OPTIMAL BODY SIZE AND AN ANIMAL'S DIET

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ABSTRACT

Within many animal taxa there is a trend for the species of larger body size to eat food of lower caloric value. For example, most large extant lizards are herbivorous. Reasonable arguments based on energetic considerations are often invoked to explain this trend, yet, while these factors set limits to feasible body size, they do not in themselves mathematically produce optimum body sizes. A simple optimization model is developed here which considers food search, capture, and eating rates and the metabolic cost of these activities for animals of different sizes. The optimization criterion is defined as the net caloric gain a consumer accrues per day. This model does produce an optimum intermediate body size which increases with food quality – not the reverse. This discrepancy is accounted for, however, because the model also predicts that body size should be even more sensitive to increases in food abundance. In nature, many poor quality foods are also relatively abundant foods, hence the consumers eating them may maximize their daily energetic profit by evolving a relatively large body size. Optimum consumer body size also decreases with increases in consumer metabolic rate and "prey" speed.

1. INTRODUCTION

Viewing the animal kingdom from a distant perspective, there are two fairly clear patterns between an animal's adult body size and the type of food that it eats. First, among many solitary carnivores and insectivores, there is a well-analyzed trend for bigger predators to consume bigger prey (see *e.g.* Hespenheide, 1973; Schoener, 1969, 1974). Beyond this, there is a tendency for animals which consume food of a low per-gram nutritional value to be of larger body size. For example, among lizards, the largest species tend to be herbivorous, the smaller species insectivorous (Pough, 1973). The largest rodents in the world, capybaras, beavers and porcupines, all consume food with a high roughage content (Walker, 1964), while their smaller relatives usually eat seeds, or insects. Dicotyledon leaves contain more protein and soluble carbohydrates than grass leaves (Gwynne and Bell, 1968). Accordingly, among African ungulates, primarily grazing species tend to be larger than those which also browse (Fig. 1). Even among grazers, species whose

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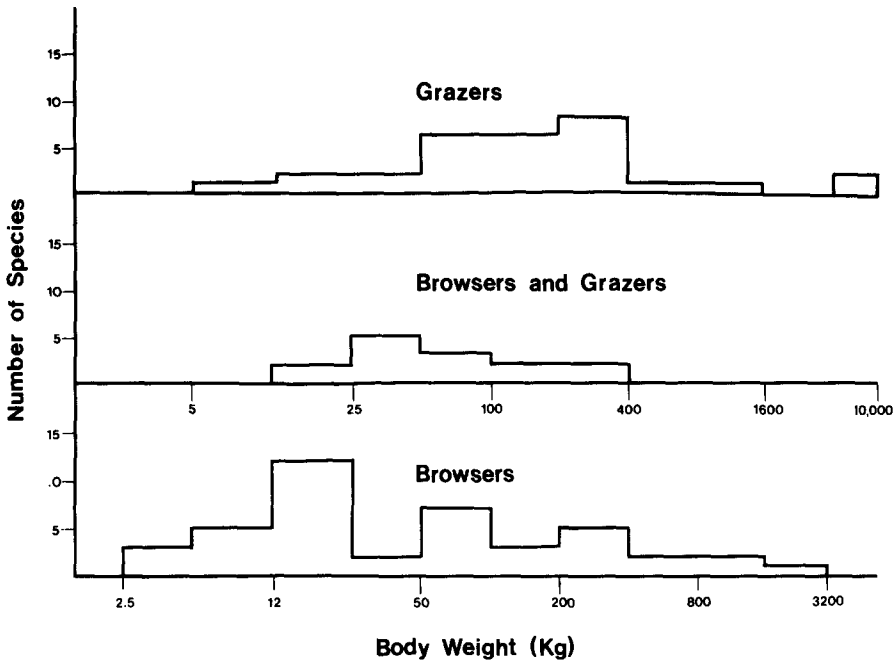
Fig. 1. The number of species of African ungulates in different body size categories given separately for species which are primarily browsers on foliage, species which either graze or eat bark, and for species which both graze and browse. The information was extracted from Dorst and Dandelot (1969). The abscissa represents typical adult body weight.

diet includes plants with thinner cell walls are generally smaller in size than those eating grass and herbs with a greater cellulose content (Bell, 1971). Small primates usually eat insects and fruit while the larger species are often folivores (Napier and Napier, 1967; Eisenberg *et al.*, 1972). Likewise, the largest of marine organisms, krill feeding whales, must ingest huge amounts of water to harvest adequate numbers of their prey.

The fossil record is also replete with examples. In the Eocene, the fox-sized ancester of the horse, *Eohippus*, had teeth that indicated a diet of soft food such as insects and fruit. Its Oligocene descendant *Mesohippus* was wolf-sized and apparently browsed on foliage. Only later with *Parahippus*, which was about the size of a pony, did grass become a dominant food source (Romer, 1966). A very similar paleontological association between rough food and large size is apparent in the ancestry of the elephant, beginning with the tapir-sized *Moeritherium* of the Eocene which had teeth indicating a diet of soft food.

