Heat loss from giant extinct reptiles

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There is disagreement in the literature about the relative rates of heat loss from a large animal surrounded by either air or water. Here, it is shown that, in most circumstances, the rate at which heat is lost by a large body is significantly greater when it is immersed in water than when it is surrounded by air, assuming that the two fluids are at the same temperature. The only circumstance when this may not apply is when comparing air with fresh water when both are at a temperature somewhere between 0 °C and 6 °C, the animal is still and water or air currents are negligible. Under these conditions, free convection in water is weak or non-existent, and so the combined effect of conduction and free convection in air becomes comparable to or even greater than that of conduction alone in water. However, in these circumstances, radiation is the dominant mode of heat loss to both media, and so heat losses are approximately the same in both air and water.

Keywords: dinosaurs; conduction; convection; radiation; heat transfer; thermoregulation

1. INTRODUCTION

The largest extant land animals are elephants. It is generally considered that their large size has required the evolution of behavioural and physiological traits to aid in the dissipation of metabolically produced heat (Wright 1984; Williams 1990; Phillips & Heath 1992). The best-known example of such a trait is the characteristically large ears of African elephants. Consideration of elephants has naturally led to speculation as to how giant extinct animals such as dinosaurs, which could have been over ten times as heavy as elephants, dissipated sufficient metabolic heat to avoid overheating (Paladino *et al.* 1997; Alexander 1998; O'Connor & Dodson 1999). The risk of overheating would be reduced if, as many believe, dinosaurs had lower metabolic rates per unit mass than extant mammals (Reid 1997). Indeed, some recent work (Seebacher *et al.* 1999) suggests that large crocodiles are useful models for thermoregulation in dinosaurs, and that the behavioural modification of microclimate (specifically moving in and out of water) is the key to understanding how giant dinosaurs avoided overheating.

When discussing how giant dinosaurs managed to avoid overheating, Alexander (1998) suggested that the difference in the rates of heat loss between air and water is trivial for animals with a mass greater than 100 kg, which is less than 5% of an adult elephant's mass. This claim is backed up by a reference to Bell (1980). If this is correct, then it will demand a considerable rethinking of our understanding of the effect of environment on the heat balance of very large animals. For example, O'Connor & Dodson (1999) suggested that 'dinosaurs with high metabolic rates could survive if they lived in or had access to standing water as a heat sink, under conditions in which the same dinosaurs on land would overheat'. Similarly, Seebacher *et al.* (1999) suggested that 'access to shade or water must have been crucial for the survival of large dinosaurs in low latitudes'. In view of the seeming contradiction between these views and that of Alexander (1998), this paper will re-examine and develop the work of Bell (1980). In particular, I will seek to

identify the ecological circumstances in which a giant ectotherm could achieve increased rates of heat loss by immersion in a large body of water.

2. AN IMPORTANT SIMPLIFICATION FOR GIANT ECTOTHERMS

There are two components to heat exchange between an animal and the environment: flow of heat between the animal's core and the skin, and flow of heat between the skin and the environment. Turner (1987) argued, on the basis of mathematical modelling, that for very large animals the second of these is so much greater than the first can safely be neglected. To put it another way, the external thermal resistance is much greater than the internal thermal resistance for these very large animals. Turner (1987) illustrates (fig. 9) that 'very large' in this context means an animal with a body over 2 m across, which translates as anything bigger than an elephant, and also that this rule still applies to such large animals even if the thermal resistance to heat flow between the skin and the environment is decreased by a factor of 100, compared with when standing in still air. Below, I will demonstrate that standing in water or in a strong wind can considerably reduce the external thermal resistance, but generally not by as much as a factor of 100. Hence, because I am considering very large animals without any fur or feather covering, I will consider only the aspect of thermal resistance describing heat flow between the animal's skin and the environment. This is equivalent to making the assumption that thermal resistance to heat flow within the animal is trivial in comparison.

