

Energetic feasibility of an obligate marine scavenger

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ABSTRACT: Many predatory species also scavenge from the carcasses of dead animals. In terrestrial ecosystems, there are species (the vultures) that meet their energy needs almost entirely by scavenging. It has been claimed that equivalent obligate scavengers would be unfeasible in aquatic ecosystems, because such organisms could not find sufficient food to meet their energetic needs. Here we use an established model of the energetics of scavenging to probe this claim quantitatively. Although the model is conservative, in that its assumptions err on the side of making scavenging energetically expensive and/or unrewarding, we conclude that an obligate scavenging fish seems entirely energetically feasible. We also consider obligate scavenging among invertebrates to be feasible. Hence it may be that obligate marine scavengers exist but remain to be discovered, or that constraints other than energetics must be invoked to explain why this foraging niche has not been filled.

KEY WORDS: Vultures · Scavenging · Food falls · Foraging · Energy balance

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INTRODUCTION

In terrestrial ecosystems, 2 distinct lineages of birds, the old-world and new-world vultures, have evolved to forage purely by scavenging on carrion (Houston 2001). Scavenging from food falls generated by dead nekton is also prevalent in marine ecosystems (reviewed in Britton & Morton 1994). Britton & Morton (1994) concluded that many predatory species, mostly benthic invertebrates and fish, are facultative scavengers, as is true of many terrestrial predators. However, unlike the vultures of terrestrial ecosystems, Britton & Morton (1994) contended that there are no obligate scavengers in the sea. Furthermore, they suggested that obligate scavenging in the sea is unlikely to evolve because of the 'spatially and temporally infrequent occurrence of natural carrion in the marine environment'. We do not find this argument convincing; carrion is also distributed unpredictably in time and space in terrestrial ecosystems. The success of vultures is considered to rest on their ability to integrate over this variation through being able to search large areas at very low transport costs (Bertram 1979, Houston 1979). Since swimming is generally faster and energetically cheaper than walking on the seabed (Martinez

1996), it seems feasible to us that a swimming marine organism could overcome the unpredictability of carrion availability in a similar way to vultures. However, this cannot be evaluated by verbal reasoning, and requires a quantitative approach. Recently, we presented a simple mathematical model used to explore the energetics of scavenging in extinct terrestrial reptiles (Ruxton & Houston 2003). In the present study we modify this model to explore, from an energetics viewpoint, the feasibility of an obligate scavenging fish. We selected fish as a well-studied group, characterised by high mobility (e.g. Dodson 1997) and efficient transport costs (Denny 1993, Bierwener 2003). An alternative strategy for an obligate scavenger would be to avoid travelling long distances in search of carrion, waiting instead for carrion to fall nearby. We consider this alternative later in this paper, and will argue that fish are less well-suited than other types of aquatic organism to this more sedentary scavenging strategy.

METHODS

Our hypothesis is that the key constraint for scavengers is generally their ability, or lack of it, to find

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food items (Ruxton & Houston 2003). This can be contrasted with predators, for whom capturing rather than discovering prey is the key constraint, and herbivores, where processing consumed food is often the key constriction on energy gain rate (Illius & Gordon 1992). 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 an area at a rate V , then it finds food items at an average rate αfV . It extracts an amount of energy E from each food item found. Hence the rate of energy gathering (E_{in}) is αfVE . The individual has a resting metabolic rate R , but searching for food requires extra energy investment at rate S . Thus, the rate of energy expenditure (E_{out}) is $R + \alpha S$, and scavengers attempt to optimise net energy gain (E_{net}) given by:

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

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

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

This can be re-arranged to provide a means of estimating the minimum standing crop of carrion (Ef , measured in $J\ m^{-2}$) that would be required to support a scavenger with a positive net energy budget:

$$(Ef)_{min} = \frac{R + \alpha S}{2\alpha vd} \quad (3)$$

We assume that the putative scavenger searches only the seabed rather than the water column, also that it is a scavenger of large food parcels (e.g. whole or part carcasses of fish and marine mammals) which generally fall rapidly through the water column, rather than much smaller particulate matter (marine snow) which remain suspended for longer periods of time. Because most large food items spend much longer on the seabed than in their brief passage through the water column, the energy density that can be discovered by a scavenger is much higher if it focuses only on the seabed.

To allow us to evaluate $(Ef)_{min}$, we need to estimate all of the parameters on the right hand side of Eq. (3): R , v , S , d and α . Since our estimates will necessarily be approximate, we try to make a scavenging existence as hard as possible. For Eq. (3), this means that where there is doubt, we will select high values of R and S and low values of α , v and d , in order to produce an over-estimate of $(Ef)_{min}$.

