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Could *Tyrannosaurus rex* have been a scavenger rather than a predator? An energetics approach

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Arguments on whether *Tyrannosaurus rex* was likely to have been an active predator or a scavenger have been based on evidence from jaw morphology and/or dentition. Here, we adopt an entirely novel approach, using energetic arguments to estimate the minimum productivity that would be required for an ecosystem to support a scavenger of the size of *T. rex*. We argue that an ecosystem as productive as the current Serengeti would provide sufficient carrion for such a scavenger. Hence, *T. rex* need not have been an active predator and could have found sufficient food purely by scavenging.

Keywords: energy flow; predation; scavenging; allometry; dinosaur

1. INTRODUCTION

Whether *Tyrannosaurus rex* was likely to have found food primarily by predation or scavenging has been debated for close to a century without resolution (Erickson *et al.* 1996; Erickson 1999). Much of this debate has used arguments based on jaw morphology and dentition. Here, we use calculations of energy gains and losses to estimate the minimum carrion productivity an ecosystem must provide in order to support an obligate scavenger of the 6 tonne (6000 kg) mass of *T. rex*. Our estimates suggest that carrion productivity equivalent to the current Serengeti would have been sufficient to support such a scavenger. Hence, we argue on the basis of physiological ecology that *T. rex* need not have been an active predator and could have found sufficient food to support itself purely by scavenging.

2. THE MODEL

Our hypothesis is that the key constraint for scavengers is generally their ability to find food items. This is in contrast to predators, where capturing rather than discovering prey is the key constraint, and herbivores, where processing consumed food is often the key restriction on energy gain rate. We assume that the scavenger spends a constant fraction (α) of its time searching for food items that are distributed with a constant uniform density (f). If, when active, the scavenger searches out area at a rate V , then it finds food items at a rate αfV . We assume that it extracts an amount of energy E from each food item found. Hence, the rate of energy gathering (E_{in}) is αfVE . We assume that the individual has a resting metabolic rate R , but that searching for food requires extra energy investment at rate S . Thus, the rate of energy expenditure (E_{out}) is given by $R + \alpha S$, and scavengers attempt to optimize net energy gain (E_{net}) given by

$$E_{\text{net}} = E_{\text{in}} - E_{\text{out}} = \alpha(fVE - S) - R. \quad (2.1)$$

If we demand that E_{net} be positive then we can rearrange equation (2.1) as a restriction on the energy density of

food available for scavenging: for a positive energy budget we demand that the density of food energy available to a scavenger is greater than a critical value given by

$$fE_{\text{min}} = \frac{\alpha S + R}{\alpha V}. \quad (2.2)$$

The right-hand side of this is the minimum energy density that an ecosystem needs to have to support a scavenger. We will now estimate this for a scavenging *T. rex* and compare this with the energy density of carrion in the extant Serengeti.

We will assume that restrictions owing to nightfall, bad weather and sleep mean that on average the scavenger can actively seek food for 50% of the 24 hour day, so we set $\alpha = 0.5$. The relationship between the mass M of a reptile in kilograms and the resting metabolic rate R in watts has been described by Schmidt-Nielsen (1984)

$$R = 0.38M^{0.83}. \quad (2.3)$$

There have been various estimates of the live mass of a full-sized *T. rex*, ranging from 3000 to 8000 kg (Farlow *et al.* 1995; Christiansen 1997; Seebacher 2001). Recent papers seem to be converging towards estimates close to 6 tonnes, so we will use a value of 6000 kg throughout this paper. Substituting this into equation (2.3) gives a value for R of 520 W. The relationship between the mass M of an ectotherm (in kg), the speed of travel v (in m s^{-1}) and the extra cost of travel S (in W) has been suggested by Bennett (1982) to be

$$S = 10.3vM^{0.64}. \quad (2.4)$$

Reptiles can sustain a speed equivalent to 10% of their maximum speed (Bennett & Ruben 1979). The maximum speed of equivalent-sized mammals and reptiles is similar (Bennett & Ruben 1979). The following relationship between mass M (in kg) and maximum speed v_{max} (in m s^{-1}) has been proposed by Alexander (1977):

$$v_{\text{max}} = 8.5M^{-0.08}. \quad (2.5)$$

Substituting $M = 6000$ in equation (2.5) gives a maximum speed for a *T. rex* of 4.2 m s^{-1} . This compares well with a recent estimate of 5 m s^{-1} based on *T. rex*'s limb mor-

