

Obligate vertebrate scavengers must be large soaring fliers

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Abstract

Among extant vertebrates, only the 23 species of vulture are obligate scavengers. We use an energetic modelling approach to explore the constraints imposed by an obligate scavenging lifestyle, and to ask whether obligate scavengers must always be avian and generally large-bodied users of soaring flight. Our model found that aerial scavengers always out-competed postulated terrestrial ones, mainly because flight allows area to be searched much more rapidly for carrion. Soaring was favoured over flapping flight because the reduction in flight speed (and so rate of area search) was more than compensated for by the decrease in the costs of transport. Large individual size is selected for if carrion is available in large packages, when obligate scavenger feed only infrequently, and so must be able to survive on body reserves in the periods between discovering food falls. In the absence of avian radiation, an obligate terrestrial scavenger seems energetically feasible, but we argue that such a beast is unlikely to have evolved. In birds, in order to become exclusive scavengers, vultures have needed to specialize for efficient soaring flight as a low energy form of travel, and as a consequence they have lost the agility needed to kill prey. In mammals, however, no comparable trade-off occurs. So for terrestrial carnivores there is probably no strong selection pressure towards being an exclusive scavenger. Indeed it will perhaps always be more advantageous to retain the flexibility of obtaining food by either predation or scavenging.

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1. Introduction

Meat-eating animals can obtain a meal either by killing their own food, or scavenging it from a carcass. Many natural ecosystems have large numbers of animals dying from disease, malnutrition or accidents that provide an easy source of meat (Houston, 1979). Despite this, obligate scavengers are very rare. Among extant vertebrates, only vultures have a diet based almost exclusively on carrion (Houston, 2001), although many other predatory birds, reptiles and mammals are opportunist scavengers. Two quite separate lineages of birds (Cathartidae and Accipitridae) have independently evolved this obligate scavenging lifestyle. Here we ask whether we can identify factors that make flying animals more efficient obligate scavengers than terrestrial ones, and consider the selective pressures acting on them. The

23 species of extant vultures are generally characterized by a large body size in comparison to other groups of birds, and by a common dependence on soaring on air currents as an alternative to flapping flight.

It has frequently been argued that soaring should be attractive to an obligate scavenger because this provides a low cost means of travel (e.g. Bertram, 1979; Houston, 1979, 2001). However, this argument does not consider the negative consequences of gliding being a relatively slow form of travel, restricting the rate at which area can be searched. In order to develop the argument more fully, verbal reasoning needs to be supported by quantitative calculation. Recently, we introduced a mathematical model of energy balance in an obligate scavenger, and used this to evaluate the feasibility of obligate scavenging among extinct dinosaurs (Ruxton and Houston, 2003). Here, we develop this model for evaluation of the energetic consequences of obligate scavenging among birds that fly by either flapping and soaring flight. This will allow us to quantify the energetics of obligate scavenging for these two broad categories of flight, and to explore the consequences of

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size of the bird for the feasibility of scavenging in a general context.

We will also extend the model to consider hypothetical mammalian and reptilian scavengers and compare these with avian ones. Although obligate scavenging in dinosaurs (and other extinct vertebrates) has often been postulated (see references in Ruxton and Houston, 2003), there has been little attempt to quantify the energetic feasibility of obligate scavenging for terrestrial animals. As with flapping and soaring birds, we would expect a trade-off between endothermy and ectothermy: endotherms have higher metabolic costs but this buys greater endurance (and so higher rates of searching). Hence, another aim of this project will be to quantify consequences of this trade-off and explore how it is affected by animal size. Finally, we will be able to compare the relative energetic feasibilities of scavenging in aerial and terrestrial taxa.

2. Methods

Our hypothesis is that the key constraint for scavengers is their ability to find food items. This can be contrasted with predators, where capturing rather than discovering prey is the main 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 uniformly distributed at density (f). If, when active, the scavenger searches out an 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 a scavenger's net energy gain (E_{net}) is given by

$$E_{net} = E_{in} - E_{out} = \alpha(EfV - S) - R. \quad (1)$$

We further assume that the area swept per unit time by the animal in its search for prey is the product of its rate of movement (v) and twice the maximum distance at which it can detect a food item (d). Substituting this into Eq. (1) gives

$$E_{net} = \alpha(2Efvd - S) - R. \quad (2)$$

We will assume that restrictions due to nightfall, bad weather and sleep mean that the scavenger can actively seek food for 50% of the day, i.e. $\alpha = 0.5$. In the appendix, we consider, as an example of a natural large mammal community, the Serengeti ecosystem in Tanzania—for which we estimate the approximate mean energy density (Ef) of carrion as 3.4 J m^{-2} (see