For internal consistency we use the same set of allometric expressions for R , v , S used by Alexander (1998) in calculations of the scaling of swimming energetics:

$$R = 0.16M^{0.78} \quad (4)$$

$$v = 0.47M^{0.17} \quad (5)$$

$$S = 2.3R = 0.37M^{0.78} \quad (6)$$

where M is the body mass in kg, R is the resting metabolic rate and S is the added cost of travel (both in watts). Alexander (1998) can be consulted for the detail of the derivation of these expressions. These values of R and S are likely to be high, because we imagine our putative scavenger to inhabit the deep-sea, where low temperatures depress the metabolic rates of fish. Measurements of metabolic rates of the cosmopolitan macrourid *Coryphaenoides armatus* suggest values of resting metabolic rate an order of magnitude lower than same-sized midwater species (Smith 1978, Bailey et al. 2002). For a 1 kg scavenger, Eq. (4) estimates R of 0.16 W, whereas Bailey et al.'s (2002) estimate for a 1 kg *C. armatus* is 0.02 W, suggesting that our value for R is likely to be an over-estimate. Empirical measurements of S are not available (Bailey et al. 2002).

On the seabed, the range of food detection has been estimated at between 15 and 70 m for the deep-sea fish *Coryphaenoides armatus* by Sainte-Marie & Hargrave (1987). Bailey & Priede (2002) consider 10 m to be a conservative estimate. We assume a very conservative value of only 1 m, in order not to favour obligate scavenging in our calculations. We imagine that detection is primarily by chemoreception, sometimes aided by sound and bioluminescence from scavengers already at the food item. Jumper & Baird (1991) presented a model describing the spread of a pulse of mate-attracting pheromone. They argued that in the deep-sea, the pheromone would spread little vertically, but expand horizontally, to be detectable at a range of 100 m in around 9 h. This again suggests that our detection distance of 1 m is very conservative. Since this detection distance will be governed primarily by the physical properties and movement of the water near the seabed, we will assume that this value is independent of the size of the scavenging fish.

Patterns of sleep, or sleep-like resting behaviour, in free-living fish are not well studied (but see Sevenster et al. 1995, Kavanau 2001), especially in bottom-feeding oceanic fish (Mattson 1990). We assume that time available for foraging is only 50% of the 24 h day (i.e. $\alpha = 0.5$), so this estimate is likely to be low and thereby bias our calculations towards making scavenging harder to sustain. Again, in the absence of guiding data, we assume that α is independent of fish size. If we substitute all these assumed data into Eq. (3) we get:

$$(Ef)_{\min} = 0.43M^{0.61} \quad (7)$$

This suggests that the minimum standing stock of carrion required increases with body mass of the scavenger, so smaller scavengers could balance their energy budget when food is available at a lower density. For a 1 kg scavenger, this density is 0.43 J m^{-2} , increasing to 1.8 J m^{-2} for a 10 kg scavenger.

DISCUSSION

Various methods of estimating the rate at which food falls to the seabed were reviewed by Stockton & DeLaca (1982). They describe what they consider to be 'large parcels of food (i.e. carcasses of fish, squids, marine mammals)', of an appropriate size for putative scavenging fish. The lowest estimate quoted in their study was $34 \text{ kg km}^{-2} \text{ d}^{-1}$. Our notional scavenger will face competition from others of its own kind and from both vertebrate and invertebrate facultative scavengers. Stockton & DeLaca (1992) also provided a survey of studies that had estimated the time from a food fall or presentation of an artificially presented bait to complete consumption: the estimates ranged from 14 to 340 h. We assume that competition is intense, so the mean time before consumption of any given part of a food fall by scavengers other than our focal individual is only 6 h. In light of the observations reported by Stockton & DeLaca (1992), this is likely to be an underestimate, again biasing our results to make obligate scavenging as challenging as possible. These assumptions mean that there is a standing crop of 8.5 kg km^{-2} available to our notional scavenger. If we conservatively assume that only 75% of this is flesh of energetic value to our scavenger, and that this flesh has an energy density of 6900 J g^{-1} (Kooyman et al. 1992), then this gives an energy density of $4.4 \times 10^7 \text{ J km}^{-2}$. If we, very conservatively, assume that assimilation efficiency is only 10%, then this gives an energy density of $4.4 \times 10^6 \text{ J km}^{-2}$ or 4.4 J m^{-2} —over twice the estimated requirement for a 10 kg scavenging fish.

We can also make an order of magnitude estimation of the population density of obligate scavengers that can be supported. Each day, we assume that 34 kg km^{-2} of carrion falls, that 75% thereof is flesh with an energy density of 6900 J g^{-1} and that assimilation efficiency is only 10%, translating to 17 600 KJ. If the scavenging fish weighs 1 kg (like *Coryphaeoides armatus*, considered earlier), then using Eqs. (4) & (6), each fish uses 30 kJ d^{-1} . Hence, the density of 1 kg scavengers that can be supported is around 600 fish km^{-2} . Density estimates for *C. armatus* range from 250 to 2000 fish km^{-2} (Drazen 2002); *C. armatus* can make up as much as 80% of the benthopelagic fish biomass

in some areas (Smith 1978). Our estimate is therefore broadly within plausible bounds.

