Anatomical and Ecological Evidence of Endothermy in Dinosaurs

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> **Recognition of endothermy in dinosaurs can explain both the success and the extinction of this group in the Mesozoic.**

Most birds and mammals are endotherms, producing at rest an order of magnitude more heat than a reptile of the same weight at the same temperature, and using high endogenous heat production to maintain a constant body temperature[1]. Living reptiles are ectothermic and rely mostly on external heat sources for temperature regulation. Traditionally, dinosaurs are pictured as ectotherms[2], but this view has been challenged recently because of resemblances in the locomotor apparatus[3-5] between dinosaurs and birds or mammals.

Anatomical Evidence

Fossil footprints and joint anatomy[5] show that dinosaurs had a fully erect gait with a very narrow trackway, and limb action severely restricted to a vertical, parasagittal plane. Large, non-dinosaurian, fossil reptiles—nareiasaurs, tapinocephalians, rhynchosaurs—had a lizard-like, sprawling gait, very short and stocky limbs, and they must have been capable of only a low sustained speed[5]. Large dinosaurs—brontosaurs, duck-bills, stegosaurs, horned dinosaurs—in contrast had relatively much longer limbs, with joint anatomy similar to that of elephants or rhinos, and probably could reach speeds equal to those of large living elephants, that is 30 km h^{-1} (ref. 6). Some small dinosaurs—ostrich dinosaurs, hypsilophodonts—had very long, gracile limbs and probably could reach top speeds similar to those in ostriches and ungulates, that is, 50–80 km h^{-1}. The cost of locomotion in mammals has been found[7] to increase linearly with speed, and the slope of this relation decreases with body weight. This cost can be estimated by the formula

$$M = 8.46W^{-0.40} S + 1.7R$$

where M is ml. O_2 g^{-1} h^{-1} consumed, W is weight in g; S is speed in km h^{-1}, and R is resting metabolism in ml. O_2 g^{-1} h^{-1}. Moberly[8] has found for the lizard *Iguana*, and I have found for the lizards *Varanus*, *Tupinambis*, *Ctenosaura* and *Uromastix*, that the cost of locomotion in these reptiles is about the same as in mammals of the same weight. At a body temperature of 35° C the maximum sustained aerobic energy output of a lizard is about six times the resting level, or about $6W^{-0.25}$ ml. O_2 g^{-1} h^{-1}, only about one-tenth to one-twentieth that of an endotherm[1,9]. Except for very short (20 s or less) anaerobic bursts, the maximum speed of a 1 kg lizard at 30–35° C is about 1–2 km h^{-1}, about one-tenth to one-twentieth that of mammals of similar weight[10]. Maximum sustained speed for a lizard-like ectotherm can be

estimated by the formula

$$S = \frac{4.3W^{-0.25}}{8.46W^{-0.40}}$$

Assuming the presence of lizard-like energetics, the maximum speed of a 100 kg ostrich dinosaur would be only 2.9 km h^{-1}, and that of a 10 ton tyrannosaur only 5.8 km h^{-1}. Clearly, dinosaurs were built for sustained speeds much higher than these, and energy metabolism in these creatures must have been like that of endotherms.

In non-aquatic reptiles, the internal nares open near the front of the palate and can be blocked by mastication of food. Mammals have an extensive secondary palate which allows elaborate mastication while maintaining continuous breathing, a necessity for endotherms. In most dinosaurs the internal nares were displaced posteriorly more than in lizards. In herbivorous dinosaurs with specialized feeding apparatuses—sauropods, duck-bills, ceratopsians, ankylosaurs—the secondary palate was especially well developed, but it is absent in herbivorous lizards.

The heart and lungs of crocodilians are the most advanced and endotherm-like of living reptiles[11]; there is a relatively great area for gaseous exchange and a complete anatomical separation of oxygenated and deoxygenated blood in the heart, and the aerobic energy output seems to reach a higher maximum than in most other reptiles. Yet the postcranial anatomy and the heart and lungs of crocodilians are more primitive than those of dinosaurs and reflect lower speeds and activity levels[5].

Birds have an air-sac system connected to the lungs that penetrates deeply into the body. Air sacs permit unidirectional flow over gaseous exchange surfaces and much more efficient oxygen extraction than in mammals[12]. In the ostrich, *Struthio camelus*, for example, air sacs allow extensive thermoregulatory panting without inducing alkalosis[12]. The vertebrae of brontosaurs and theropods had large cavities for air sacs which exited through large pneumatopores as in birds, and these dinosaurs, unlike living reptiles, probably had an avian-type lung with unidirectional flow.

