ENERGETICS AND THE DISTRIBUTION OF VAMPIRES

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ABSTRACT.—The weight fluctuations and rates of metabolism of vampires in the laboratory were examined in an attempt to describe the energy budget of vampires in the field. Their energy expenditure is limited by the size of the meal that can be transported in flight. A Desmodus of 42 grams would expend about 26 kilocalories per day, more than 90 per cent of which is committed directly to homeostasis and to the cost of handling the food. Appreciably colder environmental temperatures than those found in the tropics would increase the cost of thermoregulation, which in turn would require a meal-size beyond that which can be transported. In fact, the limits in distribution of Desmodus are correlated with the 10°C minimal winter isotherm both in Mexico and in Argentina and Chile.

There have been many studies of the energetics of organisms under laboratory or standard conditions. Such procedures have been valuable in the analysis of the physical basis of certain functions, such as temperature regulation, but these measurements of energy expenditure are by no means equal to the expenditures of animals in the field. Field expenditures are of interest, because many species have a limited supply of chemical potential energy, which means that there must be an adjustment of their expenditure to balance their income. Unfortunately, evaluating the expenditures of animals in the field at the present time is technically difficult. Yet it is often possible to use peculiarities in the habits of an animal to estimate its energy expenditure. That is what is attempted in this paper with vampire bats.

Vampire bats are believed to feed exclusively on the blood of homiotherms. They usually feed only once a night; thus the size of their meal must be adequate to support their expenditure of energy over the next 24 hours. In this paper I shall examine the factors responsible for setting the size of the meal of vampires (and therefore the size of their energy expenditure) and how these factors influence the distribution of vampires.

METHODS

The vampires Desmodus rotundus, Diaemus youngi, and Diphylla ecaudata were caught in Brasil (for localities, see McNab, 1969). Some of the vampires were post-absorptive (not fed the day or night before the day of measurement), some were fed the night before, and others were used on the afternoon of the day of capture, and thus had fed the night before in the field. Rates of metabolism were measured by means of an open system employing a Beckman paramagnetic oxygen analyzer and were corrected to STP. Body temperatures were measured with a YSI Telethermometer after each measurement of oxygen consumption.

The change in weight in some Desmodus caught in the field near Cotia, São Paulo, Brasil, was studied. Upon capture, the bats were immediately brought into the laboratory and weighed (usually about 1630 hours). They were then placed in individual cages and periodically weighed, but given no food or water to simulate normal conditions found in caves. Their body temperatures were measured at each weighing. Similar observations were made on a fruit-eating bat, Sturnira lilium, and on the white mouse, Mus musculus.
Table 1.—Longevity of unfed sanguivores.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>$T_x$ (°C)</th>
<th>RH (%)</th>
<th>Longevity (days)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phlebotomus papatasii</td>
<td>10-20</td>
<td>23</td>
<td>90</td>
<td>6.7</td>
<td>Theodore, 1936</td>
</tr>
<tr>
<td>Phlebotomus papatasii</td>
<td>10-20</td>
<td>23</td>
<td>80</td>
<td>5.5</td>
<td>Theodore, 1936</td>
</tr>
<tr>
<td>Glossina palpalis</td>
<td>92♂</td>
<td>24</td>
<td>88</td>
<td>5.6</td>
<td>Mellanby, 1936</td>
</tr>
<tr>
<td></td>
<td>56♀</td>
<td>24</td>
<td>88</td>
<td>4.5</td>
<td>Mellanby, 1936</td>
</tr>
<tr>
<td>Glossina palpalis</td>
<td>64♂</td>
<td>24</td>
<td>65</td>
<td>5.2</td>
<td>Mellanby, 1936</td>
</tr>
<tr>
<td></td>
<td>44♀</td>
<td>24</td>
<td>65</td>
<td>4.0</td>
<td>Mellanby, 1936</td>
</tr>
<tr>
<td>Desmodus rotundus</td>
<td>10</td>
<td>20</td>
<td>65</td>
<td>2.9</td>
<td>This study</td>
</tr>
</tbody>
</table>

**SIZE OF MEALS**

The size of a meal may be measured in terms of the weight of blood eaten, although the weight of a vampire before and after a meal is not a direct measure of a meal-size, inasmuch as an appreciable fraction of the water ingested as a part of the meal is excreted during feeding and soon thereafter. This behavior occurs in mosquitoes (Boorman, 1960; Freitas and Guedes, 1961), tsetse flies (Bursell, 1960), and vampires (McFarland and Wimsatt, 1969); it seems to be a means of compacting the nutritious fraction of the food for aerial transport. In fact, up to 25 per cent of the weight of a meal may be voided by vampires within the first hour of feeding (McFarland and Wimsatt, 1969), which later requires them to produce a highly concentrated urine, since protein metabolism (and hence urea production) occurs at a time when water excretion is reduced.

