Endothermy and Activity in Vertebrates

Albert F. Bennett and John A. Ruben

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Endothermy, the maintenance of a high and constant body temperature by metabolic means, is a striking adaptation in the animal kingdom. Endothermic animals expend great quantities of energy to regulate and maintain internal thermal conditions and functional processes over a wide range of environmental temperatures. In contrast to ectotherms, they are generally warmer than their environment and are often more active animals. Although endothermy appears during intense muscular activity in several otherwise ectothermic organisms, only among mammals and birds is endothermy maintained even under resting conditions. The energetic cost of this maintenance in these groups is great, and its evolution has required substantial restructuring of many systems of the vertebrate body. In spite of these costs, mammalian and avian endothermy developed along essentially parallel lines among different groups of reptilian ancestors. The selective factors influencing its evolution must have been substantial and highly significant to have made such a profound alteration in the energetics, physiology, and behavior of two major groups of vertebrates. However, there is no general agreement among vertebrate biologists as to what those selective factors were or what the sequence of events culminating in endothermy was.

The evolution of endothermy in mammals and birds has been the subject of considerable speculation (1, 2), and debate has also been raised concerning metabolic thermoregulation among the dinosaurs (3). These discussions are generally based on the assumption that the endothermic condition is the end product of selection for a high and stable body temperature per se. That is to say, the evolution of endothermy was occasioned by only thermoregulatory considerations. Consequently, attention has been centered upon the advantages of a relatively high and constant body temperature. Among the benefits cited are stability of enzymatic catalysis, independence of timing daily activity, and resistance to freezing (1). These selective factors are not necessarily significant or even advantageous in all environmental circumstances in which endothermy evolved. Thus, arguments for the evolution of endothermy are necessarily based on the assumption that the endothermic condition is the end product of selection for a high and stable body temperature per se. That is to say, the evolution of endothermy was occasioned by only thermoregulatory considerations.
tion of endothermy based on thermoreg-
ulory considerations alone tend to be
ad hoc rather than a uniform explanation
equally applicable to all groups. We sug-
gest that thermoregulation was not the
total cause of endothermy's development.
Thermoregulation has a more profound role
in the evolution of endothermy, particularly
in regard to the maintenance of a constan-
temperature. A principal factor in the evolu-
tion of endothermy was the increase in
body mass and temperature.

Summary. Resting and maximal levels of oxygen consumption of endothermic ver-
tetbrates exceed those of ectotherms by an average of five- to tenfold. Endotherms
have a much broader range of activity that can be sustained by this augmented aer-
obnic metabolism. Ectotherms are more reliant upon, and limited by, anaerobic metabo-
ism during activity. A principal factor in the evolution of endothermy was the increase
in aerobic capacities to support sustained activity.

Cost of Endothermy

Hypotheses based on only thermoreg-
ulory considerations fail to justify in
selective terms the great increments in
energy consumption demanded by endo-
thermy. The rate of resting metabolic ex-
duce is greater in endotherms than in ecto-
therms, including the lower vertebrates (fish, amphibians, and rept-
iles) and the invertebrates (4). Dif-
ferences in standard metabolic rates among these animals are due principally
to variation in body mass and temper-