Most dinosaur specimens represent animals with a live weight of 50 kg or more[5], the few smaller specimens probably representing juveniles of genera with an adult weight of 30–50 kg[5]. Although microvertebrates and mouse-sized salamanders, lizards and mammals are very common in Jurassic and Cretaceous deposits, small dinosaurs are unknown[5]. Why did dinosaurs fail to exploit the ecological possibilities of small body size utilized so successfully by other groups ?

Because large tropical endotherms have a low surface area to volume ratio, they can maintain a constant body temperature without dense superficial insulation. Elephants, rhinos, hippos, pigmy hippos, many suids and armadillos, for

example, are nearly hairless, even at birth, but very small endotherms require insulation because even relatively brief exposure to cool temperatures would strain heat production. Thus the only naked small mammals are subterranean forms, such as the naked mole rat, *Heterocephalus*, which avoid surface temperature fluctuations. Fossil skin impressions show that dinosaurs lacked any superficial insulation[2], and this factor, combined with endothermy, would have restricted dinosaurs to large body size. Small ectotherms allow body temperature to fall when environmental conditions are adverse to behavioural thermoregulation; most endotherms must maintain a constant body temperature.

The tetrapod skeleton provides reserves of calcium phosphate for internal chemical homeostasis. Endothermy places greater demands on the homeostatic capacity of bone because: (1) variations in energy metabolism are greater in endotherms—the difference between resting and maximum energy output is an order of magnitude greater than in ectotherms; (2) endotherms regulate their internal environment more closely and more continuously.

The labile fraction of bone is concentrated in the youngest layers of the most recently formed haversian systems[13], and the maintenance of large reserves of this bone depends on the number and rapidity of reconstruction of haversian systems. Rapid mineral transfer from bone to plasma also depends on bone vascularization and the minimum distance from labile bone to capillary. Mineral transfer from intercellular fluids to plasma provides minute to minute adjustment; transfer from labile bone to intercellular fluids provides hour to hour adjustment[13]. In mammals the compact bone is richly vascularized and contains large numbers of rapidly reconstructed haversian systems[14], but in living reptiles the compact bone contains few if any haversian systems with little reconstruction and is often completely avascular[15]. Similarly, the compacta in most fossil reptiles was usually poorly vascularized with little reconstruction[15], though close-packed haversian systems with evidence of rapid reconstruction are known in the specialized mammal-like reptile *Kannemeyeria*, which may have resembled mammals in various physiological aspects[15]. The bone histology of theropods, some brontosaurs and ornithischians was also mammal-like[15].

Currey has described[16] in artiodactyls a bone architecture —laminar bone—which provides a more intimate association of bone cells and capillaries than does haversian bone. Laminar bone is unknown in living reptiles but was present in *Dinodontosaurus*, a close relative of *Kannemeyeria*[16]. Laminar bone even more densely vascularized than that of artiodactyls was present in some prosauropod and brontosaur dinosaurs[16,17]. All the dinosaurs which I investigated display densely haversian or laminar bone, or both.

Energy Budgets

In a field study of the Komodo dragon (*Varanus komodoensis*), a powerful predator, Auffenberg estimated that a 50 kg lizard kills a large mammal (pig or deer) or finds a large carcass about once a month[18]. Assuming the weight of the average prey carcass is about half that of the lizard, the Komodo dragon thus takes its own body weight in prey every 60 days. Cheetahs (*Acionyx jubatus*) take their own weight in prey every 10.0 days[19]; and figures for lions (*Panthera leo*) and wild dogs (*Lycaon pictus*) are 7.7–9.1 and 6.7 days respectively[20]. Endotherms thus take prey at a rate an order of magnitude higher than ectotherms relative to body weight.

Secondary productivity (SP) is the fixation of energy into tissue by a heterotrophic population[21], and in a steady state population SP can be expressed as the weight or caloric equivalent of all individuals dying per year. In most ecto-... SP is 15, 30% of the total energy assimi-

of magnitude higher in ectotherms, but the ratio of assimilation to standing crop (SC) is an order of magnitude lower in ectotherms than in endotherms. Hence, the SP/SC ratio is similar in ectotherms and endotherms of the same size—in six of the seven small endotherms listed by Golley[21], SP was 100–300% of SC, much the same range as in small lizards[22]. The SP of a prey population is the maximum crop available to carnivores. Because endothermic carnivores require prey at a rate an order of magnitude higher than that of ectotherms, the predator SC to prey SC ratio in an ectothermic predator/prey complex should be an order of magnitude higher than in an endothermic complex.

