

## Migration

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To migrate long distances on land requires three characteristics: sufficiently large size, long striding legs, and sufficient aerobic power. Mice, for example, cannot traverse long distances, nor can large snakes and turtles. Migrating on land is harder than migrating in the sea or in the air because the energy cost of moving a given distance is highest on land and least in water (swimming is up to a dozen times more efficient than walking). Also, sea creatures can take advantage of ocean currents. Many marine fish, reptiles, and mammals migrate very long distances, sometimes across entire oceans. Insects, bats, and birds also migrate great distances, in extreme cases from pole to pole. In comparison, land migrations are rather modest. The greatest terrestrial migrators are polar mammals, who are under strong pressure to seek out the best seasonal conditions. Caribou trek up to 5000 km a year, but this movement is confined to a rather small area of 400 km across. Polar bears

move up to 2500 km a year, partly in the water. In lower latitudes strong wet-dry seasons can inspire seasonal movements. The annual migrations of saiga and Serengeti gnu cover up to 1000 km round-trip. The long migrations often attributed to plains bison and African elephants before European disruption are controversial. It is notable that caribou and gnu are specialized for migrating because they have the most energy-efficient legs known. In herding animals the size of the juveniles may be a limiting factor; migrating ungulate calves weigh at least 15 kg. Carnivores do not migrate with their herbivore prey; rather, they exploit herbivores as they move through their territory. The latter fact exposes the point that migrations are dangerous. The tendency of land animals to migrate in mass aggregations at speeds above 2 or 3 km/hr reduces their vulnerability to predation but increases the possibility of mass disasters at overcrowded water crossings. Migrations are energy-taxing and arduous journeys that are undertaken only if there are compelling advantages to doing so. This may be why few mammals migrate, and no reptiles do so.

Migrations in the fossil record are difficult to identify but are suggested by the following taphonomic characteristics. Migrating animals often take advantage of the clear run provided by shorelines (Cohen *et al.*, 1993). Therefore, mass, unidirectional trackways paralleling a shoreline are suggestive of migratory movements, especially if they were made at 2 or 3 km/hr or more. Mass aggregations can be killed by volcanic events, fast-acting epidemics, or suffer high mortality at river crossings. Mass death assemblages that are not attributable to gradual accumulation (as in droughts) are therefore strongly suggestive of migratory habits (Coombs, 1990). If a dinosaur species was limited in distribution, it probably did not migrate very far. A wider distribution is compatible with seasonal migrations but may simply indicate dispersed habitation, as per the circumpolar distribution of wolves and moose.

Almost all the larger dinosaurs had the long striding legs needed to migrate moderate distances (Fig. 1; the big-clawed, fat-bellied THERIZINOSAURS and short-limbed ANKYLOSAURS may have been exceptions). The 2–10 km/hr speeds recorded by the majority of dinosaur trackways are high enough for long-distance movements (Paul, 1994). No dinosaur had the ex-

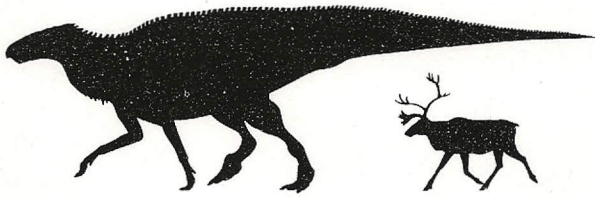


FIGURE 1 The great size of hadrosaurs may have enhanced their migratory abilities, but they lacked the extremely energy-efficient legs that make gracile caribou the longest ranging modern land animals. Figures drawn to same scale.

tremely gracile, highly energy-efficient legs of specialized long-range migrators.

The traditional view of dinosaurs as REPTILES, many semiaquatic, tended to suppress speculation that dinosaurs migrated. An exception was Huene, who suggested that bone beds of Late Triassic prosauropods were death assemblages that recorded mass migrations across a central European desert. This scenario has been challenged by recent work indicating that the bone beds accumulated gradually (Coombs, 1990).

The giant SAUROPODS of the Late Jurassic Morrison Formation have been considered potential migrators because they combined great energy needs with a seasonally dry habitat and because they may have roamed to the bordering highlands in search of large cobbles suitable for GASTROLITHS. These speculations are plausible, but there is little direct fossil evidence that sauropods migrated. Parallel sauropod Jura-Cretaceous trackways following shorelines hint at migratory behavior.