Because a vampire usually feeds only once per day (Wimsatt, 1969), its daily energy expenditure is a function of the size of its meal. In seeking the appropriate relationship between the size of the meal (which may be expressed by $\Delta W$, corrected for urinary weight loss) and the original (prefeeding) body weight ($W_o$), it is reasonable to suggest that $\Delta W/W_o \propto M/W_o = kW_o^{-0.25}$, where $M$ is the rate of metabolism (in kcal/day) and $k$ is a constant. This relationship simply states that the size of the meal relative to body weight should vary with weight in a manner similar to that of the weight-specific rate of metabolism.

Such a possibility can be tested by plotting $\log \Delta W/W_o$ against $\log W_o$: if the suggestion is correct, one would expect a linear curve that has a slope of $-0.25$. The curve fitted to data from two mosquitoes, one tsetse fly, one Triatoma (kissing bug), and two vampires has a slope equal to $-0.23$ ($r = -0.97$; Fig. 1). Thus, the data, which have a range of $10^{4.5}$ in weight, are consistent with the suggestion that the size of the blood meal is correlated with energy expenditure.

Two reservations about this analysis must be made. First, the equation relating the rate of metabolism to weight is appropriate for basal, not average,
Fig. 1.—The relation of the weight-specific size of a meal to the prefeeding body weight in flying sanguivores. Data were obtained from Boorman (1936), Bursell (1960), Freitas and Guedes (1961), and Wimsatt (1969). The value for *Diphylla ecaudata* was taken as the mean of two extremes, the minimal being the fractional increase of weight with feeding and the maximal being that value multiplied by 1.54 (from Desmodus) to correct for urinary loss.

Expenditures. It is not clear what exponent of weight would be appropriate under field conditions. Second, a vampire, unlike a sanguivorous insect, is a homoiotherm (McNab, 1969) and would therefore be expected in Fig. 1 to have a higher food consumption for its size than expected from its weight to com-
RATES OF METABOLISM IN FED AND POST-ABSORPTIVE VAMPIRES

Vampires have a high protein diet and thus would be expected to have resting rates of metabolism in the field that are appreciably above the post-absorptive levels reported by McNab (1969). If Desmodus, Diaemus, or Diphylla are fed the night before measurement, the minimal rates of metabolism at thermoneutral temperatures are about 50 per cent above basal levels (Figs. 2, 3 and 4). Consequently, fed vampires in thermoneutrality have body temperatures that are about 2°C higher than post-absorptive individuals. It is curious that the conductances of fed individuals are also above those of post-absorptive individuals, one result being that the body temperatures of fed and post-absorptive individuals are similar at temperatures below thermoneutrality.

The rates of oxygen consumption of Desmodus, measured in the laboratory...
the same day the bats were captured in the field, are identical with the values obtained from individuals that were fed in the laboratory the night before measurement (Fig. 2). Therefore, fed vampires have resting rates of metabolism equal to or above the basal rates expected from weight, even though the actual basal rates are lower than expected. It takes 30 to 40 hours after feeding in the field for vampires to reach post-absorptive levels, which means that vampires in the field will become post-absorptive only if they miss a night's feeding.

**The Weight-Dynamics of Fasting Vampires**

There is a decrease in body weight with time when food is withheld from an animal. The loss of weight during fasting tends to be a negative exponential function of time (Kleiber, 1961); in vampires this is the case after an initial period of urination and defecation (Fig. 5). The constant in the exponent is influenced by the humidity of the environment and the weight of the animal.