3. BELL'S ARGUMENT

Bell argues that for a body cooling in water, the external thermal resistance is given by

$$r_w = \frac{K}{h}, \quad (3.1)$$

where K is a constant dependent only on the fluid and not on the body, and h is the coefficient of heat transfer in Newton's law of cooling. In contrast, for a body cooling in air, he argues that the total external resistance is the sum of r_w and a second resistance (r_b) due to the boundary layer around the body. He imagines the body to be an isothermal core surrounded by a uniform thin insulating layer of negligible heat capacity (this can be thought of as the skin of the animal). The parameter h is the coefficient of heat transfer between this isothermal layer and the environment. He suggests that h will scale inversely with the linear dimension of the object, and thus as mass to the power minus one-third. Hence, r_w will increase as mass to the power one-third. He then presents empirical evidence from lizards to suggest that r_b is independent of mass. Hence, as mass increases, r_w increases but r_b does not, so eventually r_w will dominate. He concludes that for masses beyond 4–7 kg 'the boundary layer resistance can be ignored and lizards will cool equally in air or water'.

4. THEORETICAL DEVELOPMENT

Let us assume that Bell is correct and that boundary-layer resistance can be ignored. Then, the relative rates of heat loss in air and water are given by the ratio of the values of the coefficients of heat transfer, h ($\text{W m}^{-2} \text{K}^{-1}$), in the two fluids. For simplicity of presentation, we will assume the simplest possible geometry, that of a sphere of diameter d (m) entirely surrounded by the fluid. According to Bird *et al.* (1960), if heat loss is by conduction alone, then h is given by

$$h = \frac{2k}{d}, \quad (4.1)$$

where k ($\text{W m}^{-1} \text{K}^{-1}$) is the thermal conductivity (the product of the density of the fluid, its specific heat capacity and its thermal diffusivity). The thermal conductivities of air and water are substantially different. Schmidt-Nielson (1979) quoted $0.586 \text{ W m}^{-1} \text{K}^{-1}$ for water and $0.025 \text{ W m}^{-1} \text{K}^{-1}$ for air at the same temperature and pressure. Thus, heat loss by conduction is greater in water than in air.

The above argument assumes that heat is lost by conduction alone. However, even if there is no large-scale movement of the surrounding fluid (say through river currents or wind), the presence of the hot body in the fluid can set up convection currents. Heat loss by such convection can be considerable, and can dominate that lost by conduction. In order to account for both convection and conduction, Bird *et al.* (1960) suggest that the expression for h in equation (4.1) must be generalized to

$$h = \frac{2k}{d} (1 + 0.3 \sqrt[4]{Gr} \sqrt[3]{Pr}), \quad (4.2)$$

where Pr is the Prandtl number of the fluid and Gr is the Grashof number.

The (dimensionless) Prandtl number describes the relative thicknesses of the velocity and thermal boundary layers. For air, Pr is always *ca.* 0.7, varying only slightly with temperature; for water, Pr decreases from 13.4 at 0°C to 5.4 at 30°C (Denny 1993). Hence, $\sqrt[3]{Pr}$ is somewhere between two and three times as large for water as

Figure 1. The effect of temperature on the fluid properties affecting the Grashof number. Plotted is $g\beta/\nu^2$, where g is the acceleration due to gravity, and β and ν are the coefficient of thermal expansion and the kinematic viscosity of the fluid, respectively. This is the Grashof number (Gr) divided by the cube of the characteristic length (d) and the difference in temperature between the body and the fluid (ΔT). (Redrawn from Denny 1993).

for air. The (dimensionless) Grashof number is a little more complicated to explain, being dependent on both the fluid and the hot body. It is given by

$$Gr = \frac{gd^3\beta\Delta T}{\nu^2}, \quad (4.3)$$

where g is the acceleration due to gravity (9.81 m s^{-2}), d is the characteristic length of the body (the diameter of our sphere, in metres), ΔT is the difference in temperature between the body surface and the fluid (K), and β and ν are physical properties of the fluid (the coefficient of thermal expansion (K^{-1}) and the kinematic viscosity ($\text{m}^2 \text{s}^{-1}$), respectively). The combination of these physical properties varies considerably with temperature, as shown in figure 1.