Although more examples could be provided, and no doubt numerous exceptions, the available evidence begs an explanation. Because this trend occurs in such a diversity of organisms, the explanation must involve factors which are not unique to any particular taxon. For example, in most ungulates the symbiosis with fermentative bacteria allows fiber to be degraded into

fatty acids augmented by microbial protein (Hungate, 1966). This system works better the longer the turnover time in the 'fermentor' (either rumen or caecum). Since the turnover time is expected to increase with increases in body size, larger animals may be favored when roughage is a significant portion of the diet. This explanation does not explain why the same body size trend occurs in lizards or other mammals which lack fermentive guts. Secondly, it is not necessarily true that turnover time will increase with body size. The digestive half-life of a meal of hay in rabbits and cattle are very similar, about 10 to 20 hours depending on the particle size, roughage content, and meal volume (Bradt and Thacker, 1958).

Pough (1973) accounts for the absence of herbivory among smallish lizards with the statement 'such an alternative (herbivory) is not available to small lizards because of the lower energy content of plant matter and its lower digestibility.' This argument follows from the fact that an animal's total metabolic rate (cal/time) increases with body weight raised to a power of about .7, but gut volume increases with weight raised to a power of about 1.0 (see *e.g.* Schoener, 1969). As body size gets smaller, eventually the animal can no longer hold enough low quality food in its stomach to support its metabolic demands. While these energetic arguments certainly set lower limits to the range of feasible body sizes, they are not sufficient along to determine optimal body sizes. One may ask: if a slightly larger body size is better for an herbivore's energetic balance, why is not an even greater size better still? What selective trade-offs prevent body size from increasing to inexorbitant limits?

The task, therefore, is to see if a model predicting optimum body size based on energetic considerations does in fact exist, and if so, how is it influenced by food quality and abundance. Clearly, if we invoke assumptions that large prey items are more easily handled by large predators, and if we assign a log-normal distribution to food abundance versus food size, then optimum consumer body sizes will appear (Schoener, 1969). Yet, we wish to explain body size relations in animals such as herbivores, detritivores, and planktonic feeding whales where these assumptions may not be appropriate. As we shall see, our purpose can be served with a much simpler model.

2. OPTIMAL BODY SIZE

Before developing this model a disclaimer is necessary. Any optimization model must have a precise optimization function. That value of a parameter which produces the maximum value of the optimization function is considered the optimum value. Presumably, the body size of an organism has evolved to optimize its success within its particular niche. Yet, how do we quantify success? An animal's size may be viewed from two different lights. First, it represents an evolutionary compromise between maximizing immediate reproductive effort on the one hand and investing assimilated energy

into growth to increase survivorship and future reproductive success on the other (Gadgil and Bossert, 1970). Secondly, an animal's size may influence if not determine the total amount of energy the organism may secure from the environment. A complete model for finding optimal body sizes should take both these factors into consideration. It is conceivable that although a relatively large size might be the most efficient in a given habitat on the basis of maximizing food harvesting, the rapid growth necessary to achieve this size or the extended period of reproductive immaturity entailed might be decidedly disadvantageous. For age-structured populations the precise criterion of fitness is the intrinsic rate of growth, m, for each genotype in a given environment (Fisher, 1930; Charlesworth, 1970, 1973).

Such a complete model, however, is beyond the scope of this paper. Here I wish to momentarily focus on the relationship between body size and the ability to secure energy from the environment. I consider the fitness of different sized individuals as proportional to the amount of net assimilated energy that they may collect from the environment over a fixed period of time and I use this as the optimization criterion. This represents the maximum energy an individual would be able to devote to reproduction. Note, that in organisms where reproductive expenditure reaches a ceiling independent of their body size, this model is only approximate. In these species, any additional energy, which might be gained by a slightly larger size, would not be channeled into reproduction. Yet, we might expect that this greater harvesting ability would allow them more time for other activities which also would confer fitness.

Assume that the amount of food found and captured per unit time by a consumer (S) is linearly related to food abundance $F(g/m^2)$

$$S = k_1 F$$

k_1 is a constant of proportionality. Once food is found and captured the consumer eats it. Assume that the rate that food is eaten $I(g/\text{min})$ is directly related to the rate that food is captured. Yet, as food capture increases there is an upper limit to the amount of food which can be handled and digested per unit time by the consumer so that eventually $I(g/\text{time})$ asymptotically approaches some upper limit $L(g/\text{time})$. This relationship may be described by the following function:

$$I = L(1 - e^{-k_2 S}) \tag{2}$$

where k_2 represents a constant controlling the rate that I increases with S. The behavior of I with S expressed in eq. 2 corresponds to Holling's (1959) type 2 functional response. As food (F) increases from zero to infinity I increases from zero to L. It is also appropriate that L should be a function of body weight of the form

$$L = a_1 W^{q_1} \tag{3}$$

Here a_1 is a constant of proportionality. If the maximum rate that food can

be eaten is determined by the volume of the gut then q_1 should be near 1.0. For certain lizards, $a_1 = .048$ and $q_1 = 1.0$ (volume in ml and weight in grams; Avery, 1973). On the other hand, if the maximum rate of feeding is set more by the length of special mouth parts, then q_1 will be around .5 to .7 (see Schoener, 1969). Since we also require that the feeding apparatus of a larger animal will become saturated at a greater food level than that of a smaller animal, we must scale k_2 by L. After this modification and substituting eq. 3 into eq. 2 we have

