PHYSIOLOGY AND MIGRATION OF NORTH SLOPE DINOSAURS

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ABSTRACT

How did north Alaskan dinosaurs survive polar winter? The physiological adaptations of cold-water leatherback turtles cannot be applied to terrestrial dinosaurs. Migrating far to the south would have cost too much energy. High aerobic metabolisms would have allowed dinosaurs to tolerate dark winters and to migrate in order to find the best regional conditions.

INTRODUCTION

The Late Neogene Arctic has been dominated by mammals that use high rates of internal heat production to keep warm and active in the dark, cold winters. How did dinosaurs inhabiting the North Slope of Alaska cope with Late Cretaceous winters? Three primary models have been proposed. In one model dinosaurs are characterized as mammal-like, tachymetabolic endotherms (Paul, 1988). Another model is gigantothermy, a recent variant of reptilian physiological models (Spotila et al., 1991). Migration models come in two forms. One model has reptilian dinosaurs undertaking winter migrations to southerly regions that are warm and sunny enough for them to stay active (Parrish et al., 1987). In the other model either reptile or mammal-like dinosaurs moved south in order to find enough winter forage, then moved north to exloit high floral growth in the land of the midnight sun.

A consensus places the North Slope and other western North American dinosaur sites 5° to 15° latitude farther north than they are today (see Paul, 1988). The Late Cretaceous paleomagnetic pole was just north of the Bering Strait; the paleospin pole has been plotted just north of Prince Patrick Island (Paul, 1988, Fig.1).

Fossil woods show that -20° to -30 °C temperatures did not afflict a barren-ground tundra fauna on the North Slope ~70 m.y. ago. However, because the sun was below the horizon for most or all of the day, a key source of heat for bradymetabolic ectotherms was not available. The North Slope paleoclimate has been described as cool or cold temperate, and mean deep-winter paleotemperatures have been estimated from 10° down to -11 °C by various workers (see Paul, 1988; also Parrish et al., 1987; Spicer and Parrish, 1990; Horrell, 1991). Freezing conditions probably occurred at least occasionally and may have been common. The apparent absence of small to gigantic bradymetabolic amphibians and reptiles (Paul, 1988; Clemens and Nelms, 1993) may confirm that Campanian-Maastrichtian North Slope winters were cold temperate. Winter storms would have thermally loaded North Slope dinosaurs with chilling wind-chill factors and evaporative cooling (Paul, 1989).

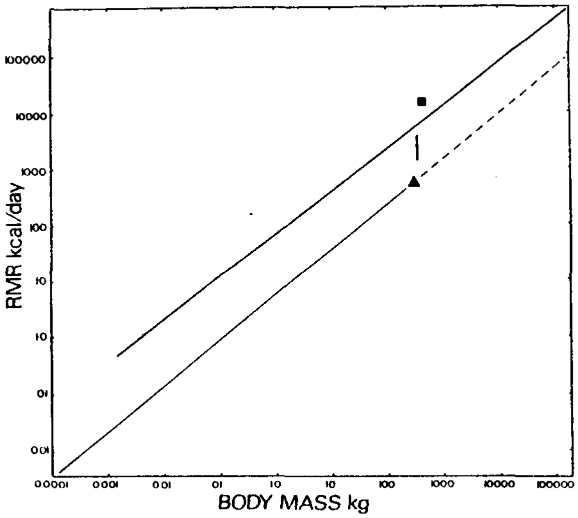

Fig.1. Comparison of resting metabolic rates of reptiles and mammals. Allometric expressions are the Kleiber curve for eutherian mammals (heavy line, RMR = 70 $M^{0.75}$, 38 °C), and reptiles including giant marine and terrestrial turtles (light line, RMR = 5.5 $M^{0.8}$, 24-30 °C, R = 0.9840, N = 135). RMR for Weddell seal indicated by square (Lockyer, 1981), for leatherback sea turtle by triangle (less consistent and higher readings in Spotila et al. [1990] indicated by vertical bar). The resting metabolism of a giant reptile is an order of magnitude lower than that of a large mammal.