For seawater at any temperature, and fresh water at temperatures above 6°C , we can see that Gr is greater for water than it is for air of the same temperature. This, combined with the values for Pr above, means that the effect of free-convective heat loss is greater for water than it is for air. However, there is an interesting exception to this, for fresh water below *ca.* 6°C .

Free convection occurs when the heating of a fluid leads to a decrease in its density, thus leading to a buoyancy force. For air at any temperature, increasing temperature (at constant pressure) always leads to expansion, and so to a reduction in density. However, this is not true for fresh water, which has a maximum density at 4°C . Hence, at low temperatures, convection may occur in air more readily than in fresh water at the same temperature. I next explore whether this effect could allow a greater heat loss to air than to water at the same temperature. Let us consider the simple case at a temperature of 4°C , where, for water, Gr is zero. Since k is about 23 times as great for water as for air, in order for equation (4.2) to be greater for air than for water we need to satisfy the following for air:

$$(1 + 0.3 \sqrt[4]{Gr} \sqrt[3]{Pr}) > 23. \quad (4.4)$$

Using the value of 0.7 for Pr , this will be satisfied provided that Gr is greater than 4.65×10^7 . From figure 1 it can be seen that $Gr \approx 1 \times 10^8 d^3 \Delta T$. Assume that the animal is using circulatory control to keep its surface temperature as high as possible in order to maximize heat loss (Turner 1987). If we assume that the body is at 40°C , so that $\Delta T = 36^\circ\text{C}$, then equation (4.4) is satisfied provided that d is greater than 23 cm. If the body were larger, say 1 m, then

$$(1 + 0.3 \sqrt[4]{Gr} \sqrt[3]{Pr}) \approx 66, \quad (4.5)$$

and so we would predict that, for such a body, the heat loss in air at 4°C through conduction and convection would be about three times that in fresh water at the same temperature.

In a situation where convection is not free but is forced by the bulk movement of the fluid past the animal (i.e. wind or water currents), then, according to Bird *et al.* (1960), equation (4.2) becomes

$$h = \frac{2k}{d} (1 + 0.3 \sqrt{Re} \sqrt[3]{Pr}), \quad (4.6)$$

where Re is the (dimensionless) Reynolds' number. Given the arguments above about the relative values of Pr and k in air and water, it is a matter of simple algebra to show that for the heat loss in air to be greater than that in water, the value of Re for air must be at least 2000 times that for water. The Reynolds' number is given by

$$Re = \frac{ud}{\nu}, \quad (4.7)$$

where u (m s^{-1}) is the speed of movement of the fluid and ν is the kinematic viscosity. This latter constant is at least eight times smaller in water than in air (Denny 1993). Hence, air must flow at least eight times as fast past the animal to produce an equivalent Reynolds' number. So, to get a Reynolds number 2000 times higher would require the air to travel at least 16 000 times faster. Hence, in almost no situations would an animal be able to lose heat faster by a combination of forced convection and conduction in air, compared with water.

Another way for an animal to lose heat is by radiation. The rate at which a body emits radiation is entirely independent of whether it is surrounded by air or water. Emitted radiation will be absorbed within a much shorter distance from the animal's body in water than in air. This would have an important effect on cooling rates, if it warmed the water surrounding the animal. However, in almost all circumstances, free or forced convection currents will prevent this from happening. Hence, the only importance of radiation for this exploration would be if there were circumstances in which it was the dominant mode of heat loss from the animal, such that the differential effects of air and water on conduction and convection would be unimportant. The coefficient of heat transfer by radiation is given by

$$h = \varepsilon \sigma (T_a + T_s)(T_a^2 + T_s^2), \quad (4.8)$$

where ε is the (dimensionless) emissivity of the animal's surface (around 0.95 for most biological materials; Haack 1986), σ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$) and T_a and T_s are the

temperatures (K) of the animal's surface and the surroundings, respectively (Turner 1985; Holman 1997). I will assume that the animal is maximizing heat loss by maximizing its surface temperature at *ca.* 40°C (313 K), and the surroundings are 20°C (293 K). Substituting these values into equation (4.8) gives a radiative-heat-transfer coefficient of 6.0.

