The magnitude of energy flow through individual animals and their populations is potentially limited by several physiological factors. These include thermal constraints affecting the time available for foraging, physiological design constraints affecting foraging mode and the rate of prey capture, and digestive constraints on how much food can be processed per day. Over short periods (hours or less), maximal rates of metabolism may determine survival during exposure to cold or when fleeing predators. Energetics, physiology and ecology can be usefully integrated within the context of the concept of maximum rate of energy flow.

Energy acquisition and allocation provide a useful framework within which to study a range of ecological problems, from the costs and consequences of behavior patterns to life history phenomena. It is generally accepted that minimization of energy expenditure is critical to the survival or ecological success of certain vertebrates (e.g. hibernation and torpor in some endotherms, low energy flow in amphibians and reptiles). Maximal rates of energy flow are probably also very important. Maximal rate of energy metabolism may determine the survival of animals in extreme situations, e.g. very low temperatures or escape from predators, and maximal energy flow may set limits on rates of production (or reproduction) which the individual animal, and the population, can achieve. Many physiological ecologists have devoted their efforts to determining the physiological and behavioral limits of animals, and the ways these constrain other aspects of animal ecology. Their studies range from biochemical studies of the enzymes of intermediary metabolism to measures of energy flow through populations.

The concept of a maximal rate of energy flow can be traced back at least to the work of Kleiber on the maximal food capacity of domestic animals, and has been explicitly incorporated into several models of animal energetics. Maximal intake can be expressed as a function of mass and temperature (Equation 1). However, the use of a parameter specific to body mass introduces the possibility of a non-linear relationship with body mass, which is not appropriate for energy balance models. Therefore, it is more appropriate to use a parameter specific to body mass and temperature (Equation 2).

Overall, the model is an attempt to incorporate the effects of temperature on energy balance and activity patterns, and to provide a framework for understanding the relationship between energy flow and population dynamics in a wide range of animals. The model is intended to be applicable to a wide range of ecological and behavioral contexts, and to provide a useful tool for predicting the effects of environmental changes on energy flow and population dynamics.

Fig. 1. Simplified model of how metabolic rate of energy flow might set limits on rates of production in an endotherm. Energy available for production is calculated as the difference between the maximal rate of intake and the energy expended for maintenance. Maintenance requirements increase with increasing air temperature due to rising costs of thermoregulation. The magnitude of the maximal rate of intake, and how it might vary with environmental conditions such as air temperature, is still unknown for almost every vertebrate in the wild. Tₚ = upper and lower temperature limits for long-term survival.

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should periodically have to retreat into burrows to cool off by conduction. This prediction was verified with telemetrically measured body temperatures. The authors estimated that the ratio of time spent foraging to time needed for cooling underground would be about 1:1 if no above-ground shade were available. Most ground squirrels foraged for longer than this, though in order to do so they had to restrict their outside activity to the 20% of the habitat which was shaded for most of the day. Thus, climatic conditions affected both the time and space available for foraging. Qualitatively similar patterns have emerged from similar studies of other species of sciurids and manikins are also being used in studies of reptiles and birds.

Decreased foraging due to reductions in time available for foraging would be expected to decrease both total daily energy expenditure and intake. This has been documented in a study of small whiptail lizards (*Cnemidophorus hyrophylalus*) in two habitats (woodland and scrub) 11 km apart, where the length of the activity period differed by a factor of more than two. In the scrub, where activity periods were shortest (probably due to less availability of shade), daily energy expenditure was 34% less and food intake was 47% less than in the woodland. The lower net rate of energy intake (intake minus expenditure) at the scrub site would be expected to result in lower rates of production. Growth and reproductive rates were not measured, but lizard body sizes and population densities were lower at the scrub site. This work emphasizes the importance of measuring proximate environmental sources of variation in life history studies.