$$I = a_1 W^{q_1}[1 - \exp(-k_2 S/(a_1 W^{q_1}))] \tag{4}$$

Notice, that at small values of S eq. 4 may be approximated by $k_2 S$. In other words, when food is very rare, the amount of food ingested per unit time is roughly independent of body weight. The implicit assumption, therefore, is that handling time (or speed of digestion) depends on W, but rate of prey encounter does not. An anonymous reviewer has pointed out that these assumptions are more transparent if the functional response of predation is modeled as a Holling hyperbola (Holling, 1965) scaled with W to obtain the same asymptotic relations. That is, we let

$$I = k_1 S/[1 + k_1 S/(a_1 W^{q_1})].$$

The functional shape of I (prey eater per unit time) versus S is similar to that in eq. 4 but the parameters have a more obvious character. k_1 now represents the rate of successful prey capture, and $1/(a_1 W^{q_1})$ is the handling time per unit prey (T_H in Holling's notation). Notice, that in these terms only the handling time is a function of W. All the qualitative conclusions which I draw from this model are valid for this Holling-type functional response as well as that of eq. 4.

Now we must consider the metabolic demands (D) of the consumer. These will also be a function of its body weight and the speed which it must travel to search and capture prey. Taylor et al. (1970) provides the required function

$$D = a_2 W^{q_2} + a_3 W^{q_3} V$$

Here V is the average speed of the consumer over a foraging period. As a first approximation, I assume V does not depend on either W or F. When we frame D in cal/day, weight in grams and speed in km/day, then for mammals

$$a_2 = .040, a_3 = .7 \ q_2 = .71, \text{ and } q_3 = .75.$$

Combining all these considerations yields the net rate of energy gain per day (E) available for reproduction

$$E = pA a_1 W^{q_1}[1 - \exp(-k_2 k_1 F/(a_1 W^{q_1}))] - [a_2 W^{q_2} + a_3 pV W^{q_3}] \tag{5}$$

Notice that the energy terms in eq. 5 are multiplied by p, the proportion of the day, which the animal is active and A, the caloric value of the assimilated food which usually will range from .5 to 4 kcal/g fresh weight. [Note that p is
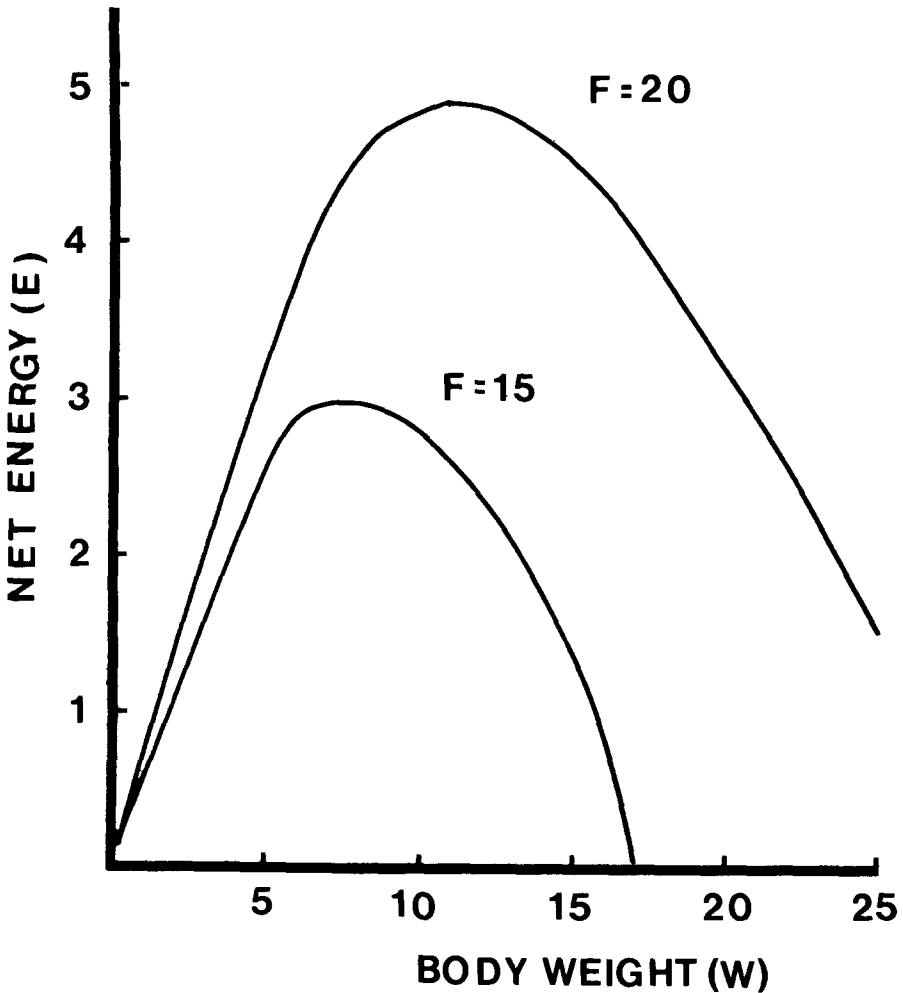
Fig. 2. The relationship between body weight (W) and net energy (E) showing the emergence of an optimal body weight ($\tilde{W}$) which increases as food abundance (F) increases. Other parameters are set as follows:
$k_1 = 1.0, p = 1, A = 1, k_2 = .15, a_1 = .2, q_1 = 1.0, a_2 = .04, q_2 = .71, a_3 = .3, q_3 = .75, V = .5$.