Table 1. Maximum aerobic power elicited by activity in small vertebrates.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass (g)</th>
<th>Aerobic power (mW/g)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scythes salmon (Decorynthus ruenca)</td>
<td>35</td>
<td>3.9</td>
<td>40</td>
</tr>
<tr>
<td>Largemouth bass (Mohroletta mohrolet)</td>
<td>150</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>Rainbow trout (Salmo gairdneri)</td>
<td>200</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>Goldfish (Carassius auratus)</td>
<td>66</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>Amphibians</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spadefoot toad (Scaphiopus hammondii)</td>
<td>40</td>
<td>7.9</td>
<td>44</td>
</tr>
<tr>
<td>Great Plains toad (Rana catesbeiana)</td>
<td>40</td>
<td>8.5</td>
<td>44</td>
</tr>
<tr>
<td>Leopard frog (Rana pipiens)</td>
<td>38</td>
<td>2.8</td>
<td>44</td>
</tr>
<tr>
<td>Reptiles</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Green iguana (Iguana iguana)</td>
<td>100</td>
<td>2.8</td>
<td>16</td>
</tr>
<tr>
<td>Racoon (Procyon lotor)</td>
<td>674</td>
<td>5.6</td>
<td>16</td>
</tr>
<tr>
<td>Desert iguana (Dipsosaurus dorsalis)</td>
<td>35</td>
<td>11.2</td>
<td>32</td>
</tr>
<tr>
<td>Geochlid lizard (Psilorhynchus cinctus)</td>
<td>548</td>
<td>2.9</td>
<td></td>
</tr>
<tr>
<td>Red-eared turtle (Pseudemys scripta)</td>
<td>305</td>
<td>5.8</td>
<td>46</td>
</tr>
<tr>
<td>Birds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red-tailed hawk (Buteo jamaicensis)</td>
<td>35</td>
<td>171</td>
<td>31</td>
</tr>
<tr>
<td>Laughing gull (Larus ridibundus)</td>
<td>322</td>
<td>71</td>
<td>31</td>
</tr>
<tr>
<td>Flicker (Colaptes auratus)</td>
<td>273</td>
<td>83</td>
<td>47</td>
</tr>
<tr>
<td>Evening grosbeak (Hesperiphora peregrina)</td>
<td>59</td>
<td>190</td>
<td>15</td>
</tr>
<tr>
<td>Mammals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Merriam's chipmunk (Eutamias merriani)</td>
<td>75</td>
<td>39</td>
<td>48</td>
</tr>
<tr>
<td>Norway rat (Rattus norvegicus)</td>
<td>286</td>
<td>27</td>
<td>49</td>
</tr>
<tr>
<td>House mouse (Mus musculus)</td>
<td>34</td>
<td>52</td>
<td></td>
</tr>
<tr>
<td>Fruit bat (Pteropus gouldii)</td>
<td>749</td>
<td>60</td>
<td>50</td>
</tr>
</tbody>
</table>

*Aerobic power was calculated at 20.9 J per milliliter of oxygen consumed. Values reported for poikilo-
therms were the greatest measured at any body temperature. Values for flying animals are the greatest report-
d for any flight speed and may not be maximal. Aerobic power per gram of scales at approximately 8-38°C
(mean 9, 14, 15).
As physical activity increases, power requirements are met by augmented aerobic metabolism. After an initial lag phase, organismal oxygen consumption rises in proportion to demand. If energet-ic demands exceed the support capacity of aerobic systems, anaerobic metabol-ism is used to supplement energy input. In vertebrates, anaerobic metabolism in-volves principally (if not exclusively) the production of lactic acid.

Among the ectothermic vertebrates, maximal oxygen consumption and aerobic scope (2) are proportionately as low as resting oxygen consumption in com-parison to the aerobic capacities of endo-therms (13). During maximal activity, oxygen consumption in the lower verte-brates can be increased an average of five- to tenfold at any single body tem-perature. Thus, at body temperatures characteristic of mammals andbirds, levels of oxygen consumption in maxi-mally active ectotherms are equal to resting levels of oxygen consumption in the former groups.

Mammals and birds during activity are also capable of increasing oxygen con-sumption by an average of five- to ten-fold (14, 15). The levels of aerobic me-tabolism achieved by endotherms are thus considerably in excess of those at-tained by lower vertebrates. For ex-ample, resting and maximal rates of oxy-gen transport in a 1-kidg iguana (Iguana iguana) at 35°C are 2 and 9 ml of oxygen per minute, respectively (16); compara-ble values for a 1-kg mammal are 9 and 54 ml of oxygen per minute (17). The ab-solute increments (aerobic scopes) are very different (4 ml compared to 45 ml of oxygen per minute). Consequently, the capacity of endotherms for supporting work aerobically exceeds that of the lower vertebrates by an order of magni-tude (Table 1). Although the resting maintenance requirements of the ecu-therm vertebrates are considerably lower, part of the price of that energetic economy is an inability to maintain high levels of aerobic power input.