Appendix A). Substituting these values into Eq. (2) gives

$$E_{net} = 0.5(6.8vd - S) - R. \quad (3)$$

This can be rearranged to provide an expression for the minimum value of the distance at which food can be detected that allows a positive energy balance:

$$d_{min} = \frac{2R + S}{6.8v}. \quad (4)$$

Our model uses minimum detection distance (d_{min}) as an index of an animal's ability to balance its energy budget: increasing d_{min} indicates that an obligate scavenging lifestyle is harder to achieve. In order to evaluate this for a given organism, we need the resting metabolic rate (R), added costs of searching for food (S) and sustainable movement speed (v). Appendix A gives published allometric equations for each of these as a function of mass (M in kg) for four different organism types: mammal, reptile, bird flying using flapping flight and bird flying using soaring.

3. Results

Initially, we make the simplistic assumption that carrion is uniformly distributed in very small packages and Fig. 1 shows clearly that for all four life history strategies the minimum detection distance (d_{min}) needed for energy balance increases with body size. For any given mass (M), a soaring bird has a lower value of d_{min} than a flapping bird, which in turn has a lower value of d_{min} than the two terrestrial life history strategies. d_{min} is lower for reptiles than for mammals for M values less than 10 kg but greater than that for mammals for masses greater than this, although the differences between the d_{min} values of these two animal types are always small.

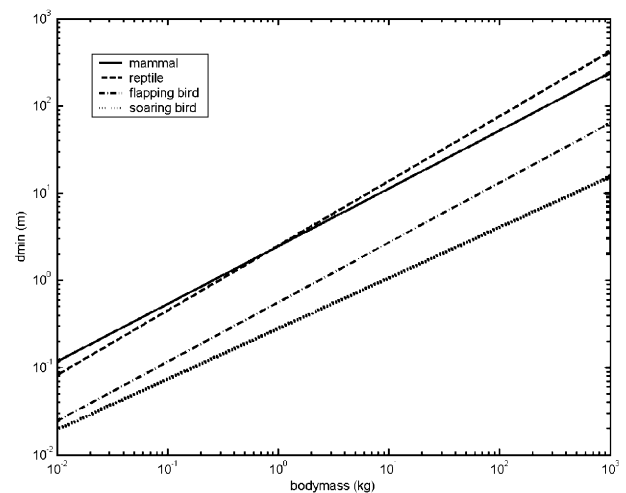


Fig. 1. The minimum distance in metres at which a scavenger of mass M (kg) must be able to detect food in order to balance its energy budget (calculated from Eq. (4)), assuming food is evenly distributed in very small packages.

However, a feature of carrion as a food source is that dead animals are not uniformly distributed in small packages but occur in large packages that are rare, highly dispersed and ephemeral. This has several consequences. An obligate scavenger may feed only infrequently, and so must be able to survive on body reserves in the periods between discovering food falls. Further, when it does feed, a single feeding bout must be sufficient to replenish these reserves. We incorporate these effects into our model in a simple way by assuming that carcasses are a specific size, and when a scavenger finds a carcass it is constrained to be unable to gather more from that carcass than the scavenger's gut capacity. That is, we assume that competition from other scavengers means that each scavenger is constrained to take only one meal from a carcass, they effectively fill their gut capacity (if they can) during this meal, but can take no more than this capacity. Hence for large carcasses where the quantity of food is not limiting, larger animals can take larger meals. This effectively increases the food density for larger scavengers, compared to smaller ones. We illustrate the consequences in Fig. 2. We only consider soaring birds and mammals here, because Fig. 1 showed that reptiles and mammals are very similar in predicted d_{\min} values and soaring birds consistently outperform flapping ones. Fig. 2a considers the situation where carcasses are 10 g in size. Scavengers weighing more than 100 g will have a gut capacity greater than this and so will be able to eat all the food that they find. In this case, the relationship between birds and mammals is similar to that in Fig. 1. However, scavengers smaller than 100 g can only consume part of a carcass, and so the effective food density available to them drops. This situation gets worse as the animal's mass (and so its gut capacity) decreases, such that for small animals d_{\min} must rise to compensate, as seen at the extreme left of Fig. 2a.