The best evidence for migrating dinosaurs are the extensive bone beds of Late Cretaceous HADROSAURS and CERATOPSIDS recently discovered in western North America from Texas to Alaska, along what used to be the western, north-south running coast of an ancient interior seaway (Hotton, 1980; Horner and Gorman, 1988; Currie, 1989). It is difficult to explain the accumulations as gradual; instead, they appear to be the result of sudden mass deaths, attributable to vulcanism or drownings at river crossings. Numbers of individuals involved in each event range from the hundreds to the tens of thousands. Age range in the bone beds is from moderately sized (and therefore mobile) juveniles to adults (the implication is that smaller juveniles either did not migrate or did so

independently). The provincial organization of western coastal dinosaur faunas into nearshore, shore, and interior, as well as distinct north-south populations (Lehman, 1996), suggests that the straight-line range of any migrations was limited in most or all cases.

The last point contradicts suggestions that Alaskan dinosaurs moved far south to avoid the polar winter. In the Late Cretaceous northern Alaska was as little as  $10^\circ$  from the north paleopole, and the Arctic Circle may have been near or in northern Alberta (Fig. 2). It has been argued that the high-latitude dinosaurs were migrating north-south in order to escape winter conditions that, although much milder than today, included extended dark, cool and perhaps freezing temperatures, and floral dormancy near the poles. Similar journeys have been suggested for Australian dinosaurs living near the south paleopole of the time. In this view dinosaurs moved toward the pole to enjoy the abundant floral growth of long summer days and then to lower latitudes in order to find winter food or to seek the warmth needed by dinosaurs with reptile-like energetics. In the latter scenario, Hotton (1980) portrayed high-latitude dino-

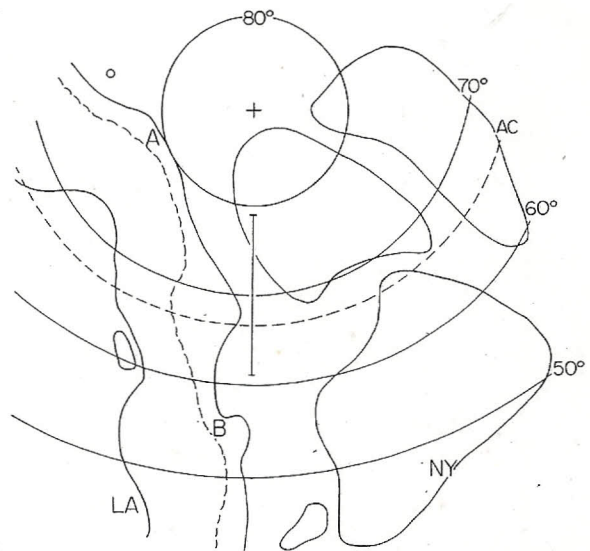


FIGURE 2 (A) North slope and (B) Montana-Wyoming indicate the possible north-south zone of migration of Late Cretaceous dinosaurs along the northwestern coast of the Niobrara seaway (cartographic distortion causes the coastal plain to appear straight rather than properly curved). The paleomagnetic pole is indicated by the open circle; the calculated spin pole by the cross. The future locations of New York and Los Angeles are marked. Scale bar = 2000 km.



saur as "happy wanderers" that moved up to 6000 km a year. To move from northern Alaska far enough south to warm reptilian bodies in the winter may have required even further movements, up to 9000 km round-trip (equal to a New York to Los Angeles round-trip). However, such long migrations may have posed insurmountable energy problems. The cost for a juvenile hadrosaur or ceratopsid of 500 kg to move 6000–9000 km was about 900,000–1,400,000 kcal. The annual active energy budget of the same juvenile reptilian dinosaurs would have been only 800,000–1,500,000 kcal, too low to power such a long trip. Nor could reptilian dinosaurs have produced enough sustainable aerobic exercise power to move at the 2 or 3 km/hr speeds typical of migrating land animals. If dinosaurs had mammal-like energetics, then they would have had the power needed for very long migrations, at least in principle. The great size of many dinosaurs also facilitated long movements. In this view the consensus that some large dinosaurs migrated is supported.

However, scenarios that portray dinosaurs as greater migrators than mammals may be excessive, and it is probable that the great majority of dinosaurs did not migrate at all. The absence of specialized, unusually energy-efficient limbs may have limited those large dinosaurs that did migrate to about 500 km straight-line one way each year. In this case, a minority of herbivorous dinosaurs near and far from the poles migrated in order to seek out the best intra-regional conditions, and to avoid overexploiting the food resources in one place, rather than to span part of a continent to find the best seasonal climatic regime (Paul, 1994). In this scenario improvements of high-latitude winter conditions were at most modest and alleviated but did not solve major thermal and food problems.

See also the following related entry:

BEHAVIOR

## References

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