There appears to be a consistent linkages between resting and maximal levels of oxygen consumption in the verte-brates. When an animal is in any given physiological state, oxygen consumption may increase an average of only five- to tenfold. This generalization is true not only for animals active at normal body temperatures but also for ectotherms over a range of body temperatures; low levels of resting oxygen consumption are associated with low levels of maximal oxygen consumption. Terpil or hiber-nating mammals are unable to achieve normothermic rates of maximal oxygen consumption until normally active body temperatures have been resumed. This low factorial increment seems to be a standard feature of vertebrate physi-ology and may represent a basic limita-tion of the capacity of the delivery or uti-lization of oxygen. For instance, blood circulation rate or the activity of mitochondria-ly enzymes may be able to increase only five-to tenfold on a short-term basis. Which system limits maximal oxygen transport in mammals is still very much in debate (17), and for the other vertebrate classes even less information is available. It is reasonable to assume, however, that these coevolved transport and utilization systems will not differ greatly from each other within an individual animal in their capacity for oxygen processing. Current knowledge does not permit the determini-nation of which mechanisms are most limiting of the capacity for oxygen transport. In general terms, oxygen uptake and transport are limited by the oxygen demand of the tissues, not by the capacity of the transport system.

Aerobic Capacity

As physical activity increases, power requirements are met by augmented aerobic metabolism. After an initial lag phase, organismal oxygen consumption rises in proportion to demand. If energet-ic demands exceed the support capacity of aerobic systems, anaerobic metabol-ism is used to supplement energy input. In vertebrates, anaerobic metabolism in-volves principally (if not exclusively) the production of lactic acid.

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Consequences for Locomotion and Sustained Activity

The differential between maximal aerobic power input in vertebrate endo-therms and ectotherms has direct con-sequences for the level and duration of activity which these animals can sustain. Aerobic metabolic rate in quadruped ani-mals while walking or running increases linearly with speed (19, 20). After maxi-mal levels of oxygen consumption are at-tained, they remain constant at higher speeds. Anaerobic metabolism provides the additional energy required at speeds in excess of that at which oxygen con-sumption becomes maximal (21). Thus, if two animals have similar costs of loco-motion, the animal with the higher aero-bic scope will be able to attain and sus-tain greater speeds aerobically. This situa-tion is evident in comparisons of the lo-comotor energetics of mammals and lizards. The net cost of transport (22) in terrestrial lizards and Mammals is very similar (19, 23); however, the mammal is able to sustain much higher speeds. In Fig. 1, oxygen consumption in a 1-kg Iguana and mammal are compared (24). Although the lizard expends less energy aerobically while walking at any given speed, the mammal can maintain a broader range of speeds (0.5 km/hour for the iguana; 4.1 km/hour for the mammal).

A comparison to aerobic potential, the cost of locomotion in terrestrial verte-brates is high, and even modest levels of activity quickly outstrip the aerobic limits of the lower vertebrates. Any ac-tivity greater than that of a slow walk in terrestrial ectotherms entails anaerobic metabolism and the production of lactic acid or the net catalysis of high-energy phosphate compounds. The metabolic power that can be obtained anaerobically far overshadows the aerobic abilities of most lower vertebrates, and moderate or high levels of activity in these animals appear to be sustainable only with the ac-tivation of anaerobiosis (25). These an-aerobic processes are capable of sup-powering muscle contractions for rather short periods, namely, 2 to 5 minutes. Consequently, these animals lack stam-nia for even moderate activity and ex-haust quickly. Recovery takes a long time and hours are sometimes required for complete restoration of the proactive physiological state (13).
Cnemidophorus murinus illustrate the Teiidae, one of the most active groups of lizards. This lizard belongs to the saurian family Coachwhip and racer snakes of this pattern of metabolic support (26). This activity, how-ever, increased 10- to 30-fold over aerobically supportable levels. This activity, how-ever, increased 10- to 30-fold over aerobically supportable levels. This activity, however, cannot be sustained. Anaerobic metabolism during activity can supple-ment, but not supplant, aerobic metabo-lism.

The anaerobic component provides more scope for activity in ectotherms than in endotherms. Maximal speeds in running mammals are generally only about twice sustainable levels (27), in comparison with 10- to 30-fold incre-ments found in lizards (28, 29). Thus, the capacities for, and consequences of, anaerobiosis play a greater role in influ-encing activity and survival of lower vertebrates than in mammals and birds. The ecto-thermic ancestors of the endothermic groups would likewise have been subject to these behavioral constraints of low stam-nas.