A tiger (*Panthera tigris*) needs to ingest a minimum of fifteen times its weight in prey a year in the wild[23] (because of loss to scavengers, twice this amount may have to be killed[19,20]). The SP/SC ratio is 25–30%[24,25] in ungulates of the size taken by tigers (deer and large antelope of 50–200 kg[23]). Thus a prey SC thirty to sixty times the tiger SC is necessary to supply the minimum food needs of the tiger. Maximum predator SC/prey SC ratio in such a community would be 1.5–3%. SP/SC ratios and food requirements per unit weight decrease with increasing body size[26], and therefore, if prey and predator are about the same size, as in the tiger-deer community, predator SC/prey SC ratios should be fairly constant for any body size in a particular climate. In one area of Rhodesia, it has been noted that lions take ungulates totalling about 1% of their number[27] and probably 1.5–3% by biomass. In Ngorongoro Crater, Tanzania, figures of 25,000 ungulates to 400 hyaenas and 80 lions[28] have been noted—a predator SC/prey SC ratio also of about 2–3%. Schaller has reported that 140,000 kg of ungulates supports six or seven tigers, a leopard and some jackals[23]—about 1% of the prey by biomass. The predator SC/prey SC of cold temperate mammal communities may be much less than 1%[25,29].

Predator/Prey Ratios

In the Early Pliocene mammal community analysed by Voorhies[30], the predator SC was about 3.9% of prey SC, excluding elephants (which are probably too large to be taken by any of the carnivores present) or 3% of prey SC including elephants (Fig. 1). Predator/prey ratios in the Pliocene community studied by Shotwell[31] were similar. For an Oligocene mammal community Clark *et al.*[32] obtained a predator SC/prey SC ranging from 2.7–8.1% for three facies, and 4.5% for the combined collections (Fig. 1). Thus in both living and fossil tropical and warm temperate mammal communities, predator SC/prey SC ratios range from 1–4.5%.

The oldest fully terrestrial tetrapod fauna known to date is from the *Tapinocephalus* Zone, mid-Permian of South Africa[33-35], where the fauna was mostly very primitive mammal-like reptiles and pareiasaurs, all of which were almost certainly ectothermic. Aquatic prey must have been unimportant, for fish and amphibians are rare. Pareiasaurs, large herbivores, are usually found articulated, in a standing posture in blue mudstone[33], a facies and mode of preservation which are virtually unknown for the rest of the fauna, indicating that pareiasaurs were ecologically separate. The ratio of number of carnivores to herbivores is 25%, much higher than in most mammalian faunas[33]. Pareiasaurs, tapinocephalians, titanosuchians and anteosaurs were all about 1,000 kg. Because skull length/body length ratios are fairly constant in primitive mammal-like reptiles, body weight for the smaller genera can be estimated by comparing the cube of the skull length to the cube of the skull length of an anteosaur (taken as 1,000 kg). For therocephalians average skull length was about 350 mm[35]; for gorgonopsians, 150 mm; for dicynodonts, 80 mm; and for anteosaurs, 720 mm[54]. Carnivore SC/herbivore SC was about 19.2%

ectothermic community were an order of magnitude greater than in mammalian communities.

Russell[36] has noted in Canadian Cretaceous deposits that field parties tend to leave behind many specimens of the commonest forms—duck-bills and ceratopsians—so that the number of duck-bill and ceratopsian specimens collected should be increased by 100% and 50% respectively to give an accurate picture of relative abundance. This correction has been incorporated in Fig. 1 and Table 1. Live weight has been estimated by using the square of the minimum shaft circumference of the limb bones—femur only for bipeds; humerus and femur for quadrupeds. Crested duck-bills with long forelimbs are treated as quadrupeds; flat-headed duck-bills with short forelimbs are treated as bipeds (Table 1). Square of minimum shaft circumference of humerus and femur of an adult *Rhinoceros unicornis*, live weight about 2,000 kg, was used as a standard (Table 1).

