How far did dinosaurs really migrate, and how hot do elephants really get?

Some points presented in the paper by Rowe et al. (Rowe et al., 2013) require discussion.

Rowe and colleagues presume that multitonne Late Cretaceous high latitude hadrosaurs migrated thousands of straightline kilometers each year to avoid severe arctic winter conditions. However, movements over such extreme distances are limited to marine and aerial creatures in the contemporary world, with many traveling many degrees of latitude to experience warm weather year round. This is practical for fliers and especially swimmers because their transport costs per unit distance traveled are modest. In contrast the longest ranged living land migrators, such as gnu and even caribou, do not move a straightline distance of more than a few hundred kilometers (Fancy et al., 1989), seasonal movements are always subregional efforts to find optimal conditions at a given time and place in the general area, and no modern land walker migrates north–south far enough to evade winter climates. This is probably because animal land locomotion is so energy inefficient that continent-spanning movements are too arduous and cost too much to be worth any gain, are excessively dangerous, would involve problems with feeding, and are hindered by geographic obstacles (Paul, 1988; Paul, 1994; Paul, 2012).

Specific to arctic hadrosaurs, most of the high latitude remains are those of juveniles too small to keep up with adults on long trips (Fiorillo, 2004). The taphonomic evidence indicates that most of the fossils were formed as the result of late winter/early spring riverine floods from mountain snowmelts (Fiorillo et al., 2010). If so, then the herds were already near or on the Alaskan North Slope as the winter ended, and lacked the time to have moved up far from the south. This is verified by Alaskan hadrosaur bone histology showing they were perennial residents that tolerated the winters, and were a distinct population from more southerly hadrosaurs whose bone microstructure is markedly different (Chinsamy et al., 2012). It is therefore well established that polar hadrosaurs were year-round residents (Paul, 1998; Paul, 1994; Paul, 2012; Fiorillo, 2004; Fiorillo et al., 2010; Chinsamy et al., 2012). It is similarly known that some giant polar southern hemisphere dinosaurs had to tolerate winter and cold and dark because there was no land to the north to migrate on (Bell and Snively, 2008; Paul, 2012). The possibility that polar hadrosaurs, or any other land animals, migrated thousands of kilometers must be ranked as very low and probably impossible, so such fictional creatures should no longer be modeled as plausible unless supporting fossil evidence is produced.

Presuming the polar hadrosaurs were permanent residents, then they rarely or never experienced warm conditions even in the summers, which were cool and cloudy (Spicer and Herman, 2010). However, giant hadrosaurs lived at all latitudes during a global warm period, so modeling their thermoregulation under high heat loads is valid. Rowe and colleagues (Rowe et al., 2013) logically used the largest, low latitude land animals available, elephants, to help understand the thermal performance of similar-sized and probably tachyenergetic dinosaurs that experienced high ambient temperatures. What is not clear is whether the captive *Elephas maximus* they utilized experienced the extreme heat loads that may be tolerated by *Loxodonta africana* living in their most hyperthermally acute habitats. Elephant herds of the coastal Namib Desert have been documented crossing expansive, shade-barren flats in daytime when air temperatures were probably above their body temperatures; their daily range can exceed 100 km and they can go without water for days (Viljoen, 1992; Bartlett and Bartlett, 1992) (D. Bartlett, personal communication). It is possible that these elephants of the arid Skeleton Coast are adapted to remain active under higher daytime heat loads than data on captive forest elephants and modeling may suggest is feasible. But they have never been sufficiently studied to determine exactly what they experience, and how they cope with intense heat. To fully understand the thermoregulation of gigantic, tachyenergetic animals will require detailed field observation of the biggest living land animals residing in the hottest habitats to discover how they do it. That, of course, will be a difficult and expensive experiment to conduct.

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Response to 'How far did dinosaurs really migrate, and how hot do elephants really get?'

The results of our study (Rowe et al., 2013) demonstrated a functionally significant relationship between heat storage and submaximal exercise in Asian elephants (*Elephas maximus*), which was sensitive to seasonal variations in radiant environmental heat. In addition, we modeled behavioral regulation (switching from diurnal to nocturnal activity) of heat storage during prolonged activity (seasonal migrations) in elephants and presumably endothermic polar hadrosaurs (*Edmontosaurus*). Furthermore, based on post-exercise behavioral observations, we discussed the importance of access to water for increased heat loss in a hot environment.

Gregory Paul expressed two general concerns. Firstly, he questioned the existence of seasonal migrations of distances greater than 1000 km, particularly in polar dinosaurs. Secondly, he questioned the use of captive Asian elephants (forest elephants) to model the thermoregulatory constraints on diurnal activity in full sun. In addition, he suggested that desert-dwelling African elephants (*Loxodonta*

africana) might be (physiologically) adapted for activity in full sun and therefore not subject to the thermoregulatory constraints on activity that we proposed in gigantic species.