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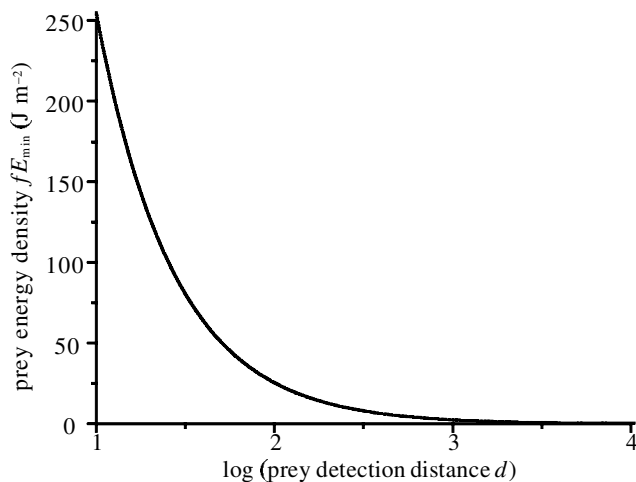


Figure 1. The minimum energy density that the ecosystem must provide to allow energy balance of the scavenger as a function of the distance in metres at which carrion can be detected, calculated from equation (2.7). The abscissa is logarithmic to the base 10 so '1' represents 10 m, '2' 100 m, '3' 1 km and '4' 10 km.

phology (Hutchinson & Garcia 2002). We will assume that sustained travelling speed, v , is 10% of our estimate, i.e. 0.42 m s^{-1} . If we substitute for v and M in equation (2.4), then this gives an added cost of travel S of 1100 W .

The rate at which an area is swept, V , is simply the sustained travel speed v multiplied by twice the distance at which food can be detected, which we will denote d . That is

$$V = 0.84d. \quad (2.6)$$

Substituting the parameter values derived in equation (2.6) into equation (2.2) gives an equation for the minimum energy density of carrion (in J m^{-2}) that could sustain an animal (fE_{min}) in terms of the distance at which it could detect carrion (d) as follows:

$$fE_{\text{min}} = \frac{2550}{d}. \quad (2.7)$$

This relationship is plotted for a range of d values from 10 m to 10 km in figure 1. To give us something to compare this against, we can estimate the energy density of carrion available each day from ungulate herbivores in the modern Serengeti ecosystem. It has been estimated that a total weight of $4 \times 10^7 \text{ kg}$ of ungulates die in the Serengeti each year (Houston 1979). Assuming that these have an mass-specific energy content of $7 \times 10^6 \text{ J kg}^{-1}$ (Peters 1983), and that the Serengeti stretches over $25\,000 \text{ km}^2$ (Sinclair & Norton-Griffiths 1979). This gives a mean energy density of $31 \text{ J m}^{-2} \text{ d}^{-1}$. When we compare this value with figure 1, we see that even if we make the conservative assumption that animals that die only remain available to *T. rex* for 24 hours (before spoiling or being consumed by other scavengers), then, if it is able to monopolize all the food it finds and can detect food at a range of 80 m, an ecosystem of similar productivity to the current Serengeti would provide sufficient food for such a scavenger.

One reason for caution in the interpretation of our results is that the allometric relations used are based on

data from extant reptiles, and consequently very few of the species used to generate the relations would have a mass approaching even 1% of our estimated mass for *T. rex*. Of our estimates, the sustainable travel speed of 0.42 m s^{-1} seems rather low for a bipedal animal with 2.5 m legs (see Fitzgerald (2002) and references therein). If we repeat our calculations assuming a sustainable running speed of 2.1 m s^{-1} , then this changes equation (2.7) to

$$fE_{\text{min}} = \frac{1600}{d}. \quad (2.8)$$

The faster running speed increases the area that can be swept for food faster than it increases the total energetic requirements of that animal, and so this leads to a reduction in the food density required to sustain the scavenger. Thus, our initial assumption of a low running speed can be seen as conservative, making a scavenging lifestyle challenging to maintain.