Maximal oxygen consumption and aerobic scope are temperature depen-dent and generally increase as body tem-peratures increase in ectothermic ani-mals (6, 12, 13). Both factors are maxi-mal at either preferred thermal levels or at the highest body temperatures toler-ated in extant reptiles. Transport of oth-er physical activities require a certain power input regardless of body temper-ature. Thus, a greater range of speeds and a greater variety of activities may be sustained aerobically at higher temper-atures. Grasser stamna and aerobically supported performance have been dem-onstrated in Iguana as body temperature rises (24). Selection operating to increase aerobic capacity would also favor the de-velopment of regulation at high body temperatures where oxygen-transport capabili-ties are maximal and a greater range of aerobic performance is possible. Another observation concerning the role of thermoregulation in the evolution of endothermy should be mentioned. If thermoregulation were generally in an equable environment, were the selective feature of greatest importance, it could have been observed in the develop-ment of the primitive reptilian physiologi-cal condition. The capacities of the ven-tilatory, respiratory, and oxygen-transport systems of extant reptiles are fully capable of sustaining resting levels of endo-thermic metabolism (29). All that would have been required is the development of an insulating coat and the full activation of oxygen-processing systems. Such a reptile would have had a greatly reduced aerobic scope but would have had func-tional anaerobic systems to support short-term activity. Thus, the oxygen delivery and utilization systems were greatly increased to supply heat and generally increase as body temper-atures where oxygen-transport systems have played an important role in the develop-ment of endothermy.

### Table 2. Production of adenosine triphosphate (ATP) during 5 minutes of maximal activity in reptiles and rodents (24).

<table>
<thead>
<tr>
<th>Animal</th>
<th>Mass (g)</th>
<th>Aerobic</th>
<th>Anaerobic</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Montane vole (Microtus montanus)</td>
<td>25</td>
<td>80</td>
<td>15</td>
<td>95</td>
</tr>
<tr>
<td>Merian’s kangaroo rat (Dipodomys merriami)</td>
<td>35</td>
<td>90</td>
<td>9</td>
<td>100</td>
</tr>
<tr>
<td>Western fence lizard (Sceloporus occidentalis)</td>
<td>13</td>
<td>24</td>
<td>22</td>
<td>46</td>
</tr>
<tr>
<td>Couchwhip and racer snakes (Coluber constrictor and Muscophorus fasciatus)</td>
<td>262</td>
<td>23</td>
<td>20</td>
<td>53</td>
</tr>
</tbody>
</table>

**Selective Factors in the Evolution of Endothermy**

The high levels of resting metabolism of endotherms are associated with high levels of maximal oxygen consumption. The attainment of this level of sustain-able energy output, and aerobic scope, is a much broader array of physiological activities and greatly enhanced the behavioral capa-bility of the vertebrates. Although the previous comparisons have been based on linear walking and running activity that can be quantified on a treadmill or by measuring velocities, they are equally applicable to any kind of behavior sup-ported through aerobic metabolism. The evolution of the complex behavior pat-terns among the birds and mammals re-quired the prior evolution of metabolic systems capable of supporting that activ-ity. We believe that this increased stam-nas and sustainable activity were impor-tant selective factors from the outset in increasing resting levels of metabolism during the evolution of endothermy. To achieve these higher levels of perform-ance, resting metabolic rate was in-creased.

The selective advantages of increased activity capacity are not subtle but rather are central to survival and repro-duction. An animal with greater stamina has an advantage that is readily com-prehensible in selective terms. It can sustain greater levels of pursuit or flight in gathering food or avoiding becoming food. It will be superior in territorial de-fense or invasion. It will be more suc-cesful in attracting mates and raising young. These advantages appear to us to be worth in-creased energetic costs, particularly since the enhanced capacity gives the possessor the ability to increase energy intake to meet new energy demands. These relations also would have pro-vided an immediate increase in stamina with a continual rise in resting metabolic rate. This condition is different from that relating to thermoregulation, in which metabolic rate must increase greatly before significant thermotolerance is at-tained. At some point after the initial metabolic increments, thermoregulatory considerations will become important and, in fact, feasible, whereas previously they were not. The advantages of a high and stable body temperature would then have caused the development of thermost-erative regulations, such as fur or feath-ers. These would retain the metabolic-cal-ly insulating heat in cool environments and serve to reduce absorption of heat from warm environments.