Carnivore SC/herbivore SC ratios for three successive Canadian Late Cretaceous rock units are 3.3%, 2.2% and 2.0% (Fig. 1; Table 2); for combined collections they are 2.9%. In the latest Cretaceous (Lance and Hell Creek, Upper Edmonton formations) predator/prey ratios are as low or lower; only a few tyrannosaur specimens are known[37], but hundreds of *Triceratops* and dozens of duck-bills have been discovered[38]. In the Late Jurassic Morrison Formation, the carnivore SC (mostly *Allosaurus*) was but a few per cent of herbivore SC (mostly giant brontosaurs, with stegosaurs and camptosaurs)[39]. High percentages of

**Table 1** Calculated Average Adult Weights of Late Cretaceous Dinosaurs

Animal	Square of minimum circumference of humerus in mm²	Square of minimum circumference of femur in mm²	Adult weight in kg	Caloric value of one specimen in A-kcal/m²/yr
Rhinoceros	433	457	2,000	
Albertosaurus		1,355	3,044	1.0
Daspletosaurus		1,582	3,556	1.2
Hadrosaurs, crested	500	2,020	5,556	1.8
Hadrosaurs, flat-headed		2,520	5,556	1.8
Ceratopsians	900	1,001	4,273	1.4
Ankylosaurs	729	900	3,662	1.2

