycogen utilized during 2 min of activity is converted to lactic acid (22, 23). Because of the large and rapidly mobilized anaerobic potential and the relatively low levels of oxygen consumption, burst activity is essentially oxygen-independent in these animals. The relative temperature-independence of lactate formation in comparison to aerobic scope (24, 26) provides the functional basis for the temperature-independence of burst behavior (22, 32, 42) and the anaerobic metabolic mode exerts an even greater influence on total metabolism at low body temperature. Although recovery from activity requires much longer at these lower temperatures, anaerobic metabolism provides the organism with a capacity for rapid activity and escape.

The relative extents of aerobic and anaerobic metabolism vary among different groups of lower vertebrates. Among small lizards interspecific variation is small; anaerobic scope varies little between species (24) and aerobic scope is mass-dependent (21, 165). Small lizards rely on anaerobiosis for burst activity. Total scope, both in its aerobic and anaerobic components, may be maximal at preferred body temperature, at least in iguanid lizards. The total energy output varies between 28 and 52 μmoles ATP

g^{-1} body weight for three species of iguanids at preferred body temperature during 2 min of activity (20, 22, 23).

Among the snakes examined, anaerobic metabolism during activity accounts for over half of the total ATP formation (138). However, aerobic and anaerobic scopes are positively correlated: Both are highest in racers (*Coluber, Masticophis*), intermediate in rattlesnakes (*Crotalus*), and lowest in boas (*Lichanura*). Minimal and maximal values for metabolism by these species during 5 min of activity differ by a factor of five: racers, 52 μmoles g^{-1}; rattlesnakes, 28 μmoles g^{-1}; boas, 10 μmoles g^{-1}. The minimal value is similar to those of turtles during activity (9–15 μmoles g^{-1}). The overall activity capacities and performance abilities of these species are well-reflected in these measurements of total metabolism.

Aerobic and anaerobic capacities of amphibians are inversely correlated in a series of species (25). The animals with the greatest aerobic scopes (e.g. *Bufo, Scaphiopus*) do not produce large amounts of lactic acid during activity; animals with high anaerobic scopes (e.g. *Rana, Batrachoseps, Hyla*) have low aerobic scopes (25, 26, 143). These differences appear to have an enzymatic basis (14, 19). This inverse relationship tends to equalize total metabolism, which ranges from 12–20 μM ATP g^{-1} for 2 min of activity. Animals that rely on burst activity for rapid escape do so by utilizing anaerobic metabolism. The more aerobically competent animals are incapable of this rapid activity and rely on static defense mechanisms: noxious skin secretions, protective postures, and counterattack (26).

Simultaneous determination of aerobic and anaerobic capacities during short-term activity has not been undertaken for fish. Measurements of oxygen consumption during activity are generally longer-term than the 1–2 min required for exhaustion. While is it premature to speculate, the data available suggest that considerable interspecific and/or interfamilial variability exists in both aerobic and anaerobic capacities. Both capacities appear greater in salmonids than in goldfish (*Carassius*) (71). In view of the considerable range of aerobic scopes reported for fish, activity metabolism in these animals may be similar to that of snakes, in which very active species have both high aerobic and anaerobic capacities.

SUMMARY

Aerobic capacities of the lower vertebrates (fish, amphibians, and reptiles) are considerably lower then those of homeothermic birds and mammals. The low rate of oxygen consumption of the former animals has decided consequences for their capacity for sustaining activity. Maximal oxygen consumption is approximately ten times the resting level, approximating that of a resting homeotherm. Since locomotor costs appear similar for

both groups, the birds and mammals have much more extensive capacities for sustained, aerobically supported activity. In contrast, the lower vertebrates rely on anaerobic metabolism (i.e. lactic acid production) to a great extent during intense activity. Anaerobic metabolism is independent of oxygen delivery systems, which operate at comparatively lower rates. Efficient in supplying energy quickly, anaerobic metabolism provides a capacity for rapid activity. It may be temperature-insensitive. It entails a long recovery period (hours), during which the animal is fatigued and unresponsive. Major differences in the aerobic and anaerobic partitioning of activity metabolism exist among different groups of lower vertebrates, but the most active animals of each group rely heavily on anaerobic metabolism to support vigorous activity.

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