Vampires have high rates of weight loss during fasting (Table 2), even higher than those of the smaller fruit-eating bat, *Sturnira*. This loss cannot be exclusively due to the metabolism of energy reserves, however, because the resting rate of oxygen consumption in *Desmodus* is equivalent to only 0.3 gram of loss of protein per 24 hours. The actual weight loss in *Desmodus* is equal to 6.8 grams per 24 hours. Such high rates of weight loss are due to high rates
Fig. 4.—The rate of metabolism and body temperature in six *Diphylla ecaudata* in relation to environmental temperature. Postabsorptive values were obtained from McNab (1969).

of evaporative water loss (McFarland and Wimsatt, 1969) and may explain why vampires normally frequent humid roosts. If a vampire could drink during the day, high rates of evaporation would not be important, but then drinking could only occur in caves that had available water and thus had high humidities.

The resistance of vampires to fasting can be measured by the response of body temperature to a change in weight. *Desmodus* normally maintains a

**Table 2.—Weight loss in mammals during inanition.**

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Body weight (kg)</th>
<th>(k^*)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>White mouse (<em>Mus musculus</em>)</td>
<td>3</td>
<td>0.019</td>
<td>0.00153</td>
<td>This study</td>
</tr>
<tr>
<td><em>Sturnira lilium</em></td>
<td>5</td>
<td>0.021</td>
<td>0.00125</td>
<td>This study</td>
</tr>
<tr>
<td><em>Desmodus rotundus</em></td>
<td>10</td>
<td>0.042</td>
<td>0.00292</td>
<td>This study</td>
</tr>
<tr>
<td>Dog</td>
<td>1</td>
<td>26.3</td>
<td>0.00015</td>
<td>Kleiber, 1961</td>
</tr>
<tr>
<td>Man</td>
<td>1</td>
<td>63.3</td>
<td>ca. 0.00015</td>
<td>Kleiber, 1961</td>
</tr>
</tbody>
</table>

* \(k = (\Delta \log_{10} W)/\Delta t\), where \(W\) (weight in % of original weight) = \(ae^{-kt}\), \(a\) is a constant, and \(t\) is time in days.*
temperature of about 35°C (McNab, 1969), but at weights less than 80 per cent of their original weights body temperature is proportional to weight (Fig. 6). It takes about 35 hours after the original weighing (at 1630 hours), or 55 hours after feeding in the field, for *Desmodus* to attain this critical weight (Figs. 5 and 6). If fasting continues, a lethal weight is reached at about 72 per cent of the original weight, which occurs some 50 hours after the original weighing, or 70 hours after feeding in the field. *Desmodus* therefore could miss feeding for two sequential nights, if the rates of weight loss recorded in the laboratory are similar to those in the field.

**An Energy Budget of *Desmodus***

Elements of the energy budget of *Desmodus* can be estimated for individuals from the colony near Cotia, São Paulo, Brasil. The energy input \( (E_t) \) in a balanced budget can be equated with the energy output \( (E_o) \), which in turn can be broken down into the energy expenditures associated with maintenance (resting) metabolism \( (E_m) \), urine loss \( (E_u) \), and fecal loss \( (E_f) \). The residual
Fig. 6.—The influence of body weight during fasting on body temperature in Desmodus rotundus. Body weight is expressed in terms of the per cent of original weight, which was measured at 1630 hours.

(unaccounted for) expenditure will be referred to as the energy equivalent of activity ($E_a$). All terms in the budget have the units of kilocalories per day (for an individual of 42 grams).

One should note here that 42 grams represents the weight of an unfed, non-pregnant adult Desmodus in Brasil. Mexican specimens in a similar state would normally weigh about 30 grams. The following energy budget can be crudely converted to a bat of 30 grams by multiplying each term by 30/42 = 0.72, all complications in the correction for weight coming from the fact that all scalar processes are proportional to weight raised to a power less than one.

The daily blood intake is estimated to be 23.8 grams by multiplying the bat’s weight at feeding by 0.57, which is the mean intake of blood expressed
relative to body weight for male vampires (Wimsatt, 1969; erroneously re-
ported in his Table 3 as 0.61). The value for males was used because females 
may have been pregnant, which would have distorted $W_o$ (see later). Inas-
much as 21.5 per cent of bovine blood are solids, because these solids are made 
up of about 86 per cent proteins, 1 per cent lipids, and 2 per cent carbohydrates 
(Wimsatt and Guerriere, 1962), and because the caloric contents of the solids 
are 5.65 kilocalories per gram of protein, 9.45 kilocalories per gram of lipid, and 
4.10 kilocalories per gram of carbohydrate (Brody, 1945), the energy intake is 
approximately 25.7 kilocalories per day.