only involved in the first and the very last term of eq. 5: when the animal is inactive, the only metabolic demand is the basal rate $a_2 W^{q_2}$]. With these modifications E will be in units of kcal/day. To find an optimum body weight, we must differentiate eq. 5 with respect to W, and see if critical points emerge. Unfortunately, the algebra involved is cumbersome and the relationship between W and E is more readily explored on a computer. Fig. 2 displays the fact that an optimum intermediate size $\tilde{W}$ does exist and that it increases with increases in F.

When all other parameters are fixed the optimum $\tilde{W}$ is approximately

linearly related to food abundance F (Fig. 3a), but increases with caloric value A with a decreasing slope (Fig. 3b). As the foraging speed of the consumer (V) increases $\tilde{W}$ hyperbolically declines (Fig. 3c). As the metabolic demands (D) increase, simulated by increasing a_2 and/or a_3, the optimum body size for a given F and A mildly decreases. For example, when a_2 is increased ten-fold, $\tilde{W}$ is halved, when the other parameters are set as in Fig. 3. If q_2 or q_3 is greater than 1, the metabolic demands of the organism increase disproportionately with weight. This might be the case for animals which must vertically climb in foraging (Taylor *et al.*, 1972). When this occurs $\tilde{W}$ is lower for a given F and A and relatively less sensitive to changes in F and A.

Optimization models involving sums of power functions are notoriously sensitive structurally to the magnitude of the exponents. The presence of an intermediate optimum may disappear entirely with only minor changes in one exponent. It should be noted that the model represented here (eq. 5) does not suffer from this weakness. An intermediate optimum persists for values of q_1, q_2, q_3, k_1, and k_2 far outside that of biological reality and the optimum weight always changes with changes in F, A, and V in the direction discussed above. In Fig. 4, I have plotted the energy intake (I) and usage (D) as a function of W for two different sets of exponents. In Fig. 4a $q_1 > q_2, q_3$ and in Fig. 4b $q_1 < q_2, q_3$. In both cases one (and only one) optimum body size is present.

What is crucial to the appearance of an optimum $\tilde{W}$ in this model is the scaling of k_2 by L in eq. 5. When eq. 4 is adjusted so that $k_2 S$ is no longer divided by L (i.e. $a_1 W^{q_1}$), the point at which I is for example 99% of its maximal value will occur at the same S in both large and small animals. When k_2 is divided by L, the food level at which larger animals feeding rate is 99% of maximum occurs at a substantially greater value of S than that of the smaller animal. It is this latter, more realistic relationship which we wish to incorporate into the model. The exact structure which I have chosen for eq. 4 is a convenient analytic form, but is not essential for an optimum body size to
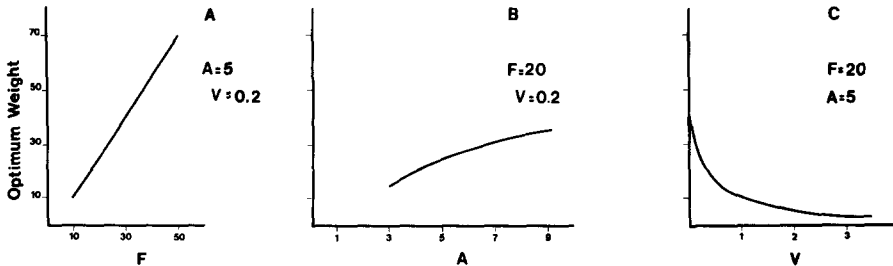

Fig. 3. (a) The relationship between optimum body size $\tilde{W}$ (g) and food abundance $F(g/m^2)$, when the other parameters in equation 5 have been specified along mammalian lines as defined below. b) The relationship between optimum body size and caloric value of the food, A (kcal/g), when the other parameters have been specified as in 3a. c) The relationship between optimum body size searching speed, V (km/day), when the other parameters in eq. 1 and 5 are specified as in 3a. Other parameters:
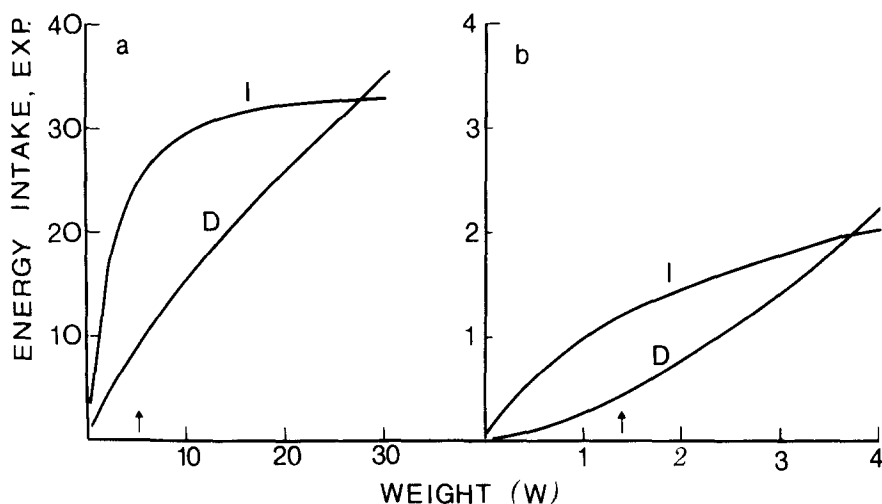$k_1 = 1.0, p = 1, k_2 = .070, a_1 = .2, q_1 = 1.0, a_2 = .04, q_2 = .71, a_3 = .3, q_3 = .75$.