The tendency for mammals and birds to regulate body temperature at com-patively high levels may also be related to increased aerobic capacity during ac-tivity. Maximal oxygen consumption and aerobic scope are temperature depen-dent and generally increase as body tem-peratures increase in ectothermic ani-mals (6, 12, 13). Both factors are maxi-mal at either preferred thermal levels or at the highest body temperatures toler-ated in extant reptiles. Transport of oth-er physical activities require a certain power input regardless of body temper-ature. Thus, a greater range of speeds and a greater variety of activities may be sustained aerobically at higher temper-atures. Grasser stamna and aerobically supported performance have been dem-onstrated in Iguana as body temperature rises (24). Selection operating to increase aerobic capacity would also favor the de-velopment of regulation at high body temperatures where oxygen-transport capabili-ties are maximal and a greater range of aerobic performance is possible. Another observation concerning the role of thermoregulation in the evolution of endothermy should be mentioned. If thermoregulation were generally in an equable environment, were the selective feature of greatest importance, it could have been observed in the develop-ment of the primitive reptilian physiologi-cal condition. The capacities of the ven-tilatory, respiratory, and oxygen-transport systems of extant reptiles are fully capable of sustaining resting levels of endo-thermic metabolism (29). All that would have been required is the development of an insulating coat and the full activation of oxygen-processing systems. Such a reptile would have had a greatly reduced aerobic scope but would have had func-tional anaerobic systems to support short-term activity. Thus, the oxygen delivery and utilization systems were greatly increased to supply heat and generally increase as body temper-atures where oxygen-transport systems have played an important role in the develop-ment of endothermy.

**Animal Reference**

Aerobic Anaerobic Total

Montane vole (Microtus montanus) 80 15 95
Meryan’s kangaroo rat (Dipodomys merriami) 90 9 100
Western fence lizard (Sceloporus occidentalis) 24 22 46
Couchwhip and racer snakes (Coluber constrictor and Muscophorus fasciatus) 23 20 53
The comparisons discussed above have been directed mainly toward terres-
trial mammals and reptiles, since both have similar locomotory energetics. 
However, the selectivity arguments appear equally well to the development of
endothermy in birds and, perhaps, in di-
osaurs. Part of the attractiveness of this hypothesis is that it does not require the development of ad hoc arguments for thermoregulatory advantages of endo-
thermy in different climates for different
groups. The greater levels of sustained 
power input may have been a factor of 
significance during the evolution of these
groups. Flapping flight requires a certain minimal level of power input that is far beyond the aerobic capacity of modern reptiles. For instance, minimum theoret-
ical and empirical power input required for level flight by a 35-g budgerigar (Mel-
opsittacus) is 3.7 W (30, 31). Maximum aerobic power of a desert iguana (Dipsos-
saurus) of equal size is 0.4 W (27). To sustain flight with this power input would require wings that are impossibly large and thin. Anaerobic metabolism cannot safely enhance this power input, since fatigues during flight could be disastrous. Consequently, fundamental enhance-
ment in the aerobic metabolic systems was required for the evolution of flying behavior characteristic of modern birds. 

Among the dinosaurs, the necessity of physiological thermoregulation has been questioned since animals of such large 

mass would, in any case, be of relatively constant body temperature (D). If these animals were endothermic or if some 
groups of dinosaurs were endothermic, the acquisition of their high metabolic rate might have been related to enhancing lev-
els of sustainable activity and not to tem-
peratures regulation per se. 

Performance During Burst Activity

The evolution of increased aerobic ability and stamina in endotherms does not have to greatly increase maxi-
mal power output and the capacity for burst 
activity. Aerobic and anaerobic contributions to 5 minutes of burst activ-
ity are summarized in Table 2 for small rodents and reptiles. Maximal energy utilization over short periods is similar in these animals and is definitely not an or-
der of magnitude different. The anaero-
bic component becomes even more prominent when shorter time periods are con-
sidered since more than half of the 
aerobic response occurs during the first 
30 seconds of activity (47), and there is an initial lag during this period before maximal levels of oxygen consumption are attained. Consequently total power input of small reptiles may even exceed that of small mammals during shorter pe-
riods of activity. These high levels of an-
eaerobic supported power input can resist in high levels of short-term behav-
ioral performance. Small lizards can ac-
celerate to speeds greater than 10 km/h in 
horizons of less than 2 m (29). Although quantitative measurements are generally lacking, maximal speeds of small lizards seem very similar to those of mammals of equal size (33).

