Food Fuels Reproductive Success

A link between diet, metabolic rate, and reproductive output gives a novel insight into mammalian energetics

Keeping an engine running at high speed is an expensive business, both in automobiles and in endothermic, or warm-blooded, animals. For instance, a mammal might require up to 30 times more food than a reptile of similar size simply to maintain its high rate of metabolism and body temperature. Although mammals generally have metabolic rates set at a higher notch than in reptiles, the range of metabolic rates displayed by different mammalian species is considerable. Questions concerning the importance of endothermy and high metabolic rates in mammals, and why some mammals have markedly higher rates than others, typically provoke reference to the ability to be active regardless of the prevailing temperature.

Mammals' relative independence of ambient temperature has undoubtedly been keenly influential in their tremendous ecological success. But, according to Brian McNab of the University of Florida, a key dimension has been largely ignored in the study of mammalian energetics. This dimension, he says, is a link between metabolic rate and reproductive output. In a recent reexamination of the subject, some of which has already been published while some is still in press, McNab concludes that high metabolic rate promotes high reproductive output in a number of different ways.

If McNab's conclusion is confirmed, the relation between metabolic rate and reproduction can be used to predict the competitive outcome between two ecologically overlapping species; and it can provide insight into the virtual rout of South American marsupial mammals when the continent joined with Central America about 3 million years ago.

"When I started to look into this in the mid-1970's I had the traditional view on metabolic rates and temperature regulation," says McNab. "But I began to be worried by the number of tropical species that had high metabolic rates, not low ones as would be expected. It was clear that metabolic rate was not simply related to climate." Another puzzle was the Arctic hare, an animal that survives the frigid Canadian tundra. "Almost all rabbits and hares, that whole group of lagomorphs, have high metabolic rates, and yet the Arctic hare has a low metabolic rate in spite of its freezing environment."

McNab surveyed the available literature on mammalian metabolic rates, reproductive characteristics, and food habits. Eventually an equation began to formulate that might explain the apparently anomalous observations on the tropical and Arctic animals. "I began to think I had a partial explanation," he says. "It seemed that a high metabolic rate might confer a reproductive advantage on a species. And the type of food a species eats might influence the metabolic rate it can achieve."

The business of seeking meaningful correlations between biological variables is beset with traps for the unwary, as McNab explicitly notes. He began to tease apart the relevant factors in the equation: these include the gestation period, postnatal growth, number of offspring, and certain population parameters. First to be examined, however, was the influence of body size and diet on metabolic rate.

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"Body size is the constant background to all these calculations," says McNab. "It is the principal variable affecting metabolic rate." There is in fact a well-established connection, known as the Kleiber relationship, which states that basal metabolic rate is proportional to body mass raised to the 3/4 power. In other words, a doubling of body mass raises metabolic rate by 68 percent. McNab was particularly interested in explanations, and consequences, of departures from this relationship.

Diet turns out to be an important determining factor in setting metabolic rate. In general, browsers have low metabolic rates, partly because of the relatively low nutritional content of leaves, partly because the frequent occurrence of toxic chemicals demands detoxification processing, and partly because, in arboreal folivores at least, the life-style is sedentary. Animals that feed on ants and termites have even lower metabolic rates because, suggests McNab, this dietary habit involves the ingestion of a significant quantity of detritus which dilutes the calorific value of the food. The presence of ants' and termites' chemical defenses, and these creatures' spotty distribution as food sources, might also contribute to the very low basal rate in mammals that depend on them. Mammals with the highest metabolic rates are grazers and meat-eaters.

The Arctic hare, incidentally, subsists on leaves and bark, a diet that immediately explains its unexpectedly low basal rate. Something of the recent history of this animal illustrates another aspect of the equation in which McNab is interested. Until about 100 years ago the Arctic hare thrived in the forests of Newfoundland whereas today it is to be found only in the more barren areas. What changed was the introduction of the snowshoe hare, a smaller animal but one, as McNab notes, with a considerably higher basal metabolic rate. The snowshoe hare quickly became established in its new location and eventually excluded the Arctic hare from its preferred habitat, the forest. McNab examined a series of competitive interactions between pairs of species of comparable size and in each case the "winner" was the one with the higher metabolic rate. McNab sought the answer to this problem in the details of reproduction and population dynamics.

An important parameter of population ecology is the exponential growth constant r. A species with a short gestation period, rapid postnatal growth, high litter number, and short generation time will have a high growth constant. McNab charted available information on these variables and examined their correlation with metabolic rates. Body size affects these variables too, but McNab found that at any given body size the effect of higher metabolic rates was to boost the population growth constant.

A high metabolic rate clearly permits a fast rate of embryonic growth in utero and a strong and sustained milk production which promotes rapid postnatal growth. The intuitive notion that an animal with a low metabolic rate might be

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able to shunt energy expenditure away from maintenance and toward reproduction appears not to hold. The "synthesis" of an offspring follows the rules for the synthesis of anything else in the body: it is enhanced by a high metabolic rate. In addition to this effect of high rates, the product of litter size and number of offspring in the litter is also raised. Overall, then, high metabolic rate correlates positively with the population growth constant.