Fig. 4. The relationship between food intake (*I*, in cal/day) and energy expenditure (*D*), in cal/day) as a function of body weight (*W*, in grams) according to eq. 4. The arrows indicate the optimum body sizes. In a) $q_1 = 1$, $q_2 = .71$, and $q_3 = .75$. In b) $\theta_1 = .7$, $q_2 = q_3 = 1.5$; also note the change in scale. For wide deviations in these exponents, an intermediate optimum W is maintained. Other parameters are set as in Fig. 2 except that $V = .8$ and $F = 10$.

arise. Many functional relationships yielding this qualitative behavior are equally suitable and yield similar results.

Recall that the implicit assumption in eq. 4 is that the constant controlling the rate of prey encounter (k_1) is itself not a function of body size. *A priori*, larger animals are expected to have larger fields of vision which may enchance their prey encounter rates. We may simulate this effect by setting (in eq. 1 and 4) $k_1 = kW^f$. If the radius of an animal's vision increases linearly with body length then *f* will be about .33, although it is not unconceivable that *f* could be as high as .5 in filter feeding organisms. This modification does not alter the models qualitative results already discussed as long as the other exponents q_1, q_2, and q_3 are held within biologically realistic levels (i.e. .1 < q_1 < 1.0 and .6 < q_2, q_3 < 2.0). If q_2 and q_3 are made unrealistically low or if *f* is much greater than .5, then for some parameter values an intermediate optimum W disappears.

3. VARIABILITY IN FORAGING SUCCESS

So far, the model predicts that a species' body size is adjusted to its food intake which is determined by food abundance and its foraging success. Since neither of these factors are expected to be constant throughout an animal's life, the model implicitly assumes they may be approximated by average values. It is instructive, however, to consider the effect of two common patterns of variation in food intake on optimal body size. First, an animal's foraging success may increase with experience and age even when

food abundance remains relatively constant. Secondly, for a fixed foraging success, food abundance commonly fluctuates on a seasonal cycle.

The first effect can be simulated by changing equation 1 to become a function of age (a)

$$S(a) = L_2 (1 - e^{-ak}) \tag{6}$$

As age increases, foraging success increases from zero to an upper limit L_2, and L_2 is linearly related to food abundance

$$L_2 = k_1 F$$

When $S(a)$ of equation 6 is substituted for S in equation 5, an intermediate optimal body size for a given age, $\tilde{W}(a)$, still persists. Furthermore, $\tilde{W}(a)$ monotonically increases with age and asymptotically approaches an upper limit $\tilde{W}_{max}$, the adult body size. The path that $\tilde{W}(a)$ takes with age determines an optimum sequence of growth increments. Fig. 5 demonstrates the behavior of this model. As expected, both $\tilde{W}_{max}$ and the absolute growth rate to $\tilde{W}_{max}$ increase with increases in F.

Ricklefs (1969) developed a model to predict optimal growth rates in parentally fed young. He incorporated the mortality of the young, their energy requirements, and their rate of growth into a function which determined the productivity of offspring. This function was maximized only when growth rate occurred as rapidly as possible. That is, no intermediate optimum was present. This result, however, hinges on his assumptions that 1) the mortality rate of the young (deaths/time) is independent of their growth rate, and 2) that growth efficiency is independent of growth rate. With these assumptions modified, an intermediate optimum will often exist (Case, 1977a). Nevertheless, the considerations involved in his model are not appropriate for organisms whose young are precocial and self-feeding. For such animals, my model demonstrates that when foraging success increases with age and experience, optimal growth rates may also exist.

Another common pattern of variability in foraging success is that caused by seasonal changes in food abundance. To simulate this pattern we may assign an oscillating nature to food availability by simply making F a sine function

$$F(t) = B \sin \frac{2\pi t}{T} + \bar{X} \tag{7}$$

Here B represents the amplitude of the fluctuation of food from peak to minimal levels and $\bar{X}$ represents the mean level. To make this a strictly seasonal cycle T should equal 365 days. After substituting $F(t)$ for F in equation 1, equation 5 must be integrated from zero to T (or 2π radians) to give the total net energy accrued over one year