The cycle of activity in Desmodus has been described by Wimsatt (1969) 
for a locality in Mexico: the peak hours of return from feeding are approxi-
mately 2 hours after the peak in exit flights. If we assume that one-fourth of 
the time outside the cave is used in flying, the partitioning of the total energy 
expenditure can be estimated.

The cost of maintenance at 20°C for the 22 hours per day in which vampires 
are in caves and 1.5 hours per day in which they are feeding and resting 
outside the cave is equal to about 18.0 kilocalories (Fig. 2), some 14.2 kilocalories 
of which are equivalent to the post-absorptive cost of maintenance (Fig. 2), 
the difference of 3.8 kilocalories being a crude measure of the cost of handling 
protein. Actually, this estimate for the heat increment is low, because it is 
greatest shortly after feeding, not some 20 hours later, when the measurements 
of oxygen consumption of field-caught animals were obtained. The amount 
of energy lost via the urine in the form of urea molecules can be estimated 
from the observation that about 1 per cent of the weight intake of blood is 
lost as urea in the urine (McFarland and Wimsatt, 1969). Thus, a bat con-
suming 23.8 grams of blood would eliminate about 0.24 gram of urea, which 
represents a loss of 0.6 kilocalorie per day. The amount of energy lost by 
defecation is equal to 5.4 kilocalories per day, assuming that 1) the grams of 
dry feces per milliliter of food intake is equal to 0.04 (based on data of Wimsatt 
and Guerriere, 1962), and that 2) the feces have the same energy content 
as protein.

From these calculations the energy expended for activity can be estimated 
by $E_a = E_i - (E_m + E_u + E_f) = 1.7$ kilocalories per day. If Desmodus expends 
energy for flight in agreement with the estimates of Tucker (1970), and if on 
the average it flies 10 kilometers per night round trip (Crespo, et al., 1961) at 
a velocity of 20 kilometers per hour, then the cost of flight for 0.5 hour per 
day would be 1.1 kilocalories. Therefore, some 1.7 - 1.1 = 0.6 kilocalorie per 
day are expended for other activities, such as movement within the caves, 
feeding, and so forth.

Any increase in energy expenditure, due to an increase in the cost of homeo-
stasis or an increase in activity, would require a larger meal. But as we have 
seen, the size of a meal is limited by the capacity of a bat to carry a load. In 
fact, the tendency of vampires to feed at the terminus of a flight (in contrast 
to insectivorous species, most of which feed in flight) may restrict them to
FIG. 7.—The contemporary distribution (shaded area) of Desmodus rotundus in Mexico and Central America in relation to the 10°C minimal isotherm for January. Extralimital records of fossil Desmodus are indicated for Florida and Cuba. Data are taken from Villa-R. (1966), Brodkorb (1959), Gut (1959), Olsen (1960), and Koopman (1958). An additional fossil locality in northern California has been reported by Hutchison (1967).

small colonies, because an increase in weight without changing body size will reduce flight speed or range in birds (Pennycuick, 1969) and undoubtedly in bats.

**Why are Vampires Limited in Distribution to the Tropics?**

*Desmodus rotundus* is a common bat between central Mexico and northern Argentina. Lyman and Wimsatt (1966) have argued that the limits of distribution are associated with a poor capacity for temperature regulation. Although vampires regulate their body temperature better than was thought by Lyman and Wimsatt, their explanation is still of merit and deserves to be re-examined in terms of the cost of temperature regulation.

*Desmodus rotundus* in Mexico is found throughout the lowlands to about 28°N on the west coast and 25°N on the east coast (Villa-R., 1966; Fig. 7). The limits of the present-day distribution in Mexico closely parallel the 10°C minimal isotherm for January (Fig. 7), and is correlated with the poor temperature regulation of *Desmodus* at ambient temperatures below 10°C (McNab, 1969). The only areas of continental United States that are presently within
FIG. 8.—The contemporary distribution (shaded area) of Desmodus rotundus in southern South America in relation to the 10°C minimal isotherm for July. Data are taken from Vieira (1942), Osgood (1943), Acosta y Lara (1950), Crespo et al. (1961), and Villa-R. and Cornejo (1969).