dinosaur carnivores occur only in obvious predator-trap deposits—local accumulations analogous to the tar pits of the California Pleistocene, such as the Cleveland-Lloyd Quarry where allosaurs of all age classes make up most of the fossils.

Energy Flow in Dinosaur Communities

An analysis of energy flow can determine whether the low percentage of carnivores was attributable to endothermy or some peculiarity of community structure—such as the

Fig. 1 Above: composition of herbivorous standing crop in fossil tetrapod communities. Numbers to right of column segments represent average adult weight for genus; height of column segment for each genus represents product of average weight and total number of specimens. Below: composition of carnivore standing crop for same fossil communities given above. Column height for herbivores and carnivores in each community drawn to same scale. Data from Boonstra[33], Russell[36], Clark *et al.*[32] and Voorhies[30].
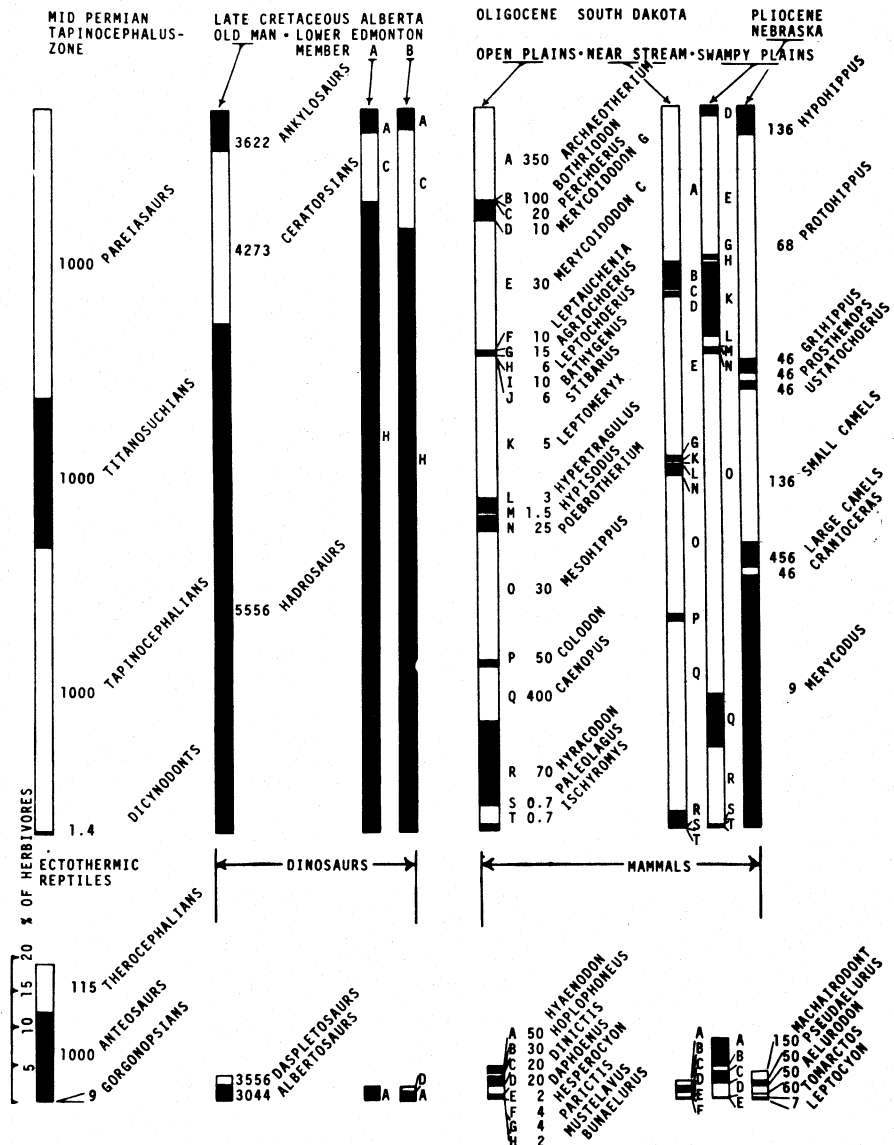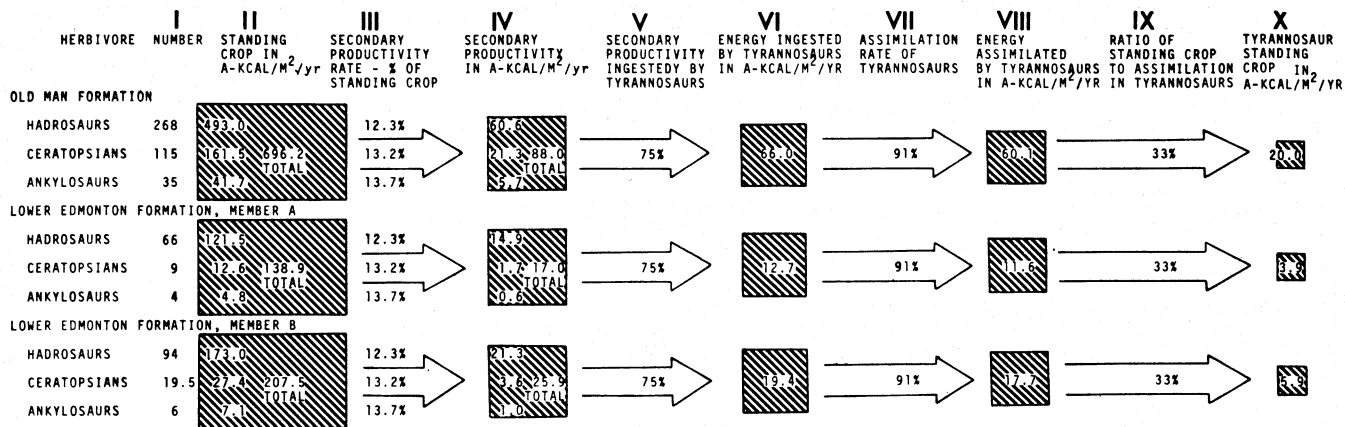
Fig. 2 Energy flow in Late Cretaceous dinosaur communities. Boxes represent energy quantities; arrows represent processes in energy transfer. Tyrannosaur standing crop (column 10) calculated from herbivore standing crop and assuming that dinosaurs were endothermic. Compare column 10 with Table 2.