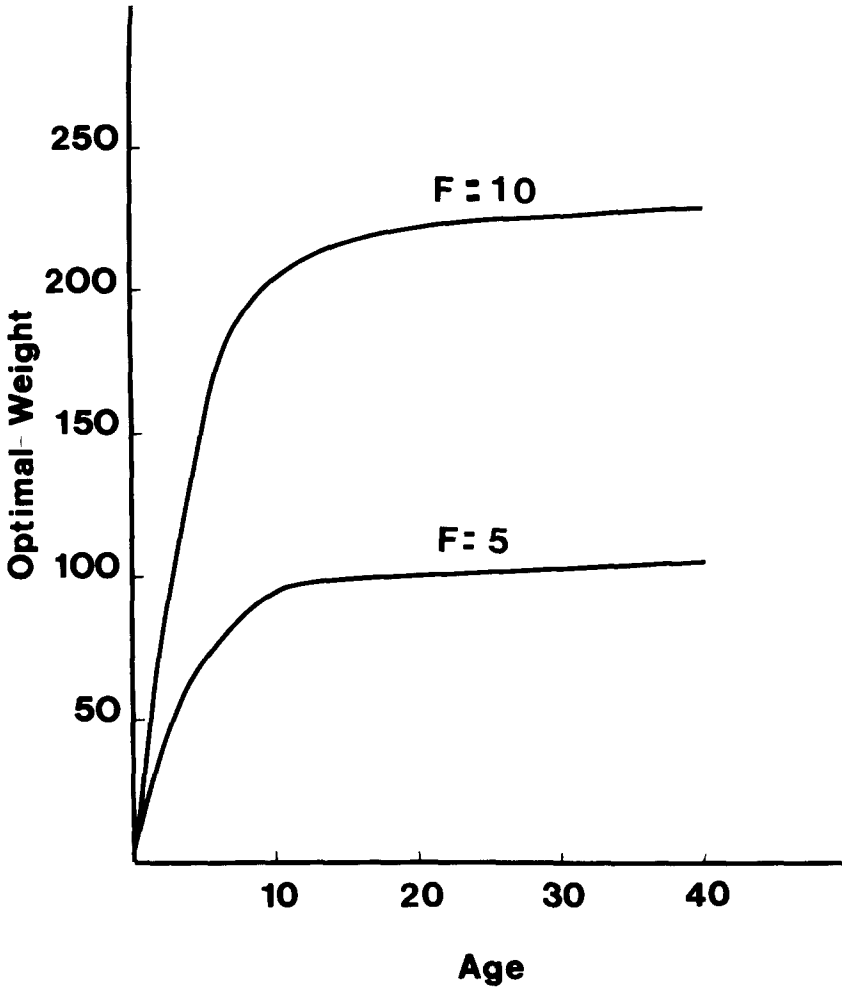$$E_t = \int_0^{2\pi} E \, dt \tag{8}$$

Fig. 5. The optimum body size *W* (a) as a function of age, for two different levels of food abundance $F = 5$ and $F = 10$. Other parameters set as in Fig. 3, except $A = 5$, $k = 10$ and $k_1 = .3$.

The relationship between E_t and $\tilde{W}$ may be readily explored on a computer using assigned values for the other parameters in the model. When this is done the essential features of the model are retained. An intermediate optimum body size still exists and it increases with $\bar{X}$, the mean level of food, and B, the amplitude of food fluctuation (Fig. 6). The fact that greater amplitudes of fluctuation favor larger body sizes, may be explained as follows. When food levels fluctuate below the animals basic energy demands, E becomes negative. But the exponents affecting energy loss when food is rare (*i.e.* q_2 and q_3) are usually lower than those affecting net energy gain when food becomes abundant again (*i.e.* q_1). Furthermore, larger animals
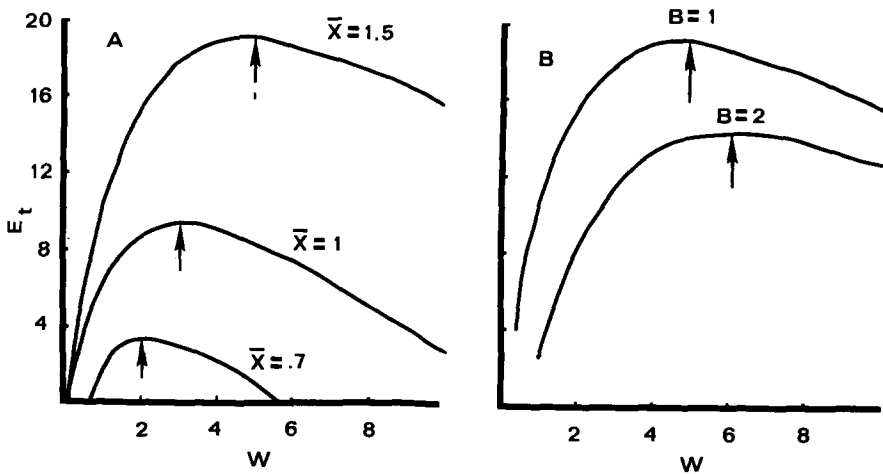
Fig. 6. The relationship between the total net energy accrued over a year's period (E_T) and body weight (W) from equations 5, 7 and 8. a) As the mean level of available food increases $\overline{X}$, The optimum body size ($\tilde{W}$) also increases. b) As the amplitude of food fluctuation (B) increases, the optimum body size also increases. Other parameters are set as follows: in a, $B = 1$ and $q_2 = 1$; in b, $\overline{X} = 1.5$ and $q_2 = 1$. In all, $a_1 = .2$, $a_2 = .1$, $q_1 = 1$ and $k = .5$.

generally can withstand food deprivation for longer periods than smaller animals, although I have not explicitly incorporated this consideration into the model (eq. 5).