...this isotherm, and presumably available for occupation by Desmodus, are near Brownsville, Texas, and in Florida south of Tampa Bay. The southern limits of distribution of Desmodus in Argentina and Chile follows the same isotherm in July (Fig. 8).

A close examination of Figs. 7 and 8 shows that vampires tend to be limited in their distribution in the tropics to lower elevations. For example, vampires are not found on the Mexican plateau; south of Mexico City Desmodus goes to higher elevations (2300 meters) than it does northward (1500 meters; Villa-R., 1966). Felten (1956) stated that Desmodus and Diphylla reach 1100 meters in El Salvador. One reviewer of this manuscript has recorded these genera at 1700 meters in Honduras. Desmodus has been found up to about 1400 meters in Guatemala (Jones, 1966). The factors limiting this distribution are not understood for at least two reasons: the mean January isotherms are generally not known for mountain localities, and it is not known whether populations at higher elevations have vertical seasonal movements. Thus, it is uncertain whether there is a different tolerance to cold temperatures involved in setting altitudinal limits. Yet, temperature profiles in Mexico and Argentina indicate that a mean January isotherm near 10°C is also correlated with the limits in altitudinal distribution in vampires.
At latitudes beyond the present position of the 10°C isotherm, cave temperatures in winter are appreciably cooler than those from caves in the tropics (for Desmodus, 13°C to 25°C; McNab, 1969). A roost temperature of 10°C, rather than 20°C, would appreciably increase the amount of energy that a vampire must expend to maintain its normal temperature: a fed vampire of 42 grams would require the expenditure of 16.9 kilocalories for 22 hours in a cave at 20°C and 27.9 kilocalories at 10°C. If the cave temperatures were as low as 5°C, the cost of maintenance would increase to 33.7 kilocalories.

Assuming that the energy loss via urine and feces remains a constant proportion of energy intake and that the absolute amount of energy consumed in activity remains constant, the total energy intake for a vampire of 42 grams living at 10°C would have to be at least 41.1 kilocalories per day, which would require an intake of 38.1 grams of blood (ΔW/W₀ = 0.91). At 5°C the intake must be at least 49.2 kilocalories per day, which is equivalent to 45.6 grams of blood (ΔW/W₀ = 1.09). These calculations suggest that vampires in a temperate environment would require meals up to twice as large as those typical of vampires in a tropical climate.

There is a limit to the size of the meal placed by the ability of a bat of a given size to carry a particular weight in flight. Crespo et al. (1970) have shown in Desmodus that the mean increase in weight with feeding that prevented flight was about 43 per cent. Such a limit may become apparent in near-term females, when they must carry both a fetus and a meal sufficient in size to sustain parent and offspring. If a fetus and associated membranes weigh about 10 grams, then ΔW/W₀ after feeding at 20°C would be (23.8 + 10)/42 = 0.80, or 0.66 after filtering and eliminating 25 per cent of the meal. (Near-term females may take smaller meals and may feed both early and late in the night.) Wing-loading is especially critical if a cold environmental temperature is an added factor demanding a large meal: at 10°C a pregnant Desmodus would have ΔW/W₀ = 1.15, and at 5°C ΔW/W₀ = 1.32. Even if 25 per cent of the blood intake is filtered and eliminated before the return flight, these ratios fall only to 0.92 and 1.05, respectively.

It is possible to increase the size of a meal by increasing W₀, but an increased weight is also correlated with an increase in the total rate of metabolism, a reduction in the maximal ratio ΔW/W₀ (Fig. 1; Pennycuick, 1969), and an increase in the cost of flight (Tucker, 1970). Therefore, there is no advantage in energetics for vampires to be large in a cold climate.

I conclude that vampires are limited in their distribution to a tropical climate because of the combination of food habits that require feeding only at the terminus of a flight and a limit placed on the maximal meal that they can carry in flight, although there may well be other factors of importance that limit distribution in the tropics. The occurrence of Desmodus as fossils at localities north of the 10°C isotherm for January in Florida (Brodkorb, 1959; Gut, 1959; Olsen, 1960) probably means that the isotherm was at least 120 miles northward of its present position in Florida at the time of the vam-
pire's residence. Presumably, the occurrence of Desmodus in northern California (Hutchison, 1967) also occurred during a warmer period.

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