In Fig. 2b we consider minimum detection distances if the food is yet more dispersed, in the form of 100 kg carcasses. This shows that a scavenger would need to be over 1 tonne in weight to have sufficient gut capacity to utilize whole carcasses, hence compared to the situation in Fig. 1, d_{\min} values are much higher, reflecting the scavengers' inability to access all the food available to them. This restriction becomes less severe for bigger and bigger scavengers, but this effect always dominates the energetic considerations shown in Fig. 1, so that for such large carcasses d_{\min} decreases (and so scavenging becoming less challenging) as body size increases.

4. Discussion

Fig. 1 showed that for reptiles, birds and mammals d_{\min} increased as the body mass increased, which means that it was becoming harder to balance the energy

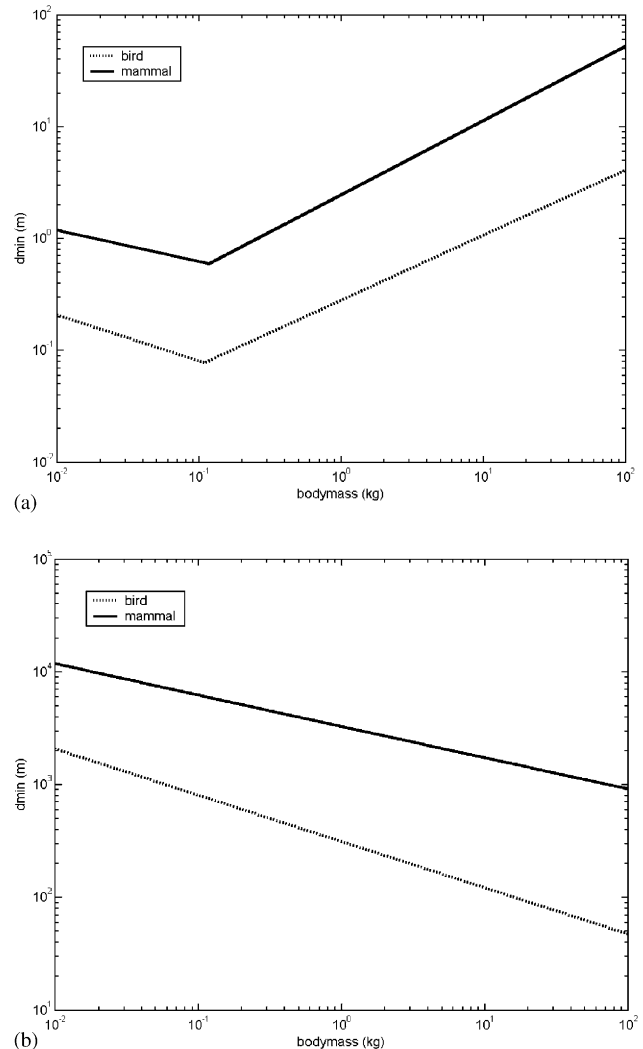


Fig. 2. Assuming gut capacity scales with mass as described in Appendix A, d_{\min} , calculated from Eq. (4) but subject to the constraint that meal size from each carcass is restricted by gut capacity. (a) 10 g carcasses; (b) 100 kg carcasses.

budget by obligate scavenging. This was due to increases in both travel costs and resting metabolic rate, both of which rose faster with body size than did the speed of movement. So larger scavengers can only exist if, with increasing mass, their ability to locate food increases faster than their increased food demands. However, Fig. 1 was based on the unrealistic assumption that the food supply was uniformly distributed in time and space as small units. When, in Fig. 2, we incorporate the stochastic and dispersed nature of the carrion food supply into the model, it demonstrates a clear evolutionary pressure towards large size for both birds and mammals when they are feeding on large carcasses. This is largely because larger animals can consume more food from each discovered food fall, and carry greater body reserves, than can small ones.

In the case of birds, body mass is ultimately constrained by the requirements of flight. Some of the larger vulture species are among the largest flying birds and find take off difficult until they have digested part of their food intake. Houston (1976, 1983) has argued that the evolutionary development of these birds has caused them to attain the highest body mass that flying conditions in their habitat will permit. So the largest species (Condors and Himalayan Griffon) occur in high mountainous regions where strong winds provide excellent soaring conditions, whilst species confined to flat lowland areas tend to be of smaller mass because they have access to weaker sources of lift. As well as the advantages of greater body mass outlined here, a large size is also obviously advantageous for a scavenger when in competitive interactions with conspecifics or other scavenging species. A feature of carrion as a food source is that large carcasses will contain far more than a single scavenger can consume, and so many individuals usually congregate at a single site and there is a high degree of competition between them. Also, a large mass has advantages in soaring flight, because flight speed is largely determined by body mass, so heavier birds can forage over a greater surface area each day (Pennycuik, 1972, 1979).