4. CONCLUSIONS

For our present purposes the most useful conclusions to draw from the model are that, under the assumptions of the present model:

(1) an optimum intermediate body size $\tilde{W}$ for a consumer does exist based solely on energetic considerations,

(2) $\tilde{W}$ decreases with increasing foraging speed and increases with food abundance, but,

(3) increases in food quality (via caloric content A) favor increases in optimum body size – not the reverse.

This finding is surprising in light of the opposite association between body size and food quality found in nature.

In one way, my model does concur with these trends in that the feasible lower limit to body size (defined as the lowest possible body size yielding a positive net energy balance) for animals eating low quality foods is greater than that of animals which eat higher quality foods. However, as we have seen, my model also shows that the optimum body size (defined as that body size receiving the greatest energy gain) is, in fact, lower for animals eating low quality food than for animals eating higher quality food. Although this dif-

ference in the behavior of an optimum and the feasible limit may seem perplexing, it is actually quite common for optimization models.

One dubious assumption involved in equation 5 is that the caloric value of food (A) does not effect either the rate of food intake (I in eq. 5) or the time available for foraging (p in eq. 5). More realistically, both of these latter functions are expected to decrease with increases in the roughage content of food since digestive turnover time will be longer. One may add these considerations into the model in any number of ways. Either a_1, k_2, or S in eq. 4 can be made to be increasing functions of A, or similarly p could be made to increase with A in eq 5. In any case, the results are unanimous: an optimum body size still exists and it still increases with increases in A (not the reverse). Only if these functions are made to increase with A but decrease with body weight (so that increases in the caloric value of food increases the net food intake relatively more for small animals than for larger animals) could an optimum body size disappear. However, I can think of no biological justification for expecting such behavior.

Hence, I predict that the association that exists in many taxa between large size and low quality food is a by-product of some other causal relationship. I suggest that the explanation lies with the common observation that most poor quality food is also relatively abundant food. Although this correlation is not without exception, it seems to be true for the foods of the relatively large animals listed in the introduction. Since the abundance of food effects $\tilde{W}$ to a greater extent than the caloric content of food in my model (Fig. 3), the correlation between large body size and abundance but low quality food is expected.

It is important to point out that there are many features which influence body size which my model does not consider. Size-selective predators may greatly alter the relative advantage of particular body sizes in their prey (Brooks and Dodson, 1965; Hecht, 1952). There are additional physical considerations which may constrain body size below the optimum levels based on energetic profit. For example, flight and perching impose physical constraints on a bird's size and form. The body size of geckos and other lizards which have evolved toe pads for vertical movement must not exceed the clinging capacity of their toes (Hecht, 1952; Andrews and Rand, 1974). For poikilotherms, the climate may place severe restraints on when and where a species may forage. These too, will be functions of body size (Spotila et al., 1973).

Finally, the body size of a consumer determines in part the size and type of foods it may eat. That is, the total available food for a consumer may be a function of its own size. A guild of species may reduce interspecific competition by consuming prey of different sizes. This, in turn, may set a limiting similarity to their body sizes (Schoener, 1974; MacArthur, 1972; Hespenheide, 1973). The result being that consumer body size can only respond to changes in overall prey abundance (via eq. 5) to the degree that competition with neighboring competitors on a body size niche gradient does not become too severe.

To the extent that these additional factors operate, optimum body size may be much different than that predicted by eq. 5. Although my model does predict certain trends in body size and diet which appear to be consistent with empirical observations within many taxa, there are some obvious inconsistencies between taxa. The fact that termites and elephants both consume woody plant tissue is a familiar example. Two further examples are illustrative. First, since reptiles are ectothermic, a reasonable assumption is that in temperate regions they are not able to forage for as long as their mammalian counterparts on both a daily and seasonal scale. On the other hand, the metabolic rate of reptiles is about ten times lower. In balance, the optimum body size of reptilian herbivores should be somewhat lower than that for mammalian herbivores in temperate habitats because $\tilde{W}$ is more sensitive to p than to changes in metabolic demands (a_2, a_3). Examining the body sizes of extant representatives of these two groups, this conclusion is borne out. The largest temperate herbivores are mammals. In tropical environments p for reptiles should be similar to that for mammals. So, if all else were equal, body sizes of reptiles should be larger than those of mammals in tropical environments. In fact, the largest extant tropical terrestrial reptiles (crocodilians and the Komodo dragon) are many times *smaller* than the largest land mammals. Of course, if all terrestrial tropical reptiles and mammals, living and extinct, are compared this prediction would be verified, assuming dinosaurs were ectothermic (Kurten 1968, 1971).