From equation (4.2), with the values of Pr and k given earlier and Gr estimated using figure 1, the values for the coefficient of heat transfer by a combination of conduction and free convection from a sphere 4 m in diameter are 8.1 and 0.04 for water and air, respectively. Comparing these values with that for radiation (6.0) suggests that when free convection applies, radiation is the dominant means of heat loss from large bodies in air, but in water convection and radiation have similar importances. Furthermore, although it is true that under the specialist situations discussed above more heat can be lost by convection and conduction in air than in water, this does not mean that more heat will be lost to air than to water to a biologically significant extent. In such circumstances, radiation is the dominant means of heat loss in both media, and so the losses in the two media will be very similar.

From equation (4.6), using $\nu = 1.7 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$ for air and $\nu = 6.610^{-7} \text{ m}^2 \text{ s}^{-1}$ for water (Denny 1993), the heat loss (the heat-transfer coefficient) by conduction and forced convection in air for the example 4 m diameter sphere would be 0.41 if the air speed was 0.1 m s^{-1} , rising to 5.6 if the air speed was 10 m s^{-1} ; in both cases these are lower than but comparable with the calculated values for radiative heat loss (6.0). Hence, radiation is an important component of heat loss in air from such a large object. In contrast, in water these values are 130 at 0.1 m s^{-1} and 1300 at 10 m s^{-1} . Thus, in water, heat losses by forced convection dominate losses through radiation, and so the heat losses to water are generally greater than to air, in circumstances where forced convection applies.

5. DISCUSSION

I have shown that, in most circumstances, the rate at which heat is lost by a body is greater when the body is immersed in water than when it is surrounded by air, assuming that the two fluids are at the same temperature. The only circumstance when this does not apply is when comparing air with fresh water, both at a temperature somewhere between 0°C and 6°C . At these temperatures, free convection in water is weak or non-existent, and so the combined effect of conduction and free convection in air can be comparable to or even greater than that of conduction alone in water. In such circumstances, heat loss will be predominantly by radiation, which is the same in air and water. Thus, only when both water and air are still and at temperatures below 6°C , is it appropriate to consider that heat losses in air and fresh water may be broadly similar for giant animals. However, when seawater is involved, or the temperature is above *ca.* 6°C , or wind or water currents occur, then water allows much more rapid heat loss than air. Hence, I have been able to find a resolution to the apparently contradictory views discussed in §1. In most circumstances, a large animal could lose more heat by standing in water. However,

when radiation is the dominant mode of heat loss, the heat loss is very similar in air and in water. Ecologically, this occurs at low environmental temperatures (under 6 °C) when the animal is not travelling and when wind or water currents are very low.

It is important to add some caveats to the above. First, if there is large-scale flow of the fluid (e.g. wind or river currents), then forced convection becomes an important avenue for heat loss. It may be that heat losses when exposed to a strong wind would be greater for an animal than if it were to retreat into the calm waters of a nearby lake. Second, ecologically, animals may not always (or indeed often) be faced with a choice between air and water at similar temperatures. The high specific heat capacity of water means that lakes and ponds are not subject to the rapid fluctuations that can occur in air temperature during the course of a day (Brönmark & Hansson 1998). Thus, during the day in summer, the air temperature may often climb above that of large bodies of water. In such circumstances, an animal needing to lose heat will generally benefit from moving into the water, both from the arguments given in this paper and because heat loss will be increased because of the lower temperature of the water compared with the air. Conversely, at night the air temperature may well be below the water temperature. Especially, if the water temperature is below 6 °C, then immersion in water may allow an animal to conserve heat, if no protective microclimates can be found on land. By considering heat loss from an idealized sphere, I can only claim to shed light on heat loss from the body of an animal. It may be that the heat loss from small appendages, such as the head, neck and legs, is an important thermoregulatory adaptation in large animals (Turner & Tracy 1983). This may also explain the function of giant sails or bony plates on the backs of several large extinct reptiles (Bennett 1996; Florides *et al.* 1999). Lastly, the simplifying assumptions used here, of a steady-state situation involving a body of uniform temperature, are open to challenge. However, the simple analysis provided here should at least offer a point of reference to those prepared to build complex models that relax these assumptions.