large size of most common dinosaurs. Energy flow may be expressed by the equation: $SC_p = (SC_h)(SPR)(I)(D)(SC_p/A)$ where SC_p is the carnivore SC, SC_h is the herbivore SC, SPR is the secondary productivity rate of herbivores expressed as per cent of SC_h, I is per cent of herbivore SP ingested by predators, D is per cent of I assimilated by predators, and A is the total yearly assimilation (energy budget) of the predators. In most discussions of energy flow[21], SC and SP are expressed in kilograms or kilocalories per acre or m². For dinosaur communities where such quantities cannot be computed, a relative unit is useful, and one A-kcal/m²/yr is defined as the caloric value of the standing crop of albertosaurs represented by one albertosaur specimen. The SC of any dinosaur thus becomes the number of specimens times the estimated body size divided by the estimated albertosaur body size (Table 2).

Environmental stress and severity of predation affect the SPR in living tetrapods. Musk oxen (*Ovibos moschatus*) in a barren ground Arctic habitat have lower SPR than warm temperate ungulates of comparable body size[39]. African elephants (*Loxodonta africana*) suffer little predation[40] and have SPR rates of only about 5%[21]. The flora of dinosaur communities indicates a mild, frost-free climate[41]. Predation on even the largest Canadian dinosaur herbivores was probably very heavy. Solitary predators with relatively small heads—cheetah[19], *Sceloporus*[22]—usually take individual prey half to a fifth their body size or smaller. Big-headed predators—lions, tigers[23,42-44], Komodo dragons[18]—frequently take prey two or even three times their body weight. Duck-bills, the largest herbivores in the Cretaceous Canadian dinosaur communities, were less than twice the adult weight of the contemporary tyrannosaurs, *Albertosaurus* and *Daspletosaurus* (Table 1)[45]. Tyrannosaurs had relatively huge heads (1,000 mm[45]) and teeth and undoubtedly could kill even the largest contemporary herbivore. The SPR rate in tropical and temperate ungulates, which are heavily preyed upon, decreases with increasing body size, much as metabolism per gram decreases as the −0.25 power of body weight[9]. The SPR of moose (*Alces alces*) in the moose-wolf com-

munity at Isle Royale is about 25%[24]; in smaller white tail deer (*Odocoileus virginianus*)[25] and in tropical ungulates[42] it is about 33 + %.

Dinosaur SPR may be estimated by the formula:

$$SPR = 0.22 \left(\frac{W}{550} \right)^{-2.50}$$

where 0.22 is a conservative estimate of SP/SC in temperate or tropical herbivores of the size of moose, 550 is the weight of an adult moose in kilograms, and W is the adult weight of the dinosaurs (Fig. 2, columns 2 and 4). Tyrannosaurs were the only carnivores powerful enough to kill and dismember duck-bills, horned dinosaurs and ankylosaurs. The next largest carnivores, *Stenonychosaurus* and dromaeosaurs[46,47], were only about 50 kg adult weight. Tyrannosaurs were long-legged, gracile, had good olfaction, and must have been the dominant scavengers and predators. At Isle Royale, moose (*Canis lupus*) are the dominant prey of wolves and, according to Jordan[24], ingest about 75 + % of the caloric value of all moose SP. Hence I, the ingestion of herbivore SP by tyrannosaurs, is estimated to be 75% (Fig. 2, columns 5 and 6). In bobcats (*Lynx rufus*), domestic cats and dogs[48], and the predatory lizard *Lacerta vivipara*[49], about 91% of ingested prey is assimilated. Tyrannosaur digestive efficiency, D, is estimated to be 91% (Fig. 2, column 7).

Low mortality rates decrease the SPR and the ratio between SC and assimilation (energy budget). Large carnivores, such as wolves, have lower mortality rates and SPR than most prey species of similar size[24,25]. Tyrannosaur mortality was probably low, much as in living elephants which are about the same size and suffer little predation. Mortality of African elephants is about 4–5% per year and the SC/assimilation ratio is about 33%[21,50]. If tyrannosaurs were endothermic with energy budgets like those of large, elephant-size mammals, SC/assimilation ratios were probably about 33% (Fig. 2, column 9). The SC_p of endothermic tyrannosaurs that should be supported by the prey SC_h can be estimated by taking 33% of the estimated assimilated prey SP, which has been calculated directly from herbivorous

Table 2 Standing Crop of Tyrannosaurs calculated from Tyannosaur Fossils and from the Energy Flow Equation

Formation	Daspletosaur specimens	Albertosaur specimens	Tyrannosaur SC as % of herbivore SC	Tyrannosaur SC in A-kcal/m²/yr	Endothermic tyrannosaur SC calculated from energy flow in A-kcal/m²/yr	Ectothermic tyrannosaur SC calculated from energy flow in A-kcal/m²/yr
Old Man	6	16	3.3	23.0	20.0	Approx. 200.0
Lower Edmonton	2	3	2.2	3.0	3.9	Approx. 39.0

dinosaur specimens (Fig. 2, columns 1 to 8). In ectotherms the SC/assimilation ratio is an order of magnitude higher than in endotherms. Thus if tyrannosaurs were ectothermic, the SC_p represented by the tyrannosaur specimens should be an order of magnitude greater than 33% of the calculated tyrannosaur energy budget.

The SC_p of endothermic tyrannosaurs that could be supported by the herbivorous dinosaur populations is 20.0 A-kcal/m²/yr for the Old Man Formation; 3.9 A-kcal/m²/yr for Member A, Lower Edmonton Formation; 5.9 A-kcal/m²/yr for Member B, Lower Edmonton Formation; and 29.8 A-kcal/m²/yr for all three (Fig. 2, column 10). If tyrannosaurs were ectothermic, these values should be an order of magnitude higher, that is, about 200.0 A-kcal/m²/yr for the Old Man Formation and about 300.0 A-kcal/m²/yr for all three formations. The actual caloric value represented by the tyrannosaur specimens (Table 2) is: 23.0 A-kcal/m²/yr for the Old Man; 3.0 A-kcal/m²/yr for Member A, Lower Edmonton; and 4.2 A-kcal/m²/yr for Member B, a total of 30.2 A-kcal/m²/yr. Thus the number of tyrannosaur specimens agrees very well with the calculated number of tyrannosaur-size endothermic predators which could be supported by the herbivorous dinosaur populations.