The second example concerns my model's prediction that the optimum body size should increase as the metabolic cost of locomotion becomes smaller. Schmidt-Nielson (1972) has compared the relative cost of locomotion in animals which swim, fly, and run. For a given speed and body size, the caloric cost of swimming is the lowest and is about an order of magnitude lower than the cost of running. Approximately, the heaviest existing reptiles are found among the sea turtles (about 450 kg) and the largest of dinosaurs appeared to be amphibious (Kurten, 1968). Since mammals are well represented in both terrestrial and marine environments, it is instructive to compare the body size range for corresponding representatives. The smallest terrestrial mammals are certain shrews with a body size of about 7 grams, while the largest extant terrestrial mammal is the African elephant (*Loxodonta africanus*) which stands about 3.3 meters tall at the shoulders and weighs about 6000 kg (Walker, 1964). The largest land mammals of all time were hornless rhinos (*Indricotherium*) of the Miocene. These animals stood nearly 5.0 meters tall (Kurten, 1971, p. 91). Since body weight increases with the cube of linear dimensions, I calculate the weight of these rhinos as

$$W_r = p^3 \, W_e$$

where $p = 5.0/3.3$, W_r is the weight of the rhino and W_e is the weight of the African elephant. This yields 30,900 kg for W_r.

The smallest totally aquatic mammal is the sea otter (*Enhydra lutris*) which

weighs about 20 kg and the largest is the blue whale (*Balaenoptera musculus*) which weighs up to $2 + 10^7$ kg (Walker, 1964). It is obvious that the size range of sea mammals is substantially larger than that of land mammals, but it is not so apparent that the upper and lower ends of the body size range have increased by nearly the same geometric factor, about three orders of magnitude. Hence, the ratio of the largest sea mammal to the smallest $(1 + 10^6)$ is very close to the corresponding ratio for land mammals (3×10^6). The congruence of this result and that predicted by my model is at first seductive, until one recalls that the energetic cost of flying is also less than running, but the upper size limit of birds (extant or extinct), is substantially lower than that of terrestrial mammals. Furthermore, ectothermic fish never reach the size of the great whales.

These contradictions attest to the influence of many of the aforementioned selective factors on optimum body size which my model simply neglects. The size of birds must be constrained by the physics of flight and bipedality. The reliance on gill-based respiration probably sets an upper limit to size in fish below that of sea mammals. If existing tropical reptiles were much larger, they might be more susceptible to endothermic predators or competitors. At least the largest existing terrestrial lizards are confined to islands with a depauperate fauna (Mertens, 1934).

A more rigorous test of the generality of my model's prediction would be to measure food abundance and food quality in a series of closely related animals which differ in body size. Some excellent mammalian candidates for such studies may be gleaned from Dorst and Dandelot (1969).

1. The savanna subspecies of the African buffalo (*Syncerus caffer caffer*) is primarily a grazer and weighs nearly 860 kg while the forest subspecies (*S.c. nanus*) browses to a greater degree and rarely exceeds 330 kg.

2. The giant forest hog (*Hylochoerus meinertzhageni*) weighs up to 120 kg, while the bush pig (*Potomochoerus porcus*) of montane forest and bush country weighs less than 45 kg. The diet of the former includes grass, herbs, leaves and roots, while the latter takes animal as well as vegetable food, but roots and bulbs seem to form the bulk of its diet.

3. The pygmy hippopotamus (*Choeropsis liberiensis*) weighs about 300 kg, inhabits swampy forests and forest streams and usually forages on land for vegetables, succulents, tender shoots, roots, grasses and fallen fruits. The larger common hippopotamus (*Hippopotamus amphibius*) weighs up to 1500 kg and is more truly aquatic inhabiting savanna lakes and ponds. It feeds primarily on grasses and aquatic plants.

Another ideal setting for testing body size predictions is by comparing island populations of a species (or genus) with adjacent related mainland representatives. For example, many rodents, bears, and iguanid lizards tend to be large on islands, while foxes, lagomorphs, artiodactyls, elephants and snakes, tend to be smaller in size than their mainland ancestors (Mertens, 1934; Foster, 1963, 1964; Cody, 1974; Case, 1977b). Islands offer unique but predictable changes in both the biotic and physical environment.

One particularly striking island mainland comparison which I have been studying is that of the lizard genus *Sauromalus*. *Sauromalus hispidus* and *S. varius* occupy various islands in the Gulf of California and are about eight times heavier than the mainland species *S. obesus*. These insular giants are probably not relicts, but are instead insular derivatives of the ancestors of the mainland species *S. obesus* (Robinson, 1973). This herbivorous, iguanid genus also has representatives on other islands in the Gulf of California which are not substantially larger in size than mainland populations (Shaw, 1945). Even on the mainland, there is a moderate difference in body size between populations of *S. obesus*. Where winter rainfall is heaviest, forage plants are more abundant and chuckawalla body size is greater (Case, 1976). Between island and adjacent mainland sites, however, this correlation is not valid. Although their present distribution may be confounded by transport by aboriginal man, the gigantic forms are restricted to islands lacking mammalian predators and competitors. Present predation rates as evidenced by tail-break frequencies are substantially greater for the mainland species and small-sized island species than for the larger insular species (Case, in prep.). A tentative hypothesis is that this reduced predation and competition has allowed some island species greater access to a wider variety of habitats and a greater time which to forage. Furthermore, any premium on the speed and mobility of small size and the concurrent lower cost of movement is greatly reduced on these islands.

ACKNOWLEDGEMENTS

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