Rates of food collection while foraging

Studies with lizards have shown how morphology and physiology may constrain foraging behavior and, ultimately, growth rates and reproductive rates. Different lizard species exhibit a range of foraging behavior from sedentary, ambush predation ('wait-ambushers') to very active, cruising predation ('wide-foragers'). Among closely related lacertid lizards in the Kalahari desert, the wide-foragers have greater cruising and sprint endurance but lower burst speed than wait-ambushers. Parallel differences are seen in metabolic patterns. The wide-foragers are able to sustain higher levels of metabolism via aerobic pathways (i.e., greater aerobic scope) while the wait-ambushers can achieve higher instantaneous (though not sustainable) power input via glycolysis (i.e., anaerobic scope). During their daily period of activity, wide-foragers appear to have higher rates of food energy intake than wait-ambushers, though they also have higher rates of energy expenditure while foraging. But the net rates of energy intake (intake minus expenditure) while foraging are higher in wide-foragers than wait-ambushers. Therefore, wide-foragers have higher instantaneous rates of production and may reach reproductive maturity more quickly. Thus, apparent trade-offs between sprint and endurance and their associated physiological bases probably affect life history characteristics.

Similar correlations between exercise physiology and predatory mode are evident among anurans, but the ecological implications of these observations require further investigation.

Rates of digestion of food

When white-throated sparrows (*Zonotrichia albicollis*) with food ad libitum are exposed to temperatures below the long-term critical minimum they apparently die of starvation rather than from inadequate homeothermic capability. This suggests that their maximum metabolic capacity is limited by their rate of energy intake and digestion rather than their rate of heat generation, at least over the measured period. The proximate factor limiting food intake and digestion rate is unknown for this species, and indeed for most animals. In ruminants the limiting factor is the time taken to break down and clear the relatively indigestible plant matter from the rumen. Similarly, the intake of a brassica diet by woodpigeons (*Columba palumbus*) is limited by the rate at which they can process the plant. Such digestive bottlenecks may also exist for animals eating very digestible foods, as indicated by some recent work on nectarivorous hummingbirds. Hummingbirds (e.g., *Selasphorus rufus*) feed 14-18 times per hour, taking less than one minute for each feeding bout. In laboratory experiments they took considerably longer to process their meals: a 100 µl meal was cleared from the crop in 15-20 min with a half-time of about 4 min (Fig. 2). Between meals in the wild, rufous hummingbirds (*Selasphorus rufus*) feed 14-18 times per hour, taking less than one minute for each feeding bout. In laboratory experiments they took considerably longer to process their meals: a 100 µl meal was cleared from the crop in 15-20 min with a half-time of about 4 min (Fig. 2). Between meals in the wild, rufous hummingbirds sit on perches, presumably waiting for the previous meal to clear the crop before initiating another feeding bout.

Digestive bottlenecks have other implications besides putting an upper limit on the metabolic capacity of animals. A key question in behavioral ecology is whether an animal is an energy maximizer that spends as much time foraging as possible, or a time minimizer that cannot benefit beyond a certain level of food intake. Field observations suggest that woodpigeons and rufous hummingbirds are time minimizers, spending 50% and 75% of their activity time resting, respectively. The laboratory digestion trials, however, suggest that they may be taking in energy as rapidly as their digestive processes permit.
In the discussion so far, the ecological implications of limits on foraging time, foraging rate and digestion rate were best understood within the framework of an animal's daily activity cycle. Two further types of constraint to energy flow within animals operate over shorter periods than the preceding ones. Now we ask what limits the peak rate of metabolism that can be sustained over minutes or hours. This rate may determine the survival of an animal during the seconds or minutes when fleeing from a predator, or of an endotherm during hours of exposure to cold, as well as affecting other aspects of the animal's ecology. Two procedures have commonly been used for measuring the upper limit for aerobic metabolism, \( V_O_{2,\text{max}} \): exercise or exposure to very cold environments. Techniques for measuring simultaneous peak rates of aerobic and anaerobic metabolism have yet to be adequately devised, though the sum of \( V_O_{2,\text{max}} \) and lactate production is sometimes used as an index (cf. Ref. 20). Whereas daily metabolic rates rarely exceed five times resting metabolism, birds and mammals can sustain metabolic rates of 5–25 times resting metabolism over a period of hours. What limits the magnitude of these rates?