Our use of d_{\min} is intended only as an index of comparative ability to balance an energy budget by scavenging, not a realistic prediction of actual detection distances. Our model makes a number of simplifying assumptions. In a natural ecosystem there is great seasonal variation in animal mortality, as well as variation in carcass density caused by animal movements. So our mean estimate of food distribution is very approximate. If there were predictable spatial variation in (time-averaged) carrion availability in a given ecosystem, then we would expect scavengers to bias their search to areas where the highest availability was expected. In order to keep our model simple, we have not considered such a “patrolling” or “loitering” search mode, although we would expect that the general conclusions of this study would be robust against the addition of such complexity, and to the addition of increasingly realistic detail about the nature of the physical environment.

Despite the simplified nature of our model, we should consider whether the general order of magnitude suggested for detection distances is realistic. The larger vultures reach 10 kg in mass, and Fig. 2b suggests that such a soaring bird, feeding on 100 kg carcasses (large antelope) will need a d_{\min} of 150 m. In contrast, a generalized lion or hyena type mammal weighing 100 kg would need a much more challenging 1 km minimum detection distance.

Apart from the general relationship of increased visual acuity with body mass (Kiltie, 2000), species adapted as scavengers might be expected to show greater

visual acuity than predicted for their body size. Popular accounts frequently cite vultures as possessing remarkable powers of vision, although there is little data to support this. Fischer (1969) carried out trials of visual acuity on tame old-world vultures and showed that they could detect patterns with an acuity eight times greater than a human observer, and there is no doubt from field observations that vultures can detect food from distances greatly in excess of 150 m, if for no other reason than the searching altitude of griffon vultures can be well in excess of 1000 m above ground. In addition, and perhaps more importantly, vultures rely heavily on watching the movements of other birds. When food searching, vultures are usually in visual contact with several other individuals, and will immediately move towards any bird they see descending to the ground. Other, yet more distant birds, will follow, and so a chain behaviour is initiated which can lead to several hundred individuals landing at a food source within an hour, although only one individual may have located the food. Houston (1974) suggested that birds might be drawn from distances of over 35 km in this way. In addition, a vulture has the great advantage of an aerial platform with an unimpeded view of the ground below. Scavenging mammals need to locate food at far greater distances. Even if their greater body mass resulted in enhanced visual acuity, the restricted depth of view caused by vegetation or undulating topographic features is likely to make a 1 km detection distance using vision completely unrealistic. It is much harder to generalize about how olfactory abilities might be influenced by body size. There is no obvious strong advantage to increased size (Farlow, 1994), but given the acute olfactory abilities of many predatory mammals such detection distances are probably feasible.

Our model is very clear in its prediction that flying is much more advantageous for a scavenger than terrestrial movement. The reason for this is that flight is so much faster and so ground can be search much more rapidly. Further, at least for visual detection, a flying bird should be able detect carrion at a greater distance than an equivalent sized terrestrial animal. Although birds have higher resting and added metabolic costs than mammals, this effect is completely mitigated by the advantage they have of a greatly increased search rate. When comparing powered and soaring flight, the far greater energy cost of flapping flight means that although a soaring bird pays a cost in reduced speed over the ground, this is always outweighed in our models by the benefits of the reduced overall energy requirements. Hence, we predict that obligate scavenging will always be favoured by soaring birds rather than ones that predominately use flapping flight.

Although we found that d_{\min} is lower for reptiles than for mammals for M values less than 10 kg but greater than that for mammals for masses greater than this, the

difference between the two life history strategies was never great. Broadly speaking, the increased metabolic costs associated with endothermy are balanced by an increase in the sustainable rate of travel. This agrees with one of the conclusions of our earlier study, that the specific metabolic physiology of the dinosaurs (whilst the subject of great and continued controversy), is of little importance to evaluating the feasibility of obligate scavenging evolving within this group (Ruxton and Houston, 2003).

Although obligate scavenging is predicted to be less attractive to the terrestrial body-forms than the avian ones, it still seems feasible. Fig. 2b indicates that a 1 tonne mammal or reptile, in an ecosystem yielding carrion at densities similar to the current Serengeti, could have met its energy requirements if it could detect carrion over a distance of the order of 400–500 m. This may be challenging, say in densely forested areas, but does not seem outside the bounds of the possible. At the current time, when birds flourish across the globe, it is no surprise that we find no obligate scavengers among the mammals and the reptiles. Terrestrial scavengers find it difficult to compete with birds because of birds' far greater travel speed. A scavenger has not only to detect food, but also reach it before competitors have eaten it. However, in previous eras before the radiation of the birds, our calculations suggest that an earth-bound vertebrate obligate scavenger could potentially have existed from an energetics perspective. Sadly, obtaining evidence for an obligate scavenging lifestyle from the fossil record will be challenging, although perhaps not impossible (Erickson, 1999).