How far did North Slope dinosaurs have to move in order to reach regions warm enough to support a reptilian thermoregulatory system, and/or to sustain high floral growth in the winter? A number of workers have suggested the Arctic Circle, which may have been in northern Alberta at that time (Paul, 1988; Wolfe and Upchurch, 1986), as the target latitude. However, that latitude was only about 5 °C warmer than the North Slope (Wolfe and Upchurch, 1986); and winter sun was not available. The transition zone from a deciduous boreal to a semitropical, fully evergreen southern flora was from central Alberta to Montana (Paul, 1988; Wolfe and Upchurch, 1986.) Leafy winter plants were too scarce to attract a large migrant population in the northern portion of the transition zone. Hotton (1980) suggested that dinosaurs migrated 3,000 km south to the Alberta-Montana border. This may have been far enough south to find abundant winter fodder but not to keep a reptile warm. To do the latter may have required reaching 55° N., where the sun shines for nearly 5 hours and rises 11° above the horizon at winter solstice. This latitude may have been at the Montana-Wyoming border at that time--some 4,500 km from the North Slope (including detours around obstacles, equal to a trip between New York and Los Angeles).

WHY GIGANTOTHERMY FAILS TO EXPLAIN NORTH SLOPE DINOSAURS

Leatherbacks (*Dermochelys coriacea*), the giant sea turtles that helped inspire the gigantothermy model, often inhabit waters as cold as 7 °C, where they maintain water-body core temperature differentials of 18+ °C. Spotila et al. (1991) asserted that the heat loss from leatherbacks in highly conductive but nonfreezing waters is as severe as that encountered by arctic dinosaurs. This is correct only if dinosaurs never experienced freezing skin temperatures.

Spotila et al. (1991) measured what they believed were high metabolic rates (MR's) in nesting leatherbacks (Fig.1). This led them to claim that there is a convergence in the MR's and thermoregulation of big reptiles and mammals. However, Lutcavage et al. (1990) consistently measured typically reptilian resting MR's in leatherbacks--values 20 times lower than those observed in seals (Fig.1). Core body temperatures only 1 °C above the 18 °C temperature of water in 1- to 6-ton basking sharks (Carey et al., 1971) indicate that they produce only a fraction of the heat generated by whales, which use very high MR's to maintain high body temperatures in cold waters (Lockyer, 1981). A gecko-to-leatherback curve confirms that the MR's of big bradymetaboles are far below those of tachymetabolic mammals (Fig.1).

There is some evidence that, like some mammals, leatherbacks can produce a modest amount of auxiliary heat with thermogenic fat (Goff and Stenson, 1988). Leatherbacks keep warm by using fat insulation and counter-current heat exchangers in their fins to retain the most amount of heat produced by fat and/or propulsive muscles as they constantly cruise. Land animals cannot benefit as much from the heat of locomotion because they do not perpetually cruise 24 hours a day, and they do not produce much locomotory heat in their main bodies. Spotila et al. (1991) acknowledge that even fat-insulated arctic dinosaurs with reptilian MR's could not have maintained elevated body core temperatures in the winter. This means that large, bradymetabolic polar dinosaurs would have experienced severe drops in body-core temperatures and become torporous. Too big to seek shelter, they would have been at risk of frostbite and tissue death.

Leatherbacks move up to 10,000 km per year between cold and warm waters at speeds of 3 to 5 km/h (Spotila et al., 1991); however, there is less to this performance than first appears. Swimming leatherbacks expend six times less energy to move a kilometer than do most land animals of similar size (Seymour, 1982). A dinosaur with a leatherback-like energy budget could, therefore, migrate only 1,700 km per year; and its aerobically sustainable speed would be only 0.5 to 0.8 km/h.