The predator SC/prey SC ratios in dinosaur communities are an order of magnitude less than in the all-ectothermic *Tapinocephalus* Zone fauna but fall within the range of living and fossil mammal communities. Analysis of energy flow strongly indicates that dinosaur energy budgets were like those of large mammals, not elephant-size lizards.

Dinosaur Success and Extinction

Abundant evidence for endothermy in dinosaurs comes from the three levels of biological organization which can be investigated through fossils—cellular (bone histology), gross anatomical (locomotor anatomy, pneumatopores, secondary palate), and community structure (low predator/prey ratios). On all these levels dinosaurs resemble advanced mammals or birds, not living reptiles. Recognition of endothermy in dinosaurs can explain both the success and the extinction of this group. The mammal-like reptiles which dominated tetrapod communities in the Permo-Triassic approached true mammals in many skeletal and presumably physiological characters, but even advanced mammal-like reptiles retained the primitive sprawling posture[5]. The most primitive living mammals (monotremes, didelphids, tenrecs, *Solenodon*) tend to regulate their body temperatures at relatively low levels (27–33° C) and have poor mechanisms for coping with either endogenous or environmentally induced heat stress[5]. Advanced mammal-like reptiles may have been similar. The locomotion, respiration and thermoregulation of dinosaurs probably resembled those of large ground birds or savannah ungulates and carnivores. Thus dinosaurs had an advantage over mammal-like reptiles in mobility and the capacity to unload high endogenous heat production during sustained, vigorous, daylight activity in a warm climate[5].

Some microfossil evidence indicates that a sudden drop in world-wide temperature occurred at the Cretaceous-Tertiary boundary[51,52]. Land tetrapod extinctions at the end of the Cretaceous were selective: many large and small ectotherms survived—salamanders, several varieties of frogs, champsosaurs, lizards, crocodilians and turtles; and small endotherms did not suffer total annihilation—many lineages of mammals and birds continued into the early Tertiary. Dinosaurs were totally wiped out. As L. S. Russell has suggested[3], the combination of large size, naked skin and endothermy may have caused the extinction of dinosaurs. In the face of sudden, prolonged cold stress, dinosaurs were too large to escape by hibernating in burrows or other micro-habitats available to small endotherms, and were unable to survive prolonged drops in their body temperature, unlike many turtles, lizards and other ectotherms. Exposure to prolonged severe cold would probably kill most of the living, naked, tropical endotherms—rhinos, hippos, elephants, armadillos—and may well have eliminated the dinosaurs, the naked, tropical endotherms of the Mesozoic.