Finally, the selection pressures driving a species towards being an exclusive scavenger, rather than a predator that scavenges opportunistically, probably differ for birds and mammals. In birds, once scavenging became a substantial contribution to the diet, there would have been the advantages outlined above to developing both a large body size and specializations for efficient soaring flight. As a consequence vultures have comparatively large body mass, large wing areas and high flight speeds. In order to retain the ability to kill prey a bird needs to be able to land with great accuracy on a target, show agility and manoeuvrability at low flight speeds, and the ability to escape rapidly if the attack should fail. Vultures show none of these abilities. In order to become exclusive scavengers, vultures have needed to specialize so highly for efficient soaring flight as a low energy form of travel that they have had to abandon the ability to kill prey. In mammals, however, we can see no comparable constraint making it necessary to abandon the ability to kill prey in order to better exploit food available from scavenging. So for terrestrial carnivores there is probably no strong selection pressure towards being an exclusive scavenger: indeed it will perhaps always be more advantageous for

them to retain the flexibility of obtaining food by either predation or scavenging.

Appendix A

A.1. Resting metabolic rates (R Watts) as a function of mass (M , kg)

For mammals, $R_m = 3.40M^{0.75}$.

For reptiles, $R_r = 0.38M^{0.83}$.

For both the flapping and soaring birds, $R_{fb} = R_{sb} = 3.8M^{0.72}$.

All from Schmidt-Nielsen (1984).

A.2. Sustainable travelling speed (v , $m s^{-1}$) as a function of mass (M , kg)

Bennett and Ruben (1979) suggest that maximum speeds are similar for mammals and reptiles, but that reptiles can sustain a speed only 10% of the maximum compared to 50% for mammals. The maximum speeds of mammals are given by Taylor et al. (1980) as $2.3M^{0.12}$. Together, these assumptions give

$$v_m = 1.15M^{0.12},$$

$$v_r = 0.23M^{0.12}.$$

Alexander (1998) gives the maximum range speed (i.e. the speed that minimizes the cost of travelling unit distance) of flapping birds as

$$v_{fb} = 16M^{0.14}$$

and suggests that this speed should be halved for soaring birds

$$v_{sb} = 8M^{0.14}.$$

A.3. Extra costs of transport (S , Watts) as a function of mass (M , kg)

For fliers, we calculate the added costs of transport at the maximum range speed. From Rayner (1995),

$$S_{fb} = 57M^{0.83} - 3.8M^{0.72}.$$

Extra costs of transport for soaring birds are generally taken as twice the resting metabolic rate (Alexander, 1998; Hedenström, 1993), so

$$S_{sb} = 7.6M^{0.72}.$$

For terrestrial animals, there is no maximum range speed, since the added cost of transport increases linearly with velocity. Calder (1996) describes the cost of moving 1 m for terrestrial homeotherms as $10.7M^{0.68}$, this gives

$$S_m = 10.7vM^{0.68}.$$

Bennett (1982), as cited by Calder (1996), has a similar relation for terrestrial ectotherms:

$$S_r = 13.5vM^{0.75}.$$

A.4. Gut capacity (G , kg)

Calder (1996) give the following relationships. For mammals:

$$G = 0.075M^{0.94}$$

for birds

$$G = 0.09M^{0.99}.$$

A.5. Energy density of the Serengeti

Ruxton and Houston (2003) argued as follows. It has been estimated that a total weight of 4×10^7 kg of ungulates die in the Serengeti each year (Houston, 1979). We assume that these have an mass-specific energy content of 7×10^6 J kg⁻¹ (Peters, 1983), and that the Serengeti stretches over 25,000 km² (Sinclair and Norton-Griffiths, 1979). This gives a mean energy density of 31 J m⁻² day⁻¹. It was also assumed that carcasses were only available for a single day (24 h) before spoiling or consumption by insects, hence the standing crop is 31 J m⁻².

However if we assume that only 60% of a carcass is flesh that is of energetic value to the scavenger, that the energy from consuming the flesh is assimilated with 80% efficiency (Smith, 1985), and that conversion of stored assimilated energy to into usable mechanical energy is achieved with 23% efficiency (Pennycuick, 1989). Then the effective energy density is reduced to 3.4 J m⁻².

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