



Optimization of short-term animal behaviour and the currency of time

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Modern ageing theory is based on the observation that oxidative metabolism causes damage that results in a gradual loss of vitality, leading to senescence and death. If animals can oxidize only a given amount of substrate in a lifetime (i.e. the 'metabolic time' is allocated from a fixed budget), then behaviour may be aimed at maximizing benefits per unit of 'metabolic time' expended. We analyse the consequences of this view for two types of behaviour that are commonly expressed as rates with respect to clock time. Examples are given of locomotory behaviour in which the animals' preferred speeds are generally interpreted as a result of maximization of energetic efficiency. The same behaviour could be expected if animals were 'speed maximizers' with respect to metabolic time. Examples are given of foraging behaviour that is also best predicted on the basis of maximization of energetic efficiency. This makes sense only if energy is allocated from a fixed budget. However, foraging animals not only expend energy but also consume it so energy cannot be considered as being allocated from a fixed budget. The same behaviour could be expected if animals were 'energy intake rate maximizers' with respect to metabolic time. This makes sense if metabolic time is allocated from a fixed budget as suggested by ageing theory. The metabolic time concept can provide a crucial link between the optimum intensity of short-term behaviour and its long-term fitness consequences. We discuss the implications of this approach for the modelling of foraging behaviour.

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An animal's physiology and behaviour can be expressed as rates, such as metabolic rate (MR; kJ/day), walking speed (m/s) or feeding rate (g/s). To model short-term behaviour, it would be helpful to consider it in relation to fitness. Fitness, which might be defined as the number of viable offspring produced in a lifetime, measures the contribution of a genotype to the future gene pool of the population. Rates of reproduction and mortality are the major proximate variables that determine the fitness of genotypes. For larger animals, measurement of these rates is difficult, as it requires long-term observations of large numbers of animals. Because the causal chains between behaviour observed today and the consequences of alternative behaviours for future reproductive success and survival are long, it is usual to assume that animals try to achieve some set of short-term goals that will contribute most to fitness. An example of this can be

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found in foraging studies. In these, it is frequently assumed that animals will maximize their rate of intake because the maximization of short-term energy intake rate would contribute most to fitness (e.g. Stephens & Krebs 1986). Such an approach seems potentially useful from at least two perspectives. First, it allows the formulation of hypotheses that can be tested in short-term experiments; second, animal behaviour may actually be organized in that way. Animals may use relatively simple rules of thumb, based on their actual state and on external information, to 'decide' which of the possible behaviours is preferred at present. In the evolutionary process, such rules of thumb may have 'surfaced' because such behaviours were, on average, effective; that is, they resulted in the genotype making a good contribution to future gene pools (e.g. Mangel & Clark 1988).

The rate at which behaviour occurs is conventionally expressed per unit of objective 'clock time'. Many time and rate variables expressed in clock time are related to mature size (M) of a species, commonly in relation to variation in specific MR (kJ/kg per day; Peters 1986). The terms 'metabolic age' and 'metabolic time' (or

'physiological time'; Calder 1984) have therefore been used in comparisons of species with widely differing *M*. Taylor (1985), for instance, used the term metabolic age in his genetic size-scaling rules (see below). Less frequently, the term metabolic time is also used to describe processes at the level of cells. Sitte et al. (1998) used the term metabolic time in relation to the effects of oxidative metabolism on cellular senescence. In all these cases, metabolic time is defined as being directly proportional to specific MR. To our knowledge, the concept of metabolic time has not been used before in analyses of short-term behaviour of individual animals. In this paper we argue that the concept of metabolic time can be usefully applied to the analysis of short-term behaviour. The approach is particularly useful in attempts to link the consequences of alternative behaviours in the short term to fitness in the long term.

We first present a background overview of the effects of specific MR across and within species on time and other rate variables, because this background is essential for the development of our argument. Subsequently, we explore how animals behave in relation to time, expressed in two different ways, using two types of behaviour that have been extensively investigated. The first, and from our perspective the simpler, is locomotory behaviour. Preferred speeds appear to be the result of a process in which both oxidative metabolism and time play a role. We analysed data collected from different species to investigate the nature of time in relation to oxidative energy expenditure during locomotion. The second type of behaviour, a very different one, is foraging. In contrast to locomotion (which, apart from time, involves energy expenditure only), the food intake resulting from foraging involves energy intake as well as energy expenditure and time. There is, however, evidence that the currency of time that is relevant to the analysis of both types of behaviour may well be the same. We finish by describing the relevance of the currency of time to research into the wider analysis of animal behaviour.