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REFERENCES

- Alexander, McN. R. 1998 All-time giants: the largest animals and their problems. *Palaeontology* **31**, 1231–1245.
- Bell, C. J. 1980 The scaling of thermal inertia in lizards. *J. Exp. Biol.* **86**, 79–85.
- Bennett, S. C. 1996 Aerodynamics and thermoregulatory function of the dorsal sail of Edaphosaurus. *Paleobiology* **22**, 496–506.
- Bird, R. B., Stewart, W. E. & Lightfoot, E. N. 1960 *Transport phenomena*. New York: John Wiley.
- Brönmark, C. & Hansson, L.-A. 1998 *The biology of lakes and ponds*. Oxford University Press.
- Denny, M. W. 1993 *Air and water: the biology and physics of life's media*. Princeton University Press.
- Florides, G. A., Wrobel, L. C., Kalogirou, S. A. & Tassou, S. A. 1999 A thermal model of reptiles and pelycosaurs. *J. Thermal Biol.* **24**, 1–13.
- Haack, S. C. 1986 A thermal model of the sailback pelycosaur. *Paleobiology* **12**, 450–458.
- Holman, J. P. 1997 *Heat transfer*, 8th ed. New York: McGraw Hill.
- O'Connor, M. P. & Dodson, P. 1999 Biophysical constraints on the thermal ecology of dinosaurs. *Paleobiology* **25**, 341–368.
- Paladino, F. V., Spotila, J. R. & Dodson, P. 1997 A blueprint for giants: modelling the physiology of page dinosaurs. In *The complete dinosaur* (ed. J. O. Farlow & M. K. Brett-Surman), pp. 491–504. Bloomington, IN: Indiana University Press.
- Phillips, P. K. & Heath, J. E. 1992 Heat exchange by the pinna of the African elephant (*Loxodonta africana*). *Comp. Biochem. Physiol. A* **101**, 693–699.
- Reid, R. E. H. 1997 Dinosaurian physiology: the case for 'intermediate' dinosaurs. In *The complete dinosaur* (ed. J. O. Farlow & M. K. Brett-Surman), pp. 449–473. Bloomington, IN: Indiana University Press.
- Schmidt-Nielsen, K. 1979 *Animal physiology*, 2nd ed. Cambridge University Press, UK.
- Seebacher, F., Grigg, G. C. & Beard, L. A. 1999 Crocodiles as dinosaurs: behavioural thermoregulation in very large ectotherms leads to high and stable body temperatures. *J. Exp. Biol.* **202**, 77–86.
- Turner, J. S. 1985 Cooling rate and size of birds' eggs—a natural isomorphic body. *J. Thermal Biol.* **10**, 101–104.
- Turner, J. S. 1987 The cardiovascular control of heat exchange: consequences for body size. *Am. Zool.* **27**, 69–79.
- Turner, J. S. & Tracy, C. R. 1983 Blood flow to appendages and the control of heat exchange in American alligators. *Physiol. Zool.* **56**, 195–200.
- Williams, T. M. 1990 Heat transfer in elephants: thermal partitioning based on skin temperature profiles. *J. Zool.* **222**, 235–245.
- Wright, P. S. 1984 Why do elephants flap their ears? *South Afr. J. Zool.* **19**, 266–269.