The relation between diet, reproduction and competitive edge now begins to emerge. All other things being equal, the one of a pair of competing species which has the higher metabolic rate will have an advantage, an advantage in terms of numbers because of an enhanced reproductive output. "All mammals will have as high a metabolic rate as their diets will allow," proposes McNab, "because of the reproductive benefits it confers."

The evolution of endothermy has often been said to be related to the regulation of body temperature in small animals and to the acquisition of nocturnal habits. "This surely was important," says McNab, "but it may well have a by-product of selection for higher reproductive output through higher metabolic rates. And the differences we see in metabolic rates between species of mammals is not because of improvements in thermoregulation or because body temperature is increased, but because of the competitive edge one species can get over another."

The suggestion that all mammals will have as high a metabolic rate (and therefore reproductive output) as possible may well be substantially true, but it runs up against another facet of population dynamics that might modify it somewhat. This has to do with reproductive "strategies" known as *r*- and *K*-selection. The former represents the production of large numbers of offspring, of which many do not survive, while the latter is applied to the devotion of substantial parental care to few offspring. In its most simplistic form, McNab's formula might seem to imply that all species will be as *r*-selected as possible.

It certainly turns out to be true that those species whose populations rise and plunge dramatically, usually tracking fluctuations in food supplies, are both *r*-selected and have high metabolic rates. But it is also true that not all species with high rates are *r*-selected. There is clearly an interplay between the quantitative reproductive benefits of high metabolic rates and the advantages of *K*-selection in environments with stable food resources.

Opossum

Most marsupials were unable to survive the challenge from placentals. The opossum did because it competes on equal metabolic terms.

Fish and Wildlife Service

With McNab's conclusion in mind, one can look at the history of mammals, specifically at the fate of the marsupials, and begin to see some rationale in it. "Although there is not a lot of information available about marsupials," says McNab, "it is clear that none of them has a high metabolic rate. Unlike the placentals, which have a very broad spread of basal rates, the marsupials are all clustered at the low end." The immediate inference is that whenever a marsupial comes up against a placental in ecological competition it is likely to be at a disadvantage.

One of the great natural experiments of all time was the joining of South and North America at the Panama Isthmus some 3 million years ago. Although there were some placental mammals on the island continent of South America before it joined with its northern neighbor, marsupials were predominant: they were the only carnivores and the major herbivores. When the great interchange of northern and southern fauna took place the marsupials did very badly indeed.

"What happened," says McNab, "was that in instances where competition between placentals and marsupials occurred under ecological circumstances that allowed placentals to have a high metabolic rate, the marsupials lost out. But when the competition was between species whose diet supported a low metabolic rate, the marsupials fared equally with the placentals. So, marsupial carnivores became extinct whereas the omnivorous opossum survived and continues to thrive."

If comparative energetics is the prime factor in the dominance of placentals over marsupials, the obvious question to ask is why marsupials do not have high metabolic rates whenever their diet would be suitable to support it?

"I can find no correlation between metabolic rate and reproductive parameters," says McNab. "The marsupial embryo is more isolated from its mother than is the case in placentals. In placentals the trophoblast, which is part of the placenta, permits extensive exchange of nutrients and gases between the two, but it is an effective block against immunological rejection of the fetus. The interface between mother and embryo in marsupials appears to be less well developed so that nutrient and gas exchange is less efficient. The possible benefits of a high maternal metabolism are therefore blocked."

If a high maternal metabolic rate cannot benefit a marsupial embryo, what about postnatal development? "Once again, the data are few," admits McNab, "but so far I have found no evidence to suggest a high metabolic rate in newborns that would be necessary to translate a rapid flow of milk into rapid growth." The rather unsatisfactory answer to all this appears to be that, although they are endothermic, marsupial mammals simply did not evolve mechanisms by which metabolic rate could be tuned to high levels.

It might be that the link between metabolic rate and reproductive output is absent or very weak, and therefore selection had nothing on which to take purchase. Or it might be that high metabolic rates have simply never arisen in the marsupial line and so its potential beneficial effects have never been expressed. There is some embryological evidence to suggest that the common ancestor between placentals and marsupials was more marsupial-like. The trick of reaching higher rates of metabolism might therefore have been the crucial factor in the evolution of placental mammals.—ROGER LEWIN

Additional Reading

1. B. K. McNab, "Food habits, energetics, and the population biology of mammals," *Am. Nat.* **116**, 106 (1980).
2. ———, "Ecological and behavioral consequences of adaptation to various food resources," in *Recent Advances in the Study of Mammalian Behavior*, J. F. Eisenberg and D. G. Kleiman, Eds. (Publ. No. 7, American Society of Mammalogists, Pittsburgh, in press).