Gigantothermic leatherbacks live in a nonfreezing, thermal environment dramatically different from the North Slope paleoclimate; they migrate at low cost; and they have a body and thermal structure very different from dinosaurs. The marine leatherback thermodynamic model is not, therefore, transferable to terrestrial dinosaurs.

WHY ULTRALONG MIGRATIONS DO NOT EXPLAIN NORTH SLOPE DINOSAURS

Spotila et al. (1991) calculated that bradymetabolic animals can migrate at least as far as tachymetaboles. However, in doing so they neglected to consider the sustained speeds at which such animals can move. A moderate pace is very energy-expensive, so much so that walking 30 to 50 km at a speed of 3 to 5 km/h is hard work. Bradymetabolic reptiles aerobically cruise at speeds of only 0.4 to 2 km/h (Fig.2). Faster sustained speeds are beyond their limited aerobic capacity (Bennett and Ruben, 1979). Anaerobic power cannot be used to sustain fast walking because it is extremely energy inefficient, can be sustained for only an hour or less, and tends to poison the subject. The evolution of long erect limbs does not allow fast, efficient walking because the cost of locomotion is similar in sprawling reptiles and in mammals of the same size (Fedak and Seeherman, 1979). Because locomotory energy costs and maximal sustained MR's both scale close to the 3/4 power (Fedak and Seeherman, 1979; Blaxter, 1989), large size does not allow dramatically faster walking speeds. The Spotila et al. (1991) projection that a dinosaur with reptilian energetics can migrate 50 km/day, or 2.8 to 4.2 km/h (allowing 6 to 12 hours rest/day), is therefore unrealistic.

High-capacity respiratory systems that work during locomotion cannot by themselves produce aerobic scopes high enough to sustain speeds over 2 to 3 km/h. Circulatory pressures also must be high in order to deliver oxygen to the muscles. High-pressure hearts have to work hard even during nontorporous rest: this helps explain why vertebrates with high aerobic scopes always have high resting MR's. A survey of mammal and dinosaur speeds shows cruising speeds of 2 to 10 km/h (Fig.2). The only viable explanation is that the maximal and minimal aerobic MR's of dinosaurs were well above those of reptiles.

Consider a migrating juvenile hadrosaur of 15 kg. Its cost of moving 6,000 to 9,000 km was about 100,000 to 150,000 kcal. If it had reptilian metabolics, its total yearly energy budget would have been only some 50,000 kcal. It probably is impossible for animals to assume migratory energy loads many times larger than their total energy budgets. Mammalian-level energetics are an order of magnitude higher and can cover the cost of very long migrations

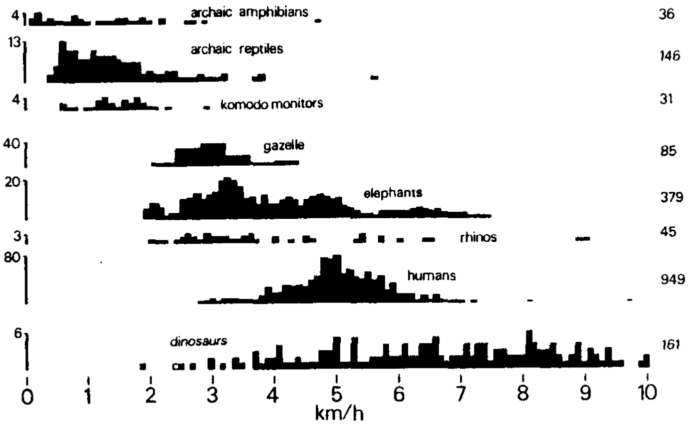

Fig.2. Observed cruising speeds in reptiles, mammals, and dinosaurs. Dinosaurs are Cretaceous tridactyl footed juveniles and adults and a large ceratopsid (open square) similar to inhabitants of the North Slope. Speeds of humans timed directly, other mammals from motion pictures (migrating gazelle from Pennycuick, 1975), fossil forms estimated from trackways per Alexander (1989). Number of observations at given speed indicated on the left, total sample sizes indicated on the right. Mammals and dinosaurs cruise at higher speeds than reptiles.