BACKGROUND

Metabolic Rate, Time and Life Span Across Species

Between species of different mature size (*M*) within broad classes (such as unicells, poikilotherms or homeotherms), specific rates, such as specific MR, tend to decrease as *M* increases (Kleiber 1961; Peters 1986). Time variables, such as the time between heartbeats and the time taken from conception to reach sexual maturity, generally increase as *M* increases. The increase is approximately in proportion to the 1/4 power of *M* within taxonomic groups (Brody 1945; Calder 1984; Schmidt-Nielsen 1984; Reiss 1991; West et al. 1999). Taylor (1965, 1980, 1985) developed genetic scaling rules that used the idea of 'metabolic age' and showed that across a range of mammalian species, key life history events occurred at similar metabolic ages, that is at similar proportions of potential life span.

Smaller animals live faster and die younger than larger ones. The modern form of the 'rate of living hypothesis'

uses this idea and proposes that cumulative oxidative damage is a good measure of the potential life span that has been 'spent' (Arking 1991). The idea of metabolic age can be extended to that of 'metabolic time', in which the flow of time varies in direct proportion to specific oxidative metabolism (Schmidt-Nielsen 1984). It is this metabolic time rather than clock time that is of relevance to the animal. Metabolic time is used in the same sense in cellular biology by Sitte et al. (1998), that is at the cellular level, metabolic time, as measured by oxidative metabolism, determines the rate of ageing.

West et al. (1999) claimed to have found an explanation, based on internal transport distances, for the systematic effects of *M* on time and rate variables, including potential life span. However, they did not give any arguments why internal transport distances should affect potential life span. Some deeper theory is needed to account for the effect of *M* on loss of vitality, ageing, senescence and death. In modern theories of ageing, such a link has been proposed. Because this link is crucial for the development of our thesis, we briefly address the question of metabolic time and potential life span within species.

Metabolic Rate, Time and Life Span Within Species

In recent decades, much has been learned about the mechanistic link between MR and ageing. There is now evidence (e.g. Finkel & Holbrook 2000) that, in aerobic organisms, oxidative stress caused by reactive oxygen species (ROS) is intimately linked to the ageing process. In brief, highly toxic ROS are inevitably formed when oxidative processes occur in cells. ROS cause damage to cellular structures including membranes, mitochondria and DNA. Although repair mechanisms exist, either not all damage is repaired or errors occur in the repair process. There is thus an accumulation of damage in the course of an organism's lifetime which causes a gradual loss of vitality, the occurrence of lesions and tumours, immune system deficiencies, ageing and, ultimately, senescence and death.

There are now several strands of evidence that ageing is directly related to oxidative stress. Although specific MR may be a good approximation of oxidative stress (e.g. Ku et al. 1993), this is not always the case. For instance, birds have longer potential life spans than mammals of the same size and with similar MR (Schmidt-Nielsen 1984). However, Barja et al. (1994) observed that per unit of oxygen consumed, mitochondria of rats, *Rattus norvegicus*, released considerably more ROS than mitochondria of pigeons, *Columba livia*, and proposed this as the explanation for the higher life expectancies of birds than mammals of the same size. Why birds differ in this respect from mammals is at present not clear, although slow avian ageing may be coupled, evolutionarily, with delayed maturity and low annual fecundity (Holmes et al. 2001). Thus, longevity is correlated with oxidative damage in comparisons involving mammals and birds, even though it is poorly correlated with cumulative oxygen consumption in this particular case. In addition,

the accumulation of oxidative damage is affected by the level of antioxidant protection and by the amount of repair activity once oxidative damage has occurred (Finkel & Holbrook 2000). The disposable soma theory (Kirkwood & Cremer 1982) has developed the argument that different species can devote a larger or smaller proportion of available resources to protection and repair. In particular, the amount of external mortality that is due to the level of predation is considered to be crucial (e.g. Cichón 1997). Different species can then have different rates of ageing at similar levels of specific MR.

There is now abundant evidence from invertebrates that an increase in protection against ROS increases vitality and potential life span without having a negative effect on MR. *Drosophila melanogaster* that were genetically modified to overexpress two antioxidant enzymes lived longer and were more active long before senescence occurred (Orr & Sohal 1994). Studies with *Caenorhabditis elegans* demonstrate a direct link between longevity and oxidative stress resistance. This was found for mutants with elevated antioxidant activities and with nematodes in which antioxidant defences were boosted by pharmacological means (Finkel & Holbrook 2000). These studies show that the modification of levels of oxidative stress is more important for loss of vitality, ageing and death than is MR as such. There are thus roles for ROS as well as for antioxidants and the repair of damage in the process.

Finally, we refer to a strand of evidence that seems particularly relevant for our thesis. Berg & Simms (1961) showed that rats that were restricted in their energy (but not nutrient) intake had longer life spans and a lower occurrence of lesions and tumours at the same age as ad libitum-fed controls. This observation has since been repeated in a wide range of species (Masoro 2000). A favoured hypothesis to explain this effect is that it acts by decreasing oxidative stress (Sohal & Weindruch 1996; Masoro 2000; Ramsey et al. 2000). Effects of energy restriction in rodents are in agreement with this hypothesis (Finkel & Holbrook 2000): energy restriction lowers the rate of ROS generation by mitochondria and prevents much of the age-associated accumulation of oxidated proteins, lipids and DNA. It also increases the ability of animals to withstand physiological stresses. These observations suggest that the ad libitum-fed animals lose their vitality sooner than the food-restricted animals as a result of the increase in accumulated oxidative damage. Then the metabolic intensity of a given genotype in the short term must have far-reaching consequences for its future fitness.

There is, then, much evidence that the proximal cause of loss of vitality, ageing, senescence and death is oxidative stress. Within genotypes, an increase in oxidative metabolism, such as that which follows the increase in energy expenditure arising from increased food intake, results in an earlier loss of vitality and ageing and a shorter potential life span. Then variation in the intensity of short-term behaviour of an animal will affect its future vitality and life span. Metabolic time may then be a time scale that is more relevant for animals than is clock time when they select a particular behavioural intensity. If a given genotype can oxidize only a given

amount of energy in its life span, then metabolic time is necessarily allocated to behaviours from a fixed budget. In that case, the optimum intensity of animal behaviour may be more properly assessed as rates in which time is expressed not in clock time but in metabolic time, that is, time that flows in direct proportion to specific MR. Evidence for this suggestion is presented below.

THE USE OF OXYGEN AND TIME IN LOCOMOTION

To go from A to B, an animal may move at a chosen speed. Among the costs associated with going from A to B are those of time and energy. The time that it takes to go from A to B is inversely proportional to speed (Fig. 1a). Consequently, oxygen consumption due to standard MR while going from A to B is also inversely proportional to speed. As illustrated below, the net energy expenditure associated with locomotion increases disproportionately with the speed of walking, running or swimming. Figure 1b shows the generally observed type of relationship between speed and O₂ consumption due to locomotion (based on an exponential model as used for fish; Peters 1986). It is evident that under some conditions, for instance during a predator attack, the animal may try to maximize its speed to escape. In such a case, the minimization of the time to cover a given distance will be far more important than the relative efficiency of locomotion. However, in the absence of such emergencies animals generally have a 'preferred speed' (arrows in Fig. 1). Apparently, animals prefer to balance somehow the advantages of a higher speed (less time is required to go from A to B) with the advantages of a lower speed (less net energy expenditure due to locomotion when going from A to B). From the relationships between speed on the one hand and time taken and energy consumed on the other (Fig. 1a, b), it is not immediately apparent how animals make this trade-off. To compare time gain with energy loss (or vice versa), two different currencies (clock time and energy expenditure) have to be expressed in a common dimension. In general, such problems do not have an easy solution (Stephens & Krebs 1986). However, in the case of locomotion, replacing clock time with metabolic time can solve this problem. Metabolic time is defined, in agreement with earlier usage of the same term, as time expressed in terms of O₂ consumption. An increase in speed will result in a decrease in oxidative metabolism due to the standard MR during locomotion because of a decrease in time required (proportional to the curve in Fig. 1a). However, an increase in speed will also result in an increase in net O₂ consumption due to locomotion per metre moved (Fig. 1b). There is now an optimum speed at which the sum of the two 'types' of O₂ consumption (i.e. the standard level and that which is directly related to locomotion) reaches a minimum level (Fig. 1c). In the literature, the same relationship is sometime expressed in its inverse form (Fig. 1d, e.g. Tolkamp & Ketelaars 1992) or in the form of the relationship between total O₂ consumption and distance moved per unit clock time (Fig. 1e, e.g. several graphs in Peters 1986). The equivalent forms shown in Fig. 1c, d, e show that there is

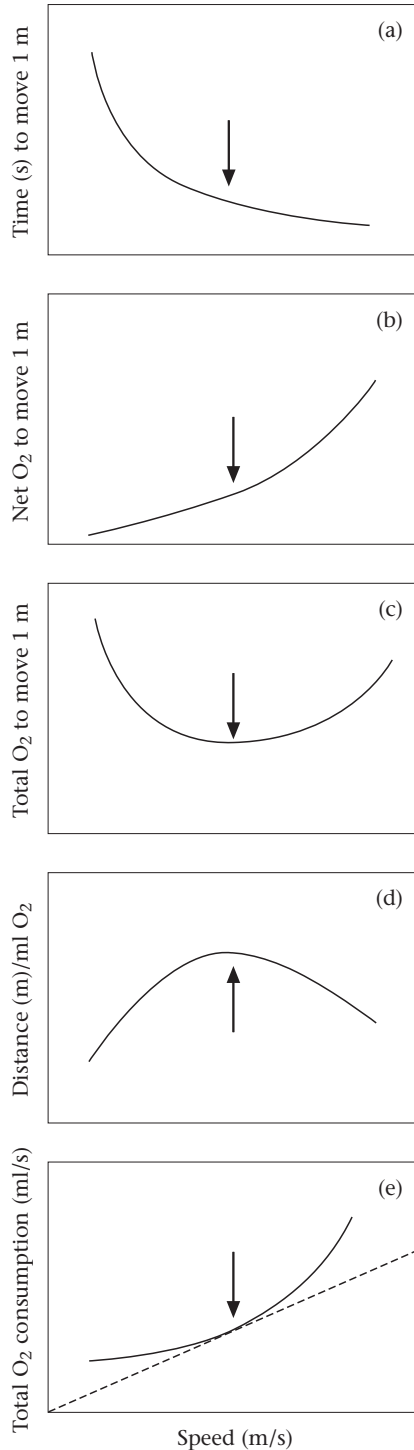


Figure 1. Effects of speed on (a) the time required to move 1 m, (b) O_2 consumption due to locomotion to move 1 m, (c) total O_2 consumption (standard plus that due to locomotion) to move 1 m, (d) the distance moved per ml of total O_2 consumed and (e) total O_2 consumption per s while moving. The arrows indicate the generally preferred speed (see text).

a speed (indicated by the arrow) at which the total O_2 consumption while going from A to B is minimized. As we show below, this optimum speed generally coincides with the animal's preferred speed.

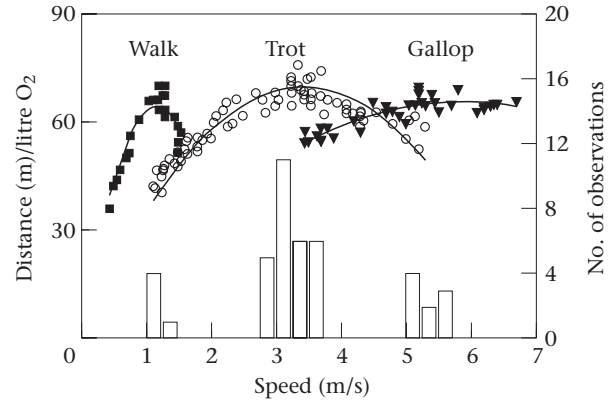


Figure 2. Effects of speed on the distance moved per litre of total O_2 consumption in walking, trotting and galloping horses (scattergram) and the frequency distribution of observed preferred speeds in each of the gaits (bars). The figure is replotted from Hoyt & Taylor (1981).

Locomotion in Horses

Hoyt & Taylor (1981) provided an elegant analysis of gait control in horses, *Equus caballus*. Horses were trained on a treadmill belt to vary their speed without changing gait, while consumption of O_2 was measured. The same horses were observed while moving freely and their preferred speeds were recorded. Their results are replotted in Fig. 2. Preferred speeds coincided with the speeds at which distance moved per litre of O_2 consumed was at its maximum (this could not be established with certainty for galloping because of technical problems). Horses, therefore, selected speeds that maximized the distance moved per unit of metabolic time.

Locomotion in Fish

In fish, the costs of swimming are usually expressed as total costs (including standard MR) which increase disproportionately with swimming speed (Peters 1986). Figure 3 shows how an increase in speed affects O_2 consumption in fish according to the model fitted to observations by Beamish (cited by Peters 1986, page 83). MR was originally expressed in watts; in Fig. 3 this was converted to ml of O_2 consumed by multiplying by 0.0486 (Blaxter 1989). The straight line through the origin touches the curve at the speed where total O_2 consumption per unit distance moved is minimal, and this is also the speed at which fish normally swim (Peters 1986; Parsons & Sylvester 1992). Normal swimming speeds coincide, therefore, with speed maximization on the basis of metabolic time. The evidence, then, is that fish maximize in the same currency while swimming as horses do when they run.

Locomotion in Birds

The relationship between speed and oxygen consumption during flight is more complex than that for running or swimming (Peters 1986). This is related to the high costs of flying at low speeds (hovering). Consequently,

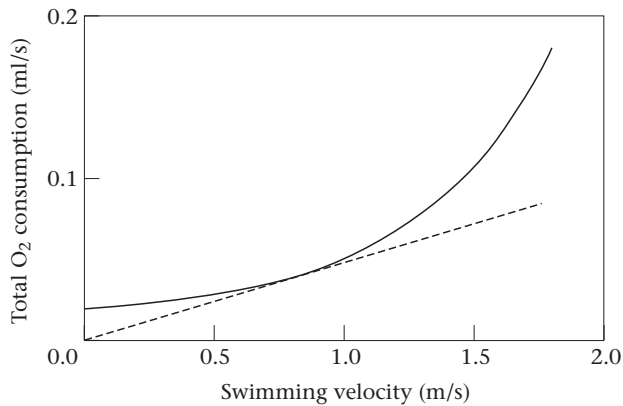


Figure 3. Total oxygen consumption in relation to swimming speed in a fish weighing 1 kg (—) and the first derivative of the curve where it goes through the origin (---). Replotted after the model supplied by Peters (1986, page 83; see also the text).

preferred flying speeds lie closer to maximum speeds than preferred running or swimming speeds (Peters 1986). Figure 4 shows the curve obtained by Tucker (as given by Peters 1986). The difference with previous figures is clear at low speeds. Nevertheless, in flight too there is an optimum speed that coincides with the maximum speed relative to metabolic time (e.g. Welham & Ydenberg 1993).

Preferred speeds in different forms of locomotion that are usually interpreted as a result of energetic efficiency maximization can thus be seen as a result of speed maximization relative to metabolic time. This also applies to humans (Ketelaars & Tolkamp 1996).

THE USE OF OXYGEN AND TIME IN FORAGING

In contrast with locomotion (an activity during which energy is consumed), foraging is aimed at increasing nutrient and energy supply, although energy will be expended in the process as well. In agreement with the assumption in many foraging models (Stephens & Krebs 1986), net energy (NE) gain can be considered the benefits of foraging. Animals have been observed (see below) to maximize NE gain per unit of energy expended, that is to maximize energetic efficiency. Efficiency maximization of foraging animals is poorly understood (Ydenberg et al. 1994) and ecologists have been sceptical about the idea. Stephens & Krebs (1986, page 9) wrote: 'There are still those [...] who confuse maximizing net rate with maximizing the ratio of benefits to costs, often called "efficiency". Although there are conditions under which maximizing efficiency makes sense (for example, allocating resources from a fixed total budget [...]), for most of the foraging problems we discuss it does not.' Indeed, an animal that consumes 8 kJ NE at an expenditure of 4 kJ is better off (in terms of NE gain) than an animal that consumes 5 kJ NE at an expenditure of 2 kJ, even if the latter is the more efficient. We agree, therefore, that efficiency maximization makes sense only when resources are allocated from a fixed total budget (Stephens & Krebs 1986). However, this does not

necessarily mean that efficiency maximization is irrelevant for most foraging problems. It is indeed difficult to see how energy can be allocated from a fixed budget if the availability of energy will depend on the foraging strategy that the animal selects. We argue, however, that it is not the energy but the capacity to oxidize energy that is allocated from a fixed total budget. Behaviour that seems to be aimed at maximizing energetic efficiency may then, in fact, be aimed at maximizing a rate with respect to metabolic time. We review below the evidence for that idea.

Bees Foraging for Protein or Energy

Bees may visit flowers to obtain protein (pollen) that differ from the flowers they visit to obtain energy (nectar). Rasheed & Harder (1997) investigated three hypotheses with regard to the currency that pollen-collecting bumblebees (*Bombus* spp.) were apparently maximizing. These included H1, pollen collected per unit clock time, and H2, pollen-collecting efficiency expressed as the amount of pollen collected per unit of energy expended. H2 predicts the same behaviour as rate maximization relative to metabolic time. Rasheed & Harder found that the behaviour was in better agreement with the latter hypothesis, that is animals maximized efficiency. They concluded that the short-term behaviour of pollen foragers results in maximization of pollen input into the colony during a forager's lifetime.

Schmid-Hempel et al. (1985) studied the foraging behaviour of honeybees, *Apis mellifera*, and tested two hypotheses concerning the currency that these animals were apparently using for some process of maximization. These were H1, foraging rate, that is the amount of nectar delivered to the colony per unit clock time, and H2, foraging efficiency expressed as the weight of nectar delivered to the colony per unit nectar expended in the foraging process. H2 predicts the same behaviour as does rate maximization relative to metabolic time. The behaviour of the bees foraging for energy was in agreement with H2, that is the bees maximized efficiency. Schmid-Hempel et al. (1985) drew attention to the fact that bees have a limited 'flight budget', as the flight metabolism of bees degenerates after a given amount of substrate has been oxidized. They concluded that maximization of foraging efficiency in the short term resulted in maximization of resources delivered to the colony in a forager's lifetime.

Biesmeijer & Toth (1998) investigated longevity and level of foraging activity in bees that specialized in different foraging tasks, that is collecting nectar or pollen. They saw remarkable differences in foraging intensity between pollen foragers (few daily flights) and nectar foragers (many daily flights). However, pollen foragers and nectar foragers performed a similar number of flights in their career, showing a direct trade-off between foraging intensity and 'foraging life span'. These observations agree with the idea that it was the amount of 'metabolic time' available to foragers that was fixed and not the amount of available energy. Therefore, what appeared as energetic efficiency maximization (which does not make sense) is

more logically interpreted as rate maximization with respect to metabolic time.

Ruminant Herbivores

Ruminants are frequently assumed to maximize forage intake rate subject to the constraint of a fixed rumen size (Mertens 1994). However, many anomalies have been observed (Weston 1982, 1996; Grovum 1987; Ketelaars & Tolkamp 1992). A particular case is where the intakes of forage by nonreproducing and lactating animals are compared. Animals of the same size, but in different physiological states, consume very different amounts of the same food (Adenuga et al. 1991; Stanley et al. 1992; Gross et al. 1996; Kaske & Groth 1997). Such observations led Ketelaars & Tolkamp (1992) to conclude that ruminants often consume less food than they are physically capable of consuming. They proposed that feed intake of ruminants can be understood only by taking into account the long-term effects of oxidative metabolism (Tolkamp & Ketelaars 1992). Their hypothesis predicts that mature ruminants maximize their NE intake rate with respect to metabolic time. The ad libitum forage intakes of mature sheep, *Ovis aries*, were predicted well using a model with parameters obtained with food-restricted fed animals. Some of the assumptions that underlie the model have been criticized (Emmans & Kyriazakis 1995), and more research is needed to develop this hypothesis more fully (NRC 2000).

Food-hoarding and Provisioning Birds

There has been an increase in interest in the concept of efficiency maximization for food-hoarding and provisioning birds. Several studies (Montgomerie et al. 1984; McLaughlin & Montgomerie 1990; Welham & Ydenberg 1993) have shown that birds neither maximized foraging rate nor minimized foraging time, but seemed instead to maximize the amount of food obtained per unit of energy expended in the process. Such behaviour makes sense if also in birds the long-term capacity to metabolize energy is allocated from a fixed total budget. Then the long-term benefits will be maximized by maximizing in the short term the foraging rate with respect to metabolic time, rather than clock time.

Implications for Foraging Models

If the cost of the time that is allocated to different behaviours requires scaling in relation to metabolic intensity, then this will have consequences for the modelling of behaviour. Many approaches in foraging studies limit predictions to very short time scales, such as a foraging bout, with patch depletion models as a typical example (Fig. 5). Clock time is generally used for the X axis. The Y axis can represent the energetic benefits of foraging, which are most appropriately expressed in terms of NE gain (e.g. Houston & McNamara 1999). NE gain can be calculated from gross energy intake by subtracting the undigested faecal energy and the digested energy that is

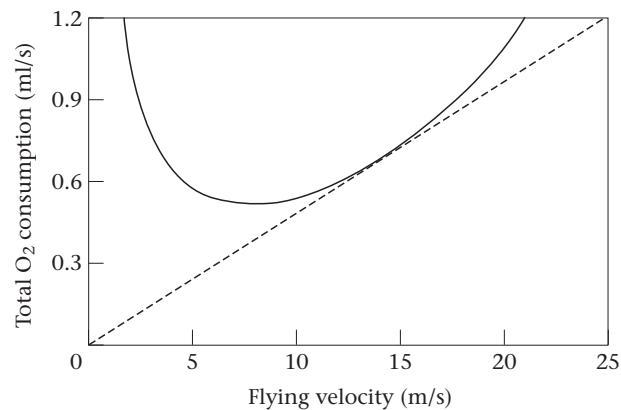


Figure 4. Total oxygen consumption in relation to flying velocity for a bird weighing 1 kg (—) and the first derivative of the curve where it goes through the origin (---). Replotted after the model supplied by Peters (1986, page 85).

metabolized during foraging. To calculate NE gain, it is not relevant whether energy is lost in the faeces or is expended during foraging, because neither is 'net' available to the animal. Only the concept of metabolic time recognizes that energy expended during foraging is metabolized and thus results in an increase in the 'loss of metabolic time'.

Figure 5 illustrates the difference between the two approaches. In the conventional approach, the energetic costs of foraging are used to 'correct' the gross energy gain to NE gain, but these have no effect on the time variable (Fig. 5a). In contrast, the concept of metabolic time assumes that, for the animal, the time scale that is relevant is one that changes proportionally with MR. Whether, and how, this approach changes predictions will depend on the average MR during travelling and the MR during patch residence time. It is evident that if, (1) MR remains the same during patch residence time and, (2) MR during travelling is the same as during patch residence time, metabolic time will be directly proportional to clock time. In such cases, the predictions will not differ between the two approaches. However, discrimination will be possible if one of the two conditions set out above is not met. A simple example of such a case is presented in Fig. 5b. The graph represents a model in which it is assumed that the MR does not change during patch residence time, that is while foraging, the NE intake rate decreases only because gross energy intake rate decreases. However, it is assumed that the animal's MR while travelling is three times that during patch residence time. In terms of metabolic time, therefore, travelling time should be accounted for as three times as costly as time spent in the patch. The result is that the predicted maximum energy intake rate is achieved at an optimum patch residence time that is about 50% longer (in clock time) than that predicted on the basis of clock time (Q versus P in Fig. 5b). Nonacs (2001) concluded from an analysis of 26 studies that, in the majority of cases observed, patch residence times were longer than those predicted by models based on rate maximization with respect to clock time. Figure 5b suggests that a difference

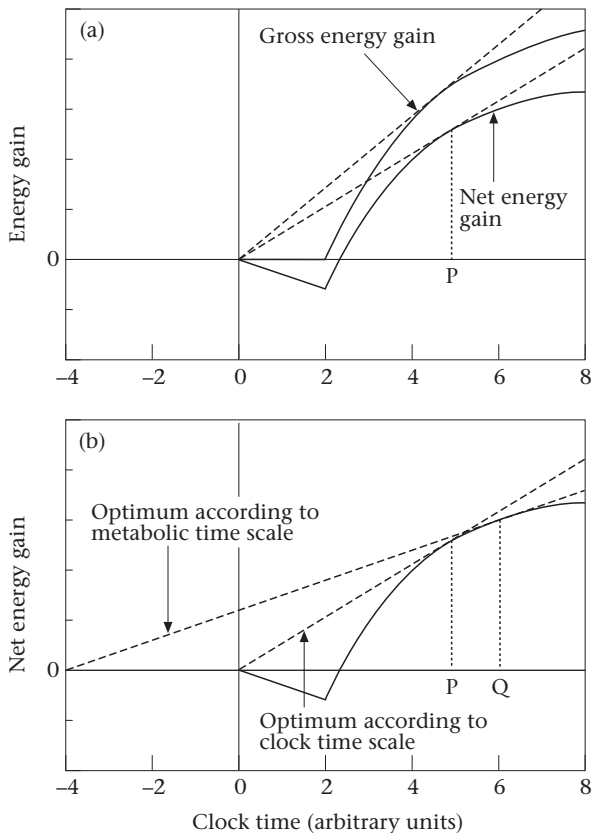


Figure 5. Two ways of correcting for energy expenditure. In the first (a), the correction affects energy gain but not the time scale; maximization of the rate of net energy gain with respect to clock time occurs at P. In the second (b), the correction affects not only energy gain but also the time scale; maximization with respect to metabolic time occurs at Q (see text for further explanation).

in MR between the travelling and residence parts of foraging could be one of the explanations. The extent to which the predictions of the two assumptions will differ depends on the extent to which MR in travel exceeds that in the patch. Similar predictions from paradigms based on efficiency or rate maximization have often hampered discrimination between hypotheses (Welham & Ydenberg 1993). Discrimination between competing hypotheses is possible only in cases where the different hypotheses predict different outcomes.

In several of the studies referred to above (e.g. Schmid-Hempel et al. 1985; McLaughlin & Montgomerie 1990; Welham & Ydenberg 1993; Ydenberg et al. 1994; Rasheed & Harder 1997), the authors compared the hypotheses of rate and energetic efficiency maximization. In all these cases, they concluded that the observations were more consistent with the latter hypothesis, which is identical to rate maximization with respect to metabolic time.

Predictions based on rate maximization with respect to metabolic time will be the same (e.g. for sugar-burning insects) or almost the same as predictions based on energetic efficiency maximization. Variation in speed (Ketelaars & Tolkamp 1996) and variation in energy intake (Tolkamp & Ketelaars 1992) may affect the respiratory quotient (the ratio of carbon dioxide produced to

O_2 consumed). The amount of O_2 consumed per unit of energy expended is then not always exactly the same. In theory, this variability could be exploited to distinguish between the two hypotheses, but doing so would require extremely accurate measurements.

Long-term versus Short-term Optimization

Figure 5 is based on the assumption that both the correction from gross to NE gain and the 'translation' of clock time to metabolic time can be made on the basis of energy expenditure during a foraging bout. In some cases, this may be realistic (nectar-foraging honeybees are an example) but in other cases it will not. A ruminant, for instance, expends some energy during a foraging bout but most energetic costs associated with ruminating, digesting, absorbing and metabolizing the food that is consumed during a bout will be made (long) after the event. It is impossible to measure at any one stage which part of the actual oxidative metabolism is associated with a given foraging bout. Thus, the model of Tolkamp & Ketelaars (1992) was based on the daily average rate of NE gain and average oxidative metabolism as measured in respiration experiments over a number of days. This raises the question of whether a bout or a day (or even a longer period of time) is the most relevant time scale for the optimization of feeding behaviour of an animal.

From studies with farm animals, it is evident that animals are extremely flexible in their short-term feeding behaviour. Large variation in bout frequency, bout size and diurnal distribution of bouts can occur without affecting average daily food intake (Tolkamp et al. 1998). This observation suggests that animals attempt to optimize food intake in the medium term and select, depending on the conditions, the most appropriate short-term behaviour. Collier & Johnson (1990, 1997) concluded similarly that the 'time window of feeding' for rats is at least a couple of days, that is rats optimize feeding behaviour with a view to their medium-term objectives. They argued that the strong emphasis on short-term behaviour has limited attention to a time window that is much narrower than the time span that is relevant for survival and reproduction. We propose that the concept of metabolic time can be useful for the development of the relationship between actual short-term behaviour and its long-term consequences. If animals have limited metabolic time available, they might do best if they maximize rates with respect to metabolic time in the medium term in order to maximize total benefits in the long term. Short- or medium-term rate maximization with respect to metabolic time can then be expected to have wide applications.

GENERAL DISCUSSION

Recent advances in the understanding of the processes involved in the gradual loss of vitality, ageing, senescence and a limited life span all point to an important role played by the ROS that inevitably are produced during oxidative metabolism. The modern version of the 'rate-of-living' hypothesis is based on the principle that an

increase in the intensity of oxidative metabolism will increase the rate at which damage accumulates in body tissues and, as a result, will directly affect the 'rate of ageing'. If so, then an increase in oxidative metabolism at any one time will be at the expense of future metabolic capacity. For species with a short absolute life span, for example nematodes and insects, the connection between oxidative damage and loss of vitality, ageing and a limited life span is well established. Evidence is accumulating that similar mechanisms play a role in vertebrates (Finkel & Holbrook 2000) including primates (Lane 2000; Roth et al. 2000). The hypothesis that metabolic time is allocated from a fixed total budget can be defended. If so, then the idea of metabolic time will be relevant to models that examine the optimization of animal behaviour.

Animal activities, such as foraging, are frequently a mixture of different behaviours, for instance locomotion and food ingestion. Both locomotion and food intake can be expressed as rates. Studies of locomotion show that animals moving at their preferred speeds are not rate maximizers with respect to clock time. Instead, their behaviour is consistent with their being rate maximizers with respect to metabolic time. In contrast, foraging models usually assume that animals are intake rate maximizers with respect to clock time. However, the foraging behaviour observed in a number of studies has been seen as evidence that animals were attempting to maximize energetic efficiency. Such behaviour can be better understood from the principle of rate maximization with respect to metabolic time. This has a number of advantages. First, it avoids the objection that energetic efficiency maximization makes sense only if energy is allocated from a fixed total budget (Stephens & Krebs 1986), which it frequently will not be. Instead, it points to the fixed budget of lifetime oxidative metabolism that an individual has. Second, it unifies the basic principles according to which behaviour is optimized for two of the major components of foraging behaviour, that is locomotion and food intake. If this is the case, models can be developed based on the idea that foraging animals are indeed rate maximizers, but with respect to metabolic time. Third, our approach generalizes what has been recognized before, that is that costs may be associated with an increase in MR. Houston & McNamara (1999, page 82), for instance, stated that 'There are general costs associated with expending energy' and gave as an example effects on the immune system. Replacing clock time with metabolic time can take account of such costs in optimization modelling. Finally, the concept of metabolic time may provide a crucial link between the rules of thumb that animals may well use to decide between different intensities of short-term behaviour and their fitness in the long term.

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