Power input and running performance levels during burst activity may thus be very similar in small reptiles and mamm-
als. These relationships explain why reptiles and amphibians are often very fleet and difficult to catch and why they may be able to outperform and outrun endotherms over shorter distances. The acquisition of high aerobic levels im-
proved capacities for stamina but not for burst activity. Consequently, ecto-
thermic vertebrates were not and are not necessarily easy prey for endotherms. Their lower energy expenditure for maintanance and thermoregulation and greater efficiencies of secondary produc-
tion permit them to occupy niches close to endotherms. Yet their pattern of ac-
tivity metabolism permit them to escape from and sometimes pursue endotherms over short distances. The evolution of endothermy has thus not improved all aspects of activity performance but only those relating to sustained behavior. 

Enhancement of Aerobic Capacities

How might the evolution of increased aerobic capacity have occurred? An ex-
amination of the diversity of modern rept-
iles can suggest adjustments possible within the reptilian metabolic frame-
work. The most active species may be expected to have maximized their potent-
ial for oxygen transport. Lizards of the genus Varanus are examples of these ca-
pacities. These are active, predatory ani-
mals with aerobic scopes and sustainable running speeds more than twice as great as lizards of similar size (2, 36). This in-
crease appears to be due to a greatly increased surface area of the lungs, high-
ly effective blood filters, and large amo-
utes of myoglobin in skeletal mus-
cles (26, 37).

Further increments in oxygen process-
ing ability would appear to require en-
ergic investments in morphological structures associated with oxygen up-
take and transport—for example, develop-
ment of an even more complex lung and ventilation system, the subdivision of

of the heart and a great increment in blood flow and pressure, and an increase in oxygen-carrying capacity of the blood. In addition, the capacity of tissue to utilize oxygen was also increased. Skeletal

muscle, the tissue with the greatest aer-
obic scope, is the principal consumer of oxygen during activity. However, skele-
tal muscle has a relatively low metabolic rate at rest and does not constitute a ma-
jor thermogenic organ in small mam-
als (38). Endothermy is not based on muscle metabolism alone but involves increments in the metabolic rates of many organs. The activity of autochon-
dinous enzymes in unperfused homogenates of liver and skeletal muscle from lizards and mammals parallels differences in aerobic metabolic rates of intact animals (8). The greater metabolic rate of the endotherms appears to be due to greater concentrations of mitochondria in its tis-
sues. If the catalytic capacity of the mitochondrial enzymes represented a larger limitation on the oxygen-Process-
ing ability of animals evolving higher metabolic rates, this capacity could have been increased with a minimum of ge-
nic alteration by increasing mitochondrial

volume. All the preceding alterations are con-
sistent with increasing capacity for both activity and physiological thermoregula-
tion. We believe these events were tightly related and that the latter would not have occurred without the former.

References and Notes


41. A. Bartholomew and V. A. Tucker, Gen.


43. F. G. Benedict, ref. 8, p. 123.

44. The following regression equations relate resting 


46. The use of the general term "energy" means the energy content of a food or tissue expressed as heat produced in a respirometer, or as calories absorbed 

47. L. J. Wilson, "Ecology of the Reptiles", T. E. Drake, Ed. (Univ. Texas Press, New Haven, 


52. The efficiency of secondary productivity (calo-

21. The velocity at which anaerobic metabolism is activated is termed the "anaerobic threshold." It is the velocity below the velocity at which oxygen consumption is maximized.

22. The slope of oxygen consumption as a function of velocity is (0).

23. The slope of the line connecting the intercept and the maximum oxygen consumption is taken from (0), intercept and the point of inflection. It may occur below the velocity at which oxygen consumption is maximized.

24. At 23% of 0% consumed and 16.7 pmole of ATP per milliliter of 0%, the anaerobic threshold is taken at 190 pmole of ATP per milliliter of 0%. Values calculated on whole body measurements on the manuscript. Supported by NSF grants PCM 77-99000 and PCM 78-21000, and NIH grant 1 KO4 AM00351-01 to A.F.B. We thank G. A. Bartholomew for comments on the manuscript.