If North Slope dinosaurs did have sufficient aerobic power to migrate long distances, would they have migrated 6,000 to 9,000 km/yr in search of the best seasonal food sources? The longest terrestrial migrations are undertaken by barren-ground caribou, which move about 5,000 km/yr (Fancy et al., 1989). Barren-ground caribou are specialized migrators with the most energy-efficient legs known (Fancy and White, 1987). The relatively heavy legs of hadrosaurs and ceratopsids probably were less efficient. This implies that the migratory performance of North Slope dinosaurs was not superior to that of caribou. Besides, even caribou remain within a region only ~400 km across (Fancy et al., 1989); no land mammal escapes arctic winters by migrating far to the south. The failure of any land mammal to move over 5,000 km/yr suggests that longer journeys are too costly even for the most aerobically capable tetrapods. It is, therefore, improbable that dinosaurs migrated continent-spanning distances to warmer climes.

DIGESTIVE FERMENTATION

Parrish et al. (1987) suggested that herbivorous polar dinosaurs were heated by digestive fermentation. Fermentation releases only 3 percent of the heat available in fodder in nonruminants (Blaxter, 1989), so it would have provided little warmth to reptilian dinosaurs (Paul, 1989).

TACHYMETABOLIC ENDOTHERMIC ARCTIC DINOSAURS

Are analogs for dinosaurs better than marine turtles available? Northern ungulates share with ceratopsids and hadrosaurs long, erect, digitigrade, hooved legs, and well-developed dental batteries. If polar dinosaurs converged with ungulates by producing lots of heat when at rest in order to maintain high circulatory pressures, they would have easily tolerated Late Cretaceous arctic winters. Subcutaneous fat could have provided insulation and additional heat if it was thermogenic. If smaller arctic dinosaurs were not insulated, hibernation was a viable option. High aerobic scopes would have given arctic dinosaurs the power needed to walk far to find the best winter conditons.

CONCLUSIONS

Using sea turtles and ultralong migrations to explain North Slope dinosaurs results in complicated, speculative, and unsatisfactory conclusions. The absence of amphibians and reptiles confirms that low MR's probably were not suitable at that place ~70 m.y. ago. Tachymetabolic endothermy is a proven metabolic system that fully explains arctic dinosaurs. Heavy fat reserves built up during the summer floral flush could be used to supplement a low-quality winter browse of twigs, bark, and rhizomes (Brouwers et al., 1987). Winter mortality probably was high, especially as energy supplies dwindled in late winter. Tyrannosaurs exploited winter conditions by preying on stressed herbivores. Migrations probably were limited to well under 5,000 km/year. Dinosaurs may have summered in interior highlands and wintered along the coast. Also possible were modest north-south parallel displacements along the coastal floodplain. Such migrations exploited--rather than escaped--the best arctic winter conditions. Being a simple and satisfactory hypothesis, the tachymetabolic endothermic model best fits the requirements of Ockham's razor. The cold resistance of arctic dinosaurs casts doubt on the possibility that an impact-induced cold snap was responsible for an extinction event that wiped out all of the dinosaurs but left ectothermic reptiles extant (Brouwers et al., 1987; Paul, 1988; Clements and Nelms, 1993). If dinosaurs did not migrate away from winters, the shortage and low quality of winter browse may have prevented their populations from growing to the point where they fully exploited the summer floral productivity of the North Slope vegetation. They probably put heavy pressure on winter floras. This suggests that the North Slope paleoflora emphasized growth over anti-browsing adaptations in the summer, and emphasized the latter in the winter.

Conditions on the Late Cretaceous North Slope appear to have been severe enough to enforce a faunal composition similar to today's--an absence of ectothermic tetrapods, tachymetabolic endothermy in the dominant tetrapods, and great annual north-south migrations undertaken only by flying endotherms.

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