[1] Gordon, M. S., Bartholomew, G. A., Grinnell, A. D., Jorgensen, C. B., and White, F. N., *Animal Function: Principles and Adaptations* (Macmillan, New York, 1968).
[2] Colbert, E. H., *Dinosaurs: Their Discovery and Their World* (Dutton, New York, 1961).
[3] Russell, L. S., *J. Paleont.*, **39**, 497 (1965).
[4] Ostrom, J. H., *Proc. N. Amer. Paleont. Conf.*, D, 347 (1969).
[5] Bakker, R. T., *Evolution*, **25**, 636 (1971).
[6] Howell, A. B., *Speed in Animals* (Univ. Chicago Press, Chicago, 1944).
[7] Taylor, C. R., Schmidt-Nielsen, K., and Raab, J. L., *Amer. J. Physiol.*, **219**, 1104 (1970).
[8] Moberly, W. R., *Comp. Biochem. Physiol.*, **27**, 21 (1968).
[9] Jansky, L., *Acta Univ. Carolinae, Biologica*, 1 (1965).
[10] Layne, J. N., and Benton, A. N., *J. Mamm.*, **35**, 103 (1954).
[11] Waterman, A. J., *Chordate Structure and Function* (Macmillan, New York, 1971).
[12] Schmidt-Nielsen, K., Kanwisher, J., Lasiewski, R. C., Cohn, J. E., and Bretz, W. L., *Condor*, **71**, 341 (1969).
[13] McLean, F. C., and Urist, M. R., *Bone* (Univ. Chicago Press, Chicago, 1968).
[14] Enlow, D. H., and Brown, S. O., *Texas J. Sci.*, **3**, 187 (1958).
[15] Enlow, D. H., and Brown, S. O., *Texas J. Sci.*, **2**, 186 (1957).
[16] Currey, J. D., *Palaeontology*, **5**, 238 (1962).
[17] Tarlo, L. B., and Mercer, J. R., *Sixteenth Symp. Vert. Palaeont. Comp. Anat.* (*Reading*) (1968).
[18] Auffenberg, W., *Animal Kingdom*, **73**, 19 (1971).
[19] Schaller, G. B., *E. Afr. Wildl. J.*, **6**, 95 (1968).
[20] Wright, B. S., *J. Wildl. Mgmt*, **24**, 1 (1960).
[21] Golley, F. B., *Amer. Zool.*, **8**, 53 (1968).
[22] Blair, W. F., *The Rusty Lizard* (Univ. Texas Press, Austin, 1960).
[23] Schaller, G. B., *The Deer and the Tiger* (Univ. Chicago Press, Chicago, 1967).
[24] Jordan, P. A., Botkin, D. B., and Wolfe, M. L., *Ecology*, **52**, 147 (1971).
[25] Wagner, F. H., in *Ecosystem Concepts in Natural Resource Management* (edit. by Van Dyne, G. M.), 284 (Academic Press, New York, 1969).
[26] Kleiber, M., *The Fire of Life* (Wiley, New York, 1961).
[27] Dasmann, R. F., and Mossmann, A. S., *J. Wildl. Mgmt*, **26**, 262 (1962).
[28] Myers, N., *Intern. Wildl.*, **2**, 34 (1971).
[29] Hornocker, M. G., *Wildl. Monog.*, 21 (1970).
[30] Voorhies, M. R., *Contr. Geol. Spec. Paper, Univ. Wyoming*, 1 (1969).
[31] Shotwell, J. A., *Ecology*, **36**, 332 (1955).
[32] Clark, J., Beerbower, J. R., and Kietze, K. K., *Fieldiana, Geol. Mem.*, 5 (1967).
[33] Boonstra, L. D., *Ann. S. Afr. Mus.*, **56** (1969).
[34] Boonstra, L. D., *Ann. S. Afr. Mus.*, **42**, 108 (1954).
[35] Boonstra, L. D., *Ann. S. Afr. Mus.*, **42**, 65 (1954).
[36] Russell, D. A., *Nat. Hist. Pap. Nat. Mus. Canad.*, 36 (1967).
[37] Osborn, H. F., *Bull. Amer. Mus. Nat. Hist.*, **35**, 733 (1917).
[38] Ostrom, J. H., and McIntosh, J. S., *Marsh's Dinosaurs* (Yale Univ. Press, New Haven, 1966).
[39] Freeman, M. M. R., *J. Wildl. Mgmt*, **35**, 103 (1971).
[40] Sikes, S. K., *The Natural History of the African Elephant* (American Elsevier, New York, 1971).
[41] Bell, W. A., *Bull. Canad. Geol. Survey*, 13 (1949).
[42] Kruuk, H., and Turner, M., *Mammalia*, **31**, 1 (1967).
[43] Hirst, S. M., *Zool. Afr.*, **4**, 199 (1969).
[44] Mitchell, B. L., Shenton, J. B., and Uys, J. C., *Zool. Afr.*, **1**, 297 (1965).
[45] Russell, D. A., *Nat. Sci. Pub. Paleont. Nat. Mus. Canad.*, 1 (1970).
[46] Colbert, E. H., and Russell, D. A., *Novitates*, 2380 (1969).
[47] Russell, D. A., *Canad. J. Earth Sci.*, **6**, 595 (1969).
[48] Golley, F. B., Petrides, G. A., Rauber, E. L., and Jenkins, J. H., *J. Wildl. Mgmt*, **29**, 442 (1965).
[49] Avery, R. A., *J. Anim. Ecol.*, **40**, 351 (1971).
[50] Laws, R. M., and Parker, I. S., in *Comparative Nutrition of Wild Animals* (edit. by Crawford, M. A.), 319 (Academic Press, London, 1968).
[51] Worsley, T. R., *Nature*, **230**, 318 (1971).
[52] Russell, D. A., *Canad. Geog. J.*, **83**, 204 (1971).