Our assumptions have erred on the side of making scavenging as energetically challenging as possible, and minimising the energy density available to the scavenger. Despite this, we suggest that an obligate scavenging fish of similar size to a turbot or small cod (~10 kg) would be feasible from an energetics perspective, although larger scavengers (e.g. typical size of a shark) could not be supported.

In this study, we have considered an obligate scavenging fish, capable of searching wide areas in order to cope with the extreme spatio-temporal unevenness in carrion availability. An alternative strategy would be to save the costs of transport and wait for carrion to fall nearby, accepting longer periods between meals. Such a strategy would be most effective in parts of the ocean where carrion food falls are spatially concentrated. Examples of such sites might include frontal systems, the convergence of currents, the base of sea cliffs and fishing grounds where a large biomass of cadavers are generated as a result of fisheries discards (Ramsey et al. 1997). However, 2 key requirements for such a 'sit-and-wait scavenger' would be the ability to use energy at a very low rate whilst inactive, and to maximise meal size (Smith & Baldwin 1982). Both these requirements would favour other taxa, such as amphipods, rather than fish. Morphologically, a large proportion of a fish is relatively metabolically expensive muscle tissue (Gartner et al. 1997) and this means that even deep-sea fish have higher mass-specific metabolic rates than amphipods (Smith & Baldwin 1982). Deep-sea amphipods are capable of storing very large quantities of food in their guts. For example, Shulenberg & Hessler (1974) observed that *Paralichella* spp. was capable of expanding its body wall such that its overall volume increased by 300 to 500%, as a result of food ingestion. Fish do not have such extreme morphological flexibility. Hence, our prediction is that obligate sit-and-wait scavengers are more likely to be amphipods than fish (see Moore & Wong 1995a,b). This links with evidence in Priede et al. (1990), that deep-sea fish species originally suspected of being largely sedentary scavengers were much more mobile than previously thought.

In terrestrial ecosystems, sacrophagid and caliphorid flies, as well as vultures, pursue a lifestyle tied in an obligate fashion to carrion (Kneidel 1984). Recently, Kaiser & Moore (1999) argued that the lysianassoid amphipod *Orchomene nanus* is an obligate scavenger of crustacean carrion. Our argument, that the density of carrion required to support an obligate scavenging lifestyle decreases with decreasing scavenger size, may provide 1 reason why *O. nanus* is relatively small (under 6 mm in length), although

Kaiser & Moore (1999) suggest that small size is advantageous, allowing access to a crab cadaver through the soft membranes around limb joints.

Although our model suggests an advantage to being a small obligate marine scavenger in terms of mean rates of energy gain and expenditure, one should offset this against the aggregated nature of carrion. Carrion is not dispersed evenly at a constant density, rather, it falls in the form of discrete 'packages'. An obligate scavenger must be able to live on its reserves in the periods between discovering food falls. Similarly, the scavenger will need to be able to replenish its reserves considerably from a single meal. Thus, the stochastic nature of food availability will provide an evolutionary pressure on large size, producing a greater ability to consume larger volumes of food at a single meal and to carry large reserves. In alliance with this, although meal size is likely to rise linearly with mass, both resting metabolic rate and transport costs are likely to increase less rapidly with increasing mass (Schmidt-Nielsen 1984, Denny 1993, Bierwener 2003). Large body size may also inadvertently increase available food, by increasing the ability to compete with other scavengers for food and/or to break through the tough integument of some carcasses. Similar arguments have been made for the generally large size of the vultures (Houston 1983), as well as for marine scavengers (Stockton & DeLaca 1982, Haedrich & Rowe 1997). One advantage that our hypothetical scavenging fish would have over vultures would be their low ectothermic metabolism, which should allow long periods between meals. Again by analogy with vultures, we should expect a scavenging fish to seek to lower their transport costs where possible; vultures make extensive use of air currents, so we would therefore expect similar use of oceanographic currents by an obligate scavenging fish (see Bailey & Priede 2002 for further discussion of the costs and benefits of different strategies for finding abyssal food falls). The use of currents to reduce the energetic cost of long-distance migration has also been demonstrated in fish (Metcalf & Arnold 1997).

Since the survey of Britton & Morton (1994), a large obligate marine scavenger has not yet been discovered. Our knowledge of the ecology of the deep-seas still lags very much behind our understanding of terrestrial ecosystems (Herring 2002). It would seem, however, that an obligate marine scavenging lifestyle is at least theoretically possible.

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