Some scientists consider that mammals (rather than reptiles) are a more appropriate model for dinosaurs (e.g. Bakker 2001). It is possible to repeat our calculations under such an assumption. Schmidt-Nielsen (1984) suggests that this would change our equation for R to

$$R = 0.38M^{0.83}, \quad (2.9)$$

increasing R substantially to 2300 W for our 6000 kg animal. Calder (1996) suggests that, for a mammal, the equation for S becomes

$$S = 10.7vM^{0.68}. \quad (2.10)$$

Bennett & Ruben (1979) suggest that the sustainable speed of mammals is 50% of their maximum speed, hence we will assume that v is 2.1 m s^{-1} . If we finally assume that α is unchanged at 0.5, then (using mammals rather than reptiles as a model) changes equation (2.7) to

$$fE_{\text{min}} = \frac{3100}{d}. \quad (2.11)$$

Hence, we see that substantial compensation for higher resting and movement costs in a mammal-like *T. rex* may come from a mammalian physiology allowing a higher sustainable rate of movement. The consequence of this is that the minimum food density required by our scavenger is only slightly increased if a mammalian model rather than a reptilian model is assumed.

3. CONCLUSIONS

Our calculation suggests that *T. rex* would be able to gather enough food to survive as a pure scavenger if a number of conditions are met. One is that the ecosystem yields the same density of carrion as the current Serengeti. Estimates of primary productivity at the place and time appropriate to *T. rex* vary widely but encompass values similar to that of the present-day Serengeti (Beerling & Woodward 2001). Any given primary productivity would have supported a greater biomass of ectothermic dinosaurs compared to the endothermic mammals that dominate the extant Serengeti (Farlow 1990). This higher biomass will more than compensate for the lower turnover rate per unit biomass that one would predict if dinosaurian herbivores

had longer lifespans than the mammalian herbivores of the extant Serengeti, on account both of their larger size and probably lower specific metabolic rates.

Another condition is that *T. rex* can detect carcasses at a distance of 80 m. Given the performance of polar bears in detecting seals over distances of kilometres (Stirling 1977) and the ability of turkey vultures to find 80% of experimentally provided chicken carcasses in tropical rainforest within 12 hours of presentation (Houston 1986), this seems likely to have been comfortably within *T. rex*'s compass. Brochu (2000) argues, on the basis of computed tomographic analysis of a fossil skull, that *T. rex* had greatly enlarged olfactory bulbs, suggestive of high olfactory acuity. Farlow (1994) suggests that the upright stance of *T. rex* could have aided carrion location, both by visual and olfactory pathways.

We also assumed that the fallen carcass was only detectable to *T. rex* for a period of 24 hours. Little is known about how long a carcass is accessible to vertebrate scavengers. Small (chicken) carcasses in tropical African forests were totally consumed by maggots within 3 days (Houston 1987). Hence, our assumption that prey is only available for 1 day seems entirely reasonable, and if anything on the low side. Our final assumption that our focal *T. rex* individual is able to find all the carcasses that fall in areas where it searches seems less plausible. It is likely that our *T. rex* would experience competition from other species and from other members of its own species. However, if we arbitrarily assume that our focal individual is only able to access 25% of the carcasses that fall, so that the ecosystem has effectively only 25% of the carrion density of the Serengeti (7.75 J m^{-2}), then (from figure 1) we see that *T. rex* would have to be able to detect prey at a distance of 330 m to balance its energy budget. This is more challenging, but still seems within the bounds of the possible, especially if, like many extant reptiles (Zug *et al.* 2001), *T. rex* had an effective sense of smell. Hence, our conclusion is that an energy budget analysis suggests that a reptile as large as *T. rex* could have survived using a purely scavenging lifestyle, providing that competition for carrion was low.

This conclusion leads to the obvious question, why is there not a *T. rex*-like scavenger on the Serengeti today? Or generally, we must ask why vultures are the only extant vertebrates that have a predominantly scavenging lifestyle. The answer may be that an avian scavenger can outcompete a terrestrial one because, as mentioned in § 1, the key requirement for a scavenger is to minimize energy expenditure while searching. Compared to terrestrial locomotion, even powered flying is faster and much less energetically expensive per distance covered (Schmidt-Nielson 1984), and birds like vultures that make extensive use of soaring have dramatically lower energy expenditure than any terrestrial scavenger could have. If *T. rex* was a scavenger, then this was probably only possible because avian radiation had yet to have a substantial effect on ecosystems.

It may well be, as suggested by Farlow (1994), that *T. rex* was an opportunist flesh eater, combining scavenging carrion with active predation. That said, our calculations suggest that total (or near total) dependence on

carrion (in the manner of extant vultures) may at least have been feasible.

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