Fossil evidence indicates that hadrosaurs were widely distributed in North America at low and high latitudes. Gregory Paul is correct in pointing out the evidence that high latitude populations may have been permanent polar residents (Bell and Snively, 2008; Chinsamy et al., 2012). However, it is likely that large ectothermic dinosaurs would succumb to a lethal level of hypothermia during exposure to several months of cold and dark polar winters (McNab and Auffenberg, 1976; Spotila et al., 1973). Therefore, while our model did not prove endothermic metabolism in hadrosaurs, permanent residency at high latitudes strengthens our argument for endothermic metabolism in polar hadrosaurs.

Furthermore, the absence of adult hadrosaurs in the fossil record, and the presence of juvenile polar hadrosaurs that were too small to escape from late spring flooding, provides evidence that at times adult polar dinosaurs were likely required to walk long distances to escape from catastrophic environmental events. We did not model heat storage in endothermic hadrosaurs during activity in cool environments. However, it is likely that our heat storage model in Asian elephants during the cool seasons – November and February trials at mean air temperatures of 13.7±3.4 and 16.2±4.0°C, respectively – are suitable models for adult endothermic hadrosaurs fleeing from spring floods.

Indeed, our models indicate that in cool conditions adult hadrosaurs could have walked approximately 21–36 km away from rising flood waters before the onset of a lethal core body temperature.

Gregory Paul is likely correct in assuming thermoregulatory variations between active Asian (forest) and African (savannah) elephants. However, heat storage during activity is a function of small surface area to body mass ratio, the rate of metabolic heat production and radiant environmental heat. Active metabolic heat production is similar in Asian and African elephants (Langman et al., 2012). The strength of our heat storage model is measured rates of active metabolic heat production (Langman et al., 2012) in the same Asian elephants we used in our study (Rowe et al., 2013). In addition, exercise trials were conducted before 10:00 h or after 17:20 h CDT, which is similar to the diurnal activity patterns in elephants (Ngene et al., 2009), including desert-dwelling elephants of the Skeleton Coast (Leggett, 2009; Leggett, 2010).

Indeed, desert-dwelling elephants of the Skeleton Coast are presented with thermoregulatory challenges, primarily exposure to direct solar radiation. Gregory Paul suggests that these challenges might be met by unique physiological adaptations that allow desert-dwelling elephants to remain active during high daytime heat loads.

Because palatable vegetation is frequently located at long distances from water sources, desert-dwelling elephants often walk longer distances than other African elephant populations (Leggett, 2009). Gregory Paul reports daily walks in desert-dwelling elephants of greater than 100 km in full sun (Viljoen, 1992; Bartlett and Bartlett, 1992) (see reference to personal communication from D. Bartlett). However, Bartlett and Bartlett (Bartlett and Bartlett, 1992) actually reported daily walks of up to 72.4 km and did not specify whether these movements were recorded during diurnal or nocturnal activity. A 72.4 km walk over 12 h could be performed at approximately 1.6 m s^{-1}, the same average walking speed recorded in African elephants during seasonal migrations of approximately 95 km (Ngene et al., 2009) and similar to the range of walking speed, from approximately 1 to 1.5 m s^{-1}, that minimized the energetic cost of locomotion in elephants (Langman et al., 2012). Furthermore, in the hot dry season, desert-dwelling elephants switched from diurnal to nocturnal walking activity (Leggett, 2010) and night-time ambient air temperatures can drop to approximately 7–10°C, well below the range of ambient air temperatures that reduced a potential lethal level of heat storage in active elephants (Rowe et al., 2013).

Gregory Paul also suggested that desert-dwelling elephants can go without water for days. Seasonal changes in the availability of water determine the movement and activity in desert-dwelling elephants (Leggett, 2009). The ephemeral Hoanib and Hoarusib River basins traverse the Skeleton Coast from east to west and serve as linear oases, where water is usually available throughout the year at spatially separated locations (Leggett, 2006). Contrary to common belief, desert-dwelling elephants spend a greater portion, approximately 10%, of their daily activity budget at water sources compared with other African elephant populations in Tanzania, Uganda and Zimbabwe, which spend approximately 3–5% of their daily activity budget at water sources (Leggett, 2009). In addition, as recorded in other elephant populations (Moss, 1988), at ambient air temperatures greater than 40°C, in the absence of standing water, adult desert-dwelling elephants use their trunks to extract water from their pharyngeal pouch and spray it over their back and ears (Leggett, 2004). Similarly, juvenile elephants used urine-soaked sand to perform the same behavior (Leggett, 2004). The appearance of going without water for days is likely an artifact of behavioral observation sample interval and not a unique physiological adaptation in desert-dwelling elephants. Therefore, rather than uniquely physiologically adapted for survival in a hyperthermal environment, desert-dwelling elephants likely utilize the same behavioral choices described in our study (Rowe et al., 2013) to meet the thermoregulatory challenges of activity in a hot environment.

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