Mobilization and/or delivery of nutrients and oxygen to the tissues

There is evidence to suggest that energy metabolism may be limited by the rate of supply of nutrients to cells. For example, free fatty acids appear to be an important substrate for thermogenesis in seasonally acclimatized animals but must be converted to acetyl coenzyme A before being completely oxidized in the mitochondria. One enzyme involved in this mobilization of fatty acids is \( \beta \)-hydroxyacyl-CoA dehydrogenase. Winter-acclimatized white-footed mice (Peromyscus leucopus) and American goldfinches (Carduelis tristis) have increased activities of this enzyme in their skeletal muscle tissue and in the mice's brown adipose tissue. What is the correlation between this enzyme and whole-animal performance? In the mice an increase of 70% in \( V_O_{2,\text{max}} \) was accompanied by an increase of 80% in the enzyme activity. In the goldfinches, summer birds with lower levels of the enzyme could not maintain elevated levels of metabolism for more than 45–60 min and became hypothermic, whereas winter birds maintained high levels of metabolism and normal body temperatures for 6–8 h. Seasonal change in \( V_O_{2,\text{max}} \) was modest in the goldfinches but, compared with other possible physiological adjustments which were investigated, the ability to mobilize body lipid rapidly seemed to be one of the key factors in the superior ability of winter goldfinches to survive cold.

There is direct evidence that the delivery of oxygen to the tissues is not a limiting factor. Pulmonary diffusing capacity does not limit \( V_O_{2,\text{max}} \) in house sparrows and rats held in cold environments and allowed to breathe an atmosphere of 33% \( O_2 \), compared with the normal level of 20%. If pulmonary diffusion were limiting, then \( V_O_{2,\text{max}} \) should have increased because the rate of \( O_2 \) diffusion is directly related to the difference between the \( O_2 \) partial pressure in air and blood; however, the values were the same.

Metabolism by tissues

Studies of endurance training have shown that increases in \( V_O_{2,\text{max}} \) are also accompanied by increases in levels of enzymes involved in the oxidation of substrates. A rigorous program of treadmill training in laboratory rats, for example, can result in significant increases in skeletal muscle citrate synthase and succinate dehydrogenase, both of which are enzymes of the Krebs cycle. These patterns might suggest that an animal's aerobic locomotory performance might be limited by metabolism at the tissue level. On the other hand, in congenic wait-ambush and wide-foraging lizards, \( V_O_{2,\text{max}} \) was 30% greater in the wide-forager but there appeared to be no differences in activities of several skeletal muscle enzymes (e.g. citrate synthase, myofibrillar ATPase).

Conclusion

The level of biological organization represented by the activity of two muscle enzymes is far removed from the level of foraging mode. There are so many other physiological factors affecting locomotory performance that it should not be surprising if differences in organismal or ecological performance cannot be accounted for by differences in a few physiological factors chosen for study. While physiological ecologists have had some success in integrating physiology and ecology, they have also uncovered instances where physiological or biochemical data are ecologically misleading or on a different scale from ecological data.

A final point of general importance is how frequently the kinds of factors described here really constrain animals in the wild. If animals maximized their rate of energy intake, and if the energy for growth and reproduction was simply the difference between metabolizable energy intake and the energy expended via respiration, then the limits to foraging time, foraging rate and digestion rate would limit production rate in the absence of other ecological limitations (e.g. food availability and predation pressure). But in many cases this view may be too simple. For instance, the growth rates that some vertebrates achieve with ad libitum feeding can be increased further with application of growth hormones. In these animals the energy budget may be actively controlled so that growth occurs at some optimum rate, presumably selected for over evolutionary time and geared to average or poor resource availability.

Maximal rates of energy flow, and their physiological or ecological bases, are known for few vertebrates. The significance of the concept for vertebrate ecology needs to be further explored, especially by the integration of laboratory and field measurements and experimental manipulations. An approach for discriminating environmental and physiological limitations in growing seabirds, for example, has been to manipulate experimentally the requirements of chicks through food deprivation or supplementation and to switch chicks of different sizes between nests. In this way it was demonstrated that food supply did not limit the growth rate of grey-backed terns (Sterna fuscata). As a final example, an approach for testing an energetic explanation for habitat
selection in roosting blackbirds has been to compare calculations of heat loss based upon field micro-meterological measures with laboratory measures of the maximal rate of heat production. The comparison showed that birds could not roost at certain locations because their rate of heat loss would exceed their peak heat production capabilities. A strength of these studies is the effective manner in which they have cast physiological measurements and concepts